Individual development, biology and evolution of the woolly mammoth

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Introduction

The woolly mammoth, *Mammuthus primigenius* (Blumenbach, 1799), is a well-known extinct elephant. Numerous researchers from different countries dedicated their work and publications to this proboscidean. Many mammoth studies are traditionally based on the morphology of the dentition. Teeth, especially third molars, are most frequent among mammoth remains. Within the last eighty years, a lot of data on the structure of soft tissues and internal organs has been made public. First steps have been made in soft tissue histology studies and in studies of the mammoth karyotype. Similarity of some DNA sequences in *M. primigenius* and *E. maximus* show that mammoths and elephants are sister groups within a monophyletic branch of Elephantidae (Osawa *et al.*, 1995; Hauf *et al.*, 1999).

Recent combined archeo-zoological studies on Late Paleolithic sites provide new fascinating information on some important features of interaction between man and mammoth during the Late Pleistocene (Anonymous, 1982; Boriskovskii, 1984; Ivanova *et al.*, 1987; Abramova, 1995; Haynes, 1985, 1989, 1999; Soffer, 1985, 1993, 1995; Frison & Todd, 1986). In addition, the woolly mammoth has become an object of many disciplines within pleistocene studies that border on paleontology and archeology, because *M. primigenius* is evidently a most widespread large mammal, whose evolution is closely connected with the environmental conditions of the Pleistocene.

Today the woolly mammoth is one of the best-studied species of extinct mammals. During recent years, a great volume of data accumulated by researchers, complex studies and new methods that had previously been applied to modern mammals only, have laid the ground for several new directions of research into the problems of the biology of the mammoth. Discoveries of natural traps and sites where large groups of mammoths died in North America (the Hot Springs site) and Russia (the Sevsk locality) have made it possible to study some peculiarities of mammoth ethology and ecology. Material of mammoth calves collected in Russia made research into the ontogenesis of the mammoth possible.

Mammoth-like elephants, of which *M. primigenius* is the most widely known representative, form a group of proboscideans (*Proboscidea* Illiger, 1811) that together with several other genera constitute the family Elephantidae Gray, 1821. In addition to mammoth-like elephants, the family comprises the genera *Stegotetrabelodon* Petrocchi, 1941, *Primelephas* Maglio, 1970, *Loxodonta* Cuvier, 1825, and *Elephas* Linnaeus, 1758 (Maglio, 1972). These groups form one family because of their common origin and because of a number of morphological similarities that are also typical of their ancestors.

Some authors (Maglio, 1972; Lister, 1996) classify all mammoth-like elephants into one genus: *Mammuthus* Burnett, 1825. The group of mammoth-like elephants in this wider interpretation includes all ancient representatives of the lineage from the Early Pleistocene, viz.., *M. subplanifrons* (Osborn, 1928), *M. africanavus* (Arambourg, 1952), *M. meridionalis* (Nesti, 1825), *M. trogontherii* (Pohlig, 1885) (also known as *M. armeniacus*(Falconer, 1857)), *M. primigenius* (Blumenbach, 1799) (Osborn, 1934; Petrocchi, 1941; Arambourg, 1952, 1970; Maglio, 1970; Maglio & Ricca, 1977).

Other authors refer *M. meridionalis* (Nesti, 1825) and *M. trogontherii* (Pohlig, 1885) to a separate genus: *Archidiskodon* Pohlig, 1888. Some authors, while acknowledging the validity of the genus *Archidiskodon* (Garutt, 1986), do not include *M. trogontherii* (Pohlig, 1885) in this genus (Foronova & Zudin, 1999; Maschenko, 1999).

The most ancient Elephantidae evolved in Africa during the Pliocene. According to paleontological evidence, elephants of both elephant-like (forms of the genus *Elephas*) and mammoth-like lineages are known from the Early Pliocene of South and Central Africa. The remains of the most ancient mammoth-like elephants have been collected from Pliocene sites of the South African Republic, Kenya and Malawi (Arambourg, 1952, 1970; Hooijer, 1955; Cooke & Coryndon, 1964; Aguirre, 1969; Beden, 1983). During the Late Pliocene (not earlier than 3.2 million years ago) the mammoth reached into Europe (Haughton, 1932; Cooke, 1965; Coppens, 1972; Lister, 1996). The subsequent evolution of the lineages took place both in Africa and Eurasia. At least from the beginning of the Late Pliocene and during the Pleistocene, mammoth-like elephants were represented mostly in Eurasia and North America, whereas the elephant-like lineage occupied southern parts of Eurasia.

Garutt (1995) suggests that both lineages descend from a common ancestor *Phanagoroloxodon mammontoides* Garutt, 1957 (an autonomous tribe Phanagoroloxodontini Garutt, 1991 in the family Elephantidae Gray, 1821). It is possible, however, that the scenario of the emergence of these two lineages was different and additional data is needed to solve this problem.

The last representative of the mammoth-like elephants, the genus *Mammuthus*, became extinct during the earlier part of the Holocene. In Africa and Asia, other members of the family, the genera *Loxodonta* and *Elephas*, have been represented by only one species each since the Late Pleistocene: *L. africana* Cuvier, 1825, and *E. maximus* L., 1758 (Shoshani & Eisenberg, 1982; Shoshani *et al.*, 1991).

Classification of all mammoth-like elephants into one genus is based on common morphological features in all representatives of the group. Mammoth-like elephants have a short and high skull with a semicircular top. The upper boundaries of the temporal grooves are indistinct. The frontal surface is relatively narrow. The narial opening is broad. The tusk alveoli diverge slightly. The tusks are strongly curved and twisted, so that they form a spiral (Garutt, 1987; Maglio, 1973; Lister, 1996). The proportions of the body and the postcranial skeleton differ substantially in the different mammoth-like elephants, as they depend on the food specialization of a given form. The early forms are adapted mostly to feeding on bushes and twigs, whereas the late forms are adapted to low bushes and grass.

Morphological transformations of the last tooth generation (M3) provide most significant evidence regarding the evolution of the mammoth-like elephants during the Pleistocene. In the most ancient forms from the Pliocene of Africa, the number of M3 plates is seven to eight (three plates per 10 cm), and the enamel is 5.5 mm thick. The height of the crown is 75% of its width. Researchers traditionally connect the progressive morphological changes in last generation teeth with the growing number of plates that compose the crown of the tooth (up to 27 in some Arctic populations of *M. primigenius*). The number of plates calculated per 10 cm rises to eleven, the enamel becomes thinner, reaching 1 mm in some late Arctic populations of *M. primigenius*. The crown height reaches 300% of its width. The eruption angle of a functional tooth decreases.

Significant transformations in skull morphology occur at the end of the Late Pleistocene. In the Early Pleistocene elephants of this group, the skull is relatively lower. The narial opening is situated above the level of the orbits. The skull width in the area of the supraorbital processes is smaller than the width of the occiput. The occipital bones are not strictly vertical. The tusks are relatively short. The tusk alveoli are directed forward and downward. The condyles are oval and displaced (relatively) to the rear part of the skull. The lower jaw of the Early Pleistocene forms has a long symphyseal part and a mental process directed forward and downward. The body of the lower jaw is relatively low and long. The ascending branches are directed upward and backward, at a sharp angle with the horizontal surface (Garutt, 1987; Osborn, 1942; Maglio, 1973; Lister, 1996). Morphological and exterior changes in the Late Pleistocene mammoths are connected with their life under cold climatic conditions: no other representatives of the family Elephantidae, or the whole order Proboscidea, have ever been forced to adapt to similar conditions. Precisely these changes in morphology determine, from the taxonomic point of view, the distinction between the earlier mammoth-like elephants (Pliocene-Early Pleistocene) and the genus *Mammuthus*.

The last representative of the group, *M. primigenius*, occupies a particular place among mammoth-like elephants, because it was well adapted to an extremely cold climate and a narrow feeding basis during winter. A quick evolution of mammoth-like elephants through a sequence of forms is observed during the Pleistocene and, evidently, during the first millennia of the Holocene (Vartanyan *et al.*, 1993; Garutt *et al.*, 1995; Averianov *et al.*, 1995).

The morphology of last generation teeth in different genera of elephants of the genus *Mammuthus* has been the main objective of studies over the last 70-90 years because these teeth have distinctive features that allow quantitative studies (Garutt, 1954, 1966; Dubrovo, 1960, 1964, 1966, 1975, 1990; Sher & Garutt, 1985a, 1985b; Foronova & Zudin, 1999; Pavlov, 1881; Dietrich, 1912; Maglio, 1973).

The biological system of mammoth-like elephants is based on peculiarities of changes in the morphology of last generation teeth in different species of this group. Gromova (1968), however, suggests that the process was not linear and varied in time in different populations. In populations of the latest *M. columbi* from the Dent locality (USA) and *M. primigenius* from the Sevsk locality (Russia) the enamel has grown thicker (reaching a mean value of 2 mm for M3) and the number of plates was reduced (20-21 for M3 specimens from Sevsk) (Maschenko, 1995; Saunders, 1995, 1999).

By the end of the Pleistocene, a fast microevolutionary process in the latest representatives of the genus *Mammuthus* had resulted in the formation of a number of geographically distinct and insular populations of *M. primigenius* and *M. columbi* that might be classified as subspecies (Golovko, 1958; Rusanov, 1968; Alekseeva, 1990; Lazarev & Tomskaia, 1987). Insular populations and some continental ones exhibit extremely small dimensions within the dimensional variability frames of the latest representatives of the genus *Mammuthus* (Vangengeim, 1961; Vereshchagin, 1972, 1977; Coope & Lister, 1987; Garutt *et al.*, 1993; Shoshani *et al.*, 1991; Maschenko *et al.*, 1993).

Today it is evident that the forms with distinctive systematic features were followed by the forms with 'intermediate' morphology, and so on (at the end of the Middle and the beginning of the Late Pleistocene). At the end of the Late Pleistocene, populations of *M. primigenius* existed, whose variability hardly fits within the frames of generic variability. It is possible that during certain periods of the Pleistocene *M. trogontherii* and *M. primigenius* co-existed.

Some data indicates different speeds of change in tooth structure in distinct populations of mammoth-like elephants (Sher *et al.*, 1995). These show morphological changes in last generation teeth that cannot be unambiguously interpreted as a testimony of transition to a new evolutionary stage and, consequently, to a new taxon (species or genus) within the mammoth-like elephants. During certain periods of the Pleistocene inadaptive changes played a great role in some populations. This role was much greater than that of gradual evolution in all mammoth-like elephants during the major part of their existence. On the other hand, morphology and biology of the woolly mammoth distinguish this species not only from all other representatives of the mammoth-like elephants, but practically from all other elephants.

The polydirectional evolution of mammoth-like elephants during the Pleistocene does not permit unambiguous interpretation of the group's phylogeny. The same is true of the determination of the taxonomic rank for some groups with 'mixed' morphology and the interpretation of relations within the group of mammoth-like elephants. The biological system of the species and subspecies of *Mammuthus* is faced with the synchronous existence of different morphotypes within one territory and the impossibility to establish whether morphologically close but geographically distinct forms existed simultaneously (Vangengeim, 1961; Gromova, 1965; Sher *et al.*, 1995; Lister, 1996; Todd & Roth, 1996).

The peculiarities of the historical development of the genus *Mammuthus* and especially its scope within the family Elephantidae are still questionable. Researchers use three different schemes to determine the composition of the genus *Mammuthus*. Each comprises different numbers of genera of mammoth-like elephants. To compose the schemes, authors use roughly the same data (features), however, interpret them differently. Taking into consideration the complications inherent to the interpretative usage of some features and the subjectivity in the assessment of their diagnostic value, one may propose to consider the evolution of mammoth-like elephants and the genus *Mammuthus* on the basis of peculiarities of individual development of representatives of the genus. For example, emergence and formation of first generation teeth and skeletal bones in the ontogenesis of *M. primigenius* repeat some peculiarities typical of more ancient mammoth-like elephants. This provides new information on evolutionary relations within the group.

Some peculiarities of the ontogenesis of *M. primigenius* and their comparison with the peculiarities in modern *E. maximus* and *L. africana* reveal similarities between modern elephants and the mammoth. This similarity and some other data on mammoth biology suggest a certain similarity in physiology and provide possibilities for extrapolation of some peculiarities of the biology of modern elephants to the extinct species *M. primigenius*, for which they cannot be established directly. Research into the ontogenesis of *M. primigenius* is most interesting in this respect. In spite of abundant studies of the mammoth, data on the individual development of representatives of the species is scarce. In ontogenetic research, the most significant information is provided by studies of morphological features in the formation process of dentition and skeleton. These are studies of the formation of the first to third generation teeth (dp2-dp4), of the deciduous (di) and of the permanent (I) tusks. In studies of the formation of the skull, the lower jaw, and the postcranial skeleton, changes of their proportions give important information. In studies of the skull, this is especially true for the sutures and their fusion. In studies of the long bones, the main information sources are the growth zones in the shafts, the stages of formation of the epiphyses and the timing of their fusion. The vertebras provide important information on the formation of neural arches and their fusion with the vertebral centres.

Abbreviations

PIN - Paleontological Institute, Russian Academy of Sciences (Moscow); GIN - Geological Institute, Russian Academy of Sciences (Moscow); ZIN - Zoological Institute, Russian Academy of Sciences (St Petersburg); IAE - Institute of Archeology and Ethnography, Siberian Branch, Russian Academy of Sciences (Novosibirsk); IHMC - Institute of the History of Material Culture, Russian Academy of Sciences (St Petersburg); SDM - State Darwinian Museum (Moscow); TPI - Tiraspol Pedagogical Insitute (Tiraspol).

Material and method

Material

A unique collection of mammoth remains from the Sevsk locality (Bryansk region, Russia) provided the main material used in this study. The collection includes over 3,700 mammoth bones, among them five almost complete skeletons of calves of different ages and two incomplete skeletons of adults. The material was collected during the 1988-1991 field campaigns by the author and his team, and was subscribed under collection number PIN 4355. Additional material of mammoth calves came from different Late Pleistocene localities in Russia (PIN 301, 778, 2069, 2323, and 4531).

The second large quantity of material came from the collection of mammoth calf remains at the Zoological Institute, St Petersburg, Russia (ZIN 6448, 20564, 25550, 25860, 28284, 28392, 28877, 28880, 29070, 29841, 29844, 29875, 29880, 30924 to 30928, 30934, 30936, 30937, 30947, 31250, 31252, 31272, 31277, 31278, 31517, 31540, 31541, 31689, 31740, 31771 to 31774, 31835 to 31837, 32572, 34201, 34378, 34416, 34418, 34419, 34421, 34426, 34427). These specimens, 152 in total, were collected from Late Pleistocene sites from Siberia (Kostionki 1, Kostionki 14, Kostionki 19, and Kostionki 21) and from the Russian Plain (the paleolithic sites Elisevichi and Judinovo, Desna river basin, and the Bryansk region). Their radiocarbon dates range from 13,650 to 24,100 years, in other words, they fall into different stages of the Late Würm glaciation (Aslanov *et al.*, 1972; Anonymous, 1982; Boriskovskii, 1984). Many specimens studied are marked only with field numbers of the institution they come from.

The world's only known partial skeleton of a mammoth foetus is used in this work and was identified by the author in the collection of the IAE. The skeleton, collected from the Shestakovo Late Paleolithic site comprises 26 bones of a single foetus in a late stage of prenatal development. The material is marked only with field numbers of the institute. The radiocarbon date of the site is 20,000 years (Okladnikov & Molodin, 1980-1981).

Molars of the first (dp2), second (dp3) and third (dp4) generation of the most ancient representatives of the mammoth-like elephants (*Archidiskodon*) from the East European Khapry locality (Rostov region, Russia; stored at ZIN and GIN), a skull, a fragmentary lower jaw, and several postcranial bones of a mammoth calf from the Yamal Peninsula (GIN 77) were also studied by the author. For comparison, material of modern Asiatic elephants from the collections of the PIN and the SDM (Moscow, Russia) was studied. The number of these specimens, including the skeletons of adults and calves, skulls, lower jaws, isolated teeth, and postcranial bones amounts up to 2,000.

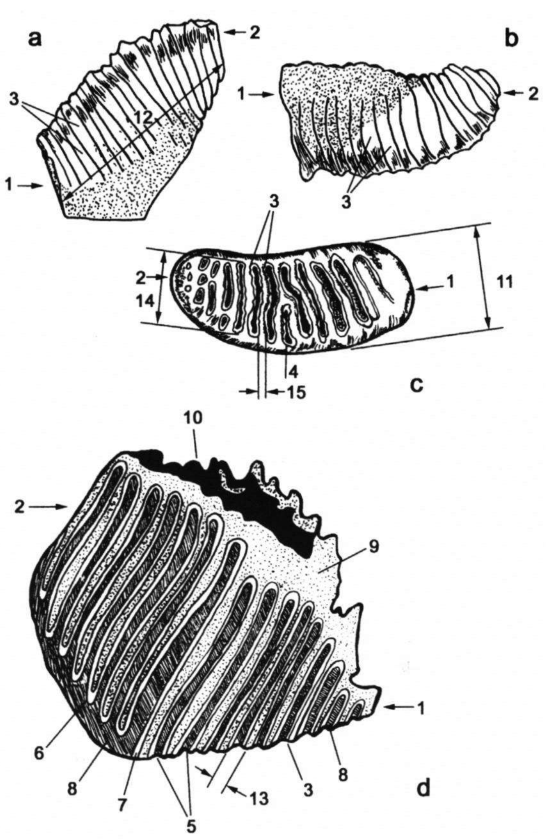

Fig. 1. Schematic structure of an elephant M3 (Garutt & Foronova, 1977): a = M^3; b = M_3; c = masticatory surface (left M^3); d = longitudinal section of tooth crown. 1 = anterior edge; 2 = posterior edge; 3 = enamel plates; 4 = inserted (additional) plate; 5 = worn plates; 6 = unworn plates; 7 = enamel; 8 = cement; 9 = dentine; 10 = root cavity base; 11 = crown width; 12 = crown length; 13 = interplate distance; 14 = plate width; 15 = interplate width.

Schematische weergave van de M3 van een olifant (Garutt & Foronova, 1977): a = M^3; b = M_3; c = kauwvlakte (linker M^3); d = dwarsdoorsnede door de kroon. 1 = voorrand van de kies; 2 = achterrand van de kies; 3 = glazuurplaten; 4 = toegevoegde, extra plaat; 5 = afgesleten platen; 6 = onafgesleten platen; 7 = glazuur; 8 = cement; 9 = tandbeen; 10 = pulpholte; 11 = kroonbreedte; 12 = kroonlengte; 13 = afstand tussen de platen; 14 = plaatbreedte; 15 = breedte tussen de platen

Cadavers of mammoth calves were used as additional comparative material: a circa one-month-old calf from Yamal Peninsula (ZIN 34201, described by Tikhonov & Khabry, 1989; Hamada *et al.*, 1992; Kuzmina, 1999), and a six-months-old calf from the Kirgiliach river, Susman district, Magadan region (ZIN 70188, described by Vereshchagin, 1981; Vereshchagin & Tikhonov, 1999).

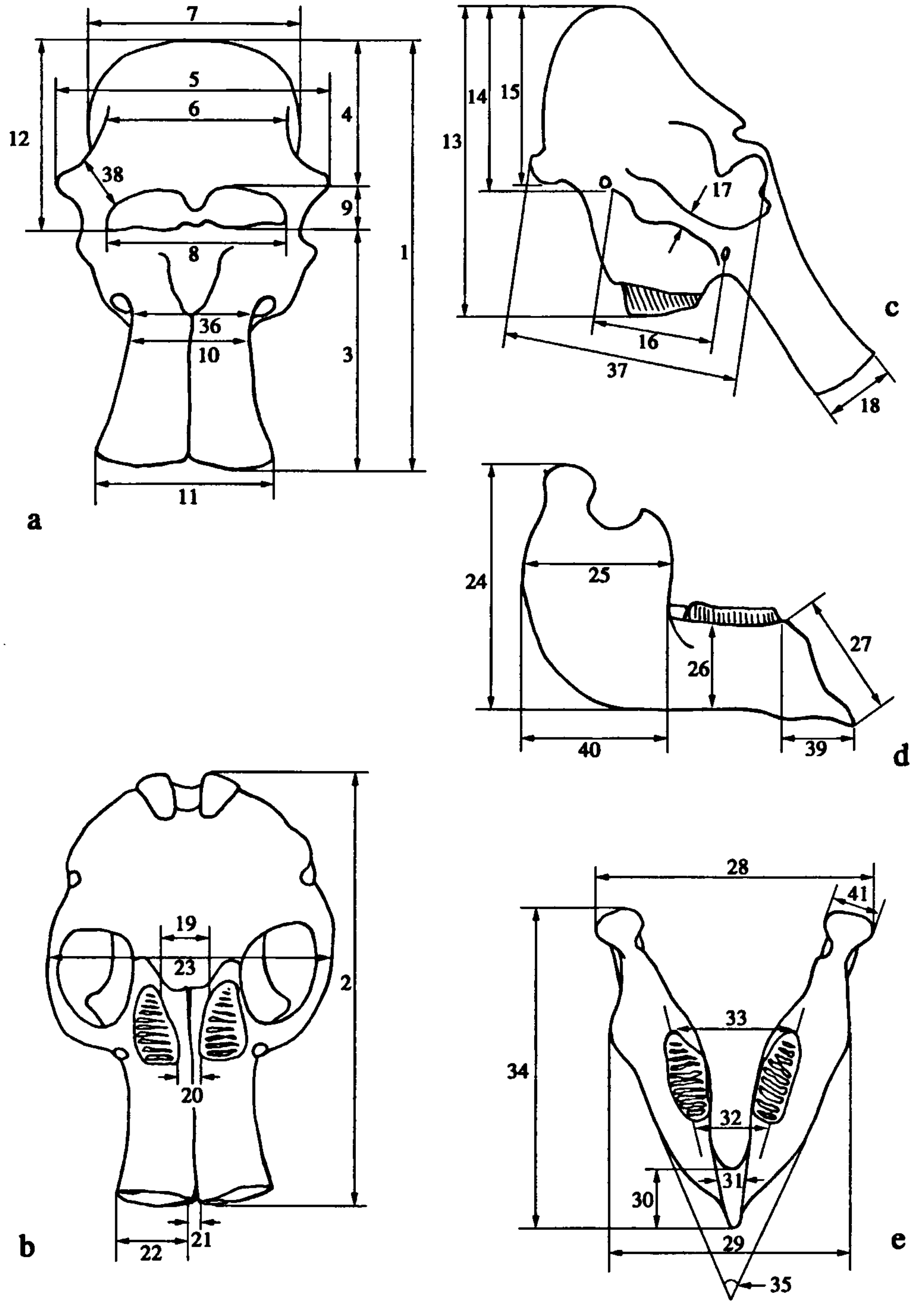

Fig. 2. Elephant skull (a, b, c) and lower jaw (d, e) measurements (after Garutt, 1954, and Beden, 1983). 1 = parietal length (from the skull apex to the lower edge of intermaxillary bones); 2 = condylobasal length (from the upper edge of occipital condyles to the lower edge of intermaxillary bones); 3 = premaxillary length (from the front edge of premaxillar bones to the lower edge of nasal opening); 4 = forehead length (from the skull apex to the upper edge of nasal opening); 5 = postorbital processes width; 6 = forehead shortest length; 7 = occiput greatest width; 8 = nasal opening greatest width; 9 = nasal opening height (greatest); 10 = premaxillary shortest width; 11 = premaxillary width at the level of tusk alveoles ends; 12 = forehead and nasal opening combined length; 13 = skull height (from the vertex to the level of teeth masticatory surface); 14 = skull height (from the apex to the lower edge of external acoustic passage); 15 = skull height (from the apex to the level of the occipital condyle lower surface); 16 = zygomatic arch length (from the external acoustic passage to the suborbital opening); 17 = minimal height and width of zygomatic arch; 18 = vertical alveolar diameter; 19 = distance between the inner edges of alveoli; 20 = distance between the front edges of alveoli; 21 = distance from the tusk to the suture between the intermaxillary bones; 22 = horizontal alveolar diameter; 23 = greatest zygomatic width; 24 = lower jaw depth; 25 = greatest height of the ascending branch; 26 = height of the horizontal branch under the middle of a functional tooth; 27 = length of interalveolar crest; 28 = greatest jaw width; 29 = greatest width of horizontal branches; 30 = symphysis length; 31 = greatest symphysis width; 32 = distance between the horizontal branches at the level of posterior edge of alveoli (along middle line of masticatory surface of the crowns); 33 = distance between the horizontal branches (at the level of anterior edge of alveoli); 34 = greatest length of the lower jaw; 35 = angle of convergence of branches; 36 = premaxillary bones width at the level suborbital openings; 37 = skull length (from the posterior edge of occipital condyle to the anterior edge of nasal opening); 38 = shortest width (from the frontal crest to the upper edge of nasal opening); 39 = distance between the anterior edge of mental process to the level of anterior edges of alveoli; 40 = distance between the base of ascending branch to its posterior edge; 41 = longitudinal and transversal diameters through condyl.

In fig. 2. worden de meetpunten van de schedel (a, b, c) en onderkaak (d, e) van olifanten schematisch weergegeven (naar Garutt, 1954, en Beden, 1983). 1 = parietale lengte (van kruin tot ondergrens tussenkaaksbeenderen); 2 = condylobasale lengte (van bovengrens achterhoofdsknobbels tot ondergrens tussenkaaksbeenderen); 3 = premaxillare lengte (van de voorrand van de premaxilla tot de onderrand neusopening); 4 = voorhoofdslengte (van kruin tot bovenrand van de neusopening); 5 = breedte van het postorbitale uitsteeksel; 6 = kortste voorhoofdslengte; 7 = grootste achterhoofdsbreedte; 8 = grootste breedte neusopening; 9 = grootste hoogte neusopening; 10 = kleinste breedte premaxillare beenderen; 11 = breedte premaxillare beenderen ter hoogte van eindpunt tandkas voor de stoottand; 12 = lengte van voorhoofd plus neusopening; 13 = schedelhoogte van kruin tot niveau van de kauwvlaktes); 14 = schedelhoogte van kruin tot onderrand uitwendige gehoorgang; 15 = schedelhoogte van kruin tot ondergrens achterhoofdsknobbel); 16 = jukbooglengte van uitwendige gehoorgang tot opening onder het oog; 17 = minimale hoogte en breedte van de jukboog; 18 = verticale middellijn van tandkas; 19, 20 = afstand tussen de binnenranden en voorranden van de tandkassen; 21 = afstand van de stoottand tot de verbindingslijn van tussenkaaksbeenderen; 22 = horizontale middellijn van de alveole; 23 = grootste breedte jukbeenderen; 24 = diepte onderkaak; 25 = grootste hoogte opgaande tak; 26 = hoogte horizontale tak midden onder functionele kies; 27 = lengte van richel tussen tandkassen; 28 = grootste onderkaaksbreedte; 29 = grootste breedte horizontale takken; 30 = symphysislengte; 31 = grootste symphysisbreedte; 32 = afstand tussen de horizontale takken ter hoogte van de achterrand van de tandkassen (langs de middellijn van de kauwvlaktes); 33 = afstand tussen de horizontale takken ter hoogte van de voorrand van de tandkassen; 34 = grootste onderkaakslengte; 35 = convergentiehoek van de onderkaakstakken; 36 = breedte van tussenkaaksbeen ter hoogte van de suborbitale openingen; 37 = schedellengte van achtergrens achterhoofdsknobbel tot voorrand neusopening; 38 = kleinste breedte van voorhoofdsrichel tot bovenrand neusopening; 39 = afstand tussen voorgrens van processus mentale tot niveau van de voorranden van de tandkassen; 40 = afstand tussen basis van de opgaande tak tot aan zijn achterste begrenzing; 41 = middellijn door gewrichtskop.

Dp2 and dp3 specimens (GIN 300, and ZIN 30012, 29071, and 25094(1)) that belong to the genus *Archidiskodon* from the Khapry locality (Volovaya Gorge and Aksaysk, Rostov region, Russia) and the Cimbal locality (Taman Peninsula) were studied. All fossil elephant remains referred to the genus *Archidiskodon* from these localities belong to the most ancient representatives of the genus from East Europe. The geological age of these localities evidently corresponds to the middle Villafranchian (Vereshchagin, 1957; Garutt *et al.*, 1975). First, second and third generation teeth referable to *M. trogontherii* were studied in the collection of the ZIN (nos. 14046, 14896, 31642(2), 29963, 29986, and 31643(2)). They come from different localities in the Odessa region, Ukraine, and Bashkiria, Russia.

Method

Measurements of skulls, lower jaws and postcranial bones were taken according to Garutt (1954, modified by Agenbroad, 1994), and is illustrated in figures 1, 2, and 3. All indexes are based on the figures thus obtained. The anatomical nomenclature adopted by Zalenskii (1903), Boas & Paulli (1925), and Eales (1926) was used in the description of postcranials. Tooth measurements were taken according to the scheme developed by Garutt & Foronova (fig. 1a-d); according to common usage, the masticatory surface is always considered to be the upper (top) part and the root is considered to be the lower part of a tooth.

Dentition

The dentition of elephants and mammoths is considerably reduced. It comprises two generations of incisors and a succession of masticatory teeth. The first pair of (deciduous) incisors of the maxillary is marked di. The second pair of incisors is represented by permanent tusks marked I. The first three generations of masticatory teeth (marked dp2, dp3, and dp4), and the next three generations of masticatory teeth (marked M1, M2, and M3). Elephants' teeth function sequentially and are substituted when worn out. The change occurs in horizontal direction: the next tooth moves forward to take the place of the previous one. Normally, each half of the jaw bears one or two functioning teeth. The crown is formed by parallel enamel plates with an orientation transversely to the longitudinal axis of the crown (fig. 1). The plates vary in number, depending on the tooth generation, which makes it possible to identify the generation even of an isolated tooth. To make identification more precise and to minimize mistakes, specimens with teeth in the process of substitution were selected. In plate counts, the anterior and posterior talons, if present, were considered to represent a plate. Several (three and more) enamel columns with a single base were considered a talon.

All elephantid teeth, apart from permanent tusks, have roots. According to the material studied, dp$_2$ has one or two roots, dp^2 two or three roots, dp$_3$ and dp$_4$ both have two roots, and dp^3 and dp^4 have two main and several additional roots. The M1 through M3 generations have a rather consistent root system with one anterior, one middle, and one posterior root (Sher & Garutt, 1985a, 1985b).

The tooth plates consist of dentine and are covered with an enamel layer; interplate gaps are filled with cement. Bases of plates and roots are also covered with cement. On the teeth of the generations dp2 through M1, cement appears first on the top of the anterior plate, followed by the other plates, and eventually covers each plate from top to base (from masticatory surface to crown base).

Upper and lower teeth in elephantids differ, and may be identified even in isolated specimens. In the generations dp2 through M3, the crowns of the upper teeth usually are wider than those of the lower teeth. Roughly spoken, upper tooth crowns tend to get narrower from top to root, whereas lower tooth crowns tend to widen at the root. The crowns of upper teeth are lingually concave, whereas the crowns of lower teeth are buccally concave. Upper and lower dp2 differ in size (upper tooth crowns are longer and wider), in the number of roots (two to three in upper teeth, one to two in the lower), and in the number of

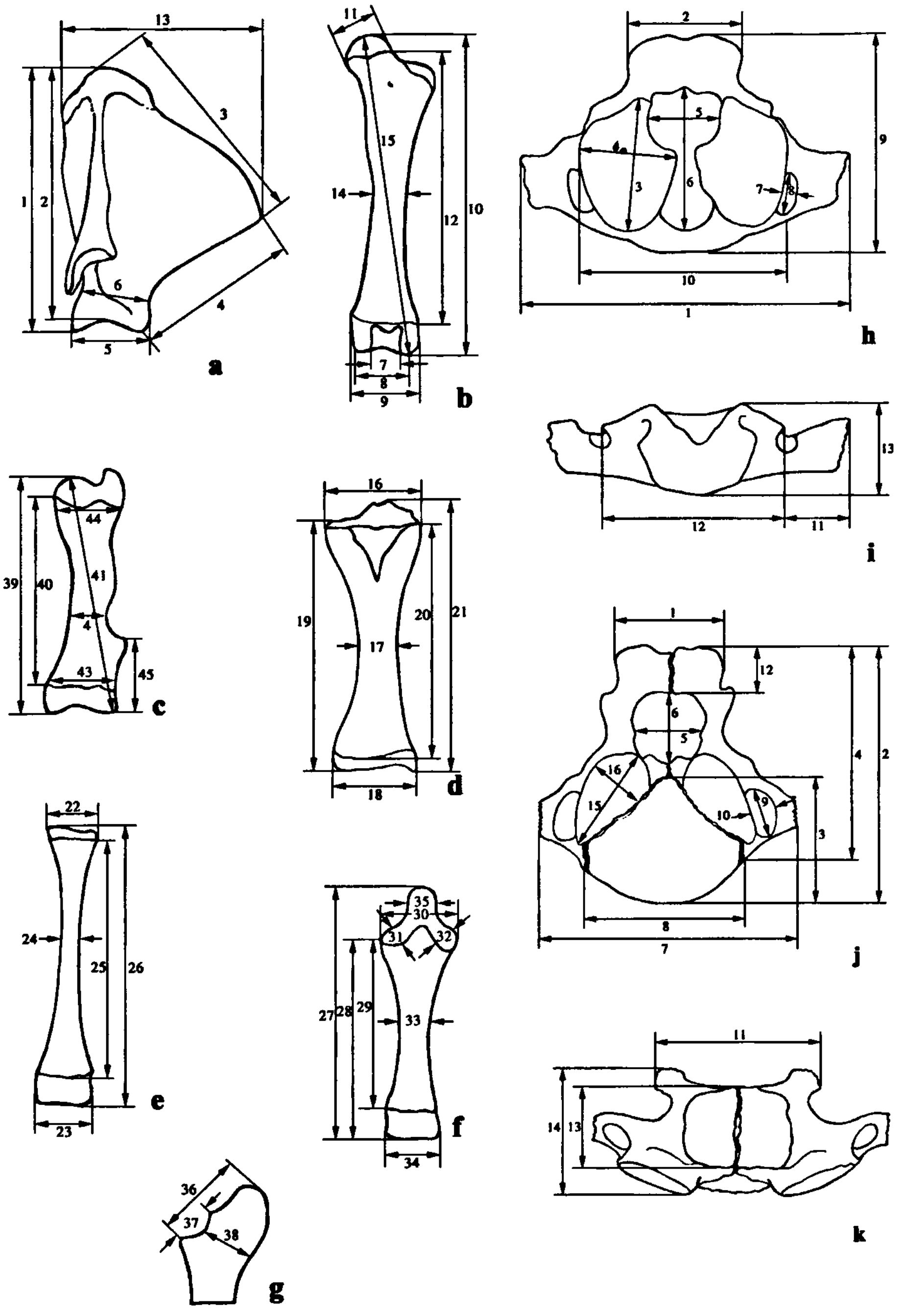

Fig. 3. Measurements of elephant postcranial bones: a = scapula; b = femur; c = humerus; d = tibia; e = radius; f = ulna; g = proximal end of the elbow bone, side view; h = atlas, front view; i = atlas, upper view; j = axis, front view; k = axis, upper view. 1 = greatest length; 2 = length to the middle of glenoid fossa; 3 = width of upper edge; 4 = width of posterior edge; 5 = head greatest width; 6 = neck width; 7 = kneecap facet width; 8 = bloc width; 9 = medio-lateral and antero-posterior diameters of distal shaft end; 10 = greatest length; 11 = longitudinal and transversal diameters through the head; 12 = shaft length; 13 = greatest shaft width; 14 = smallest shaft width; 15 = distance between lateral condyle and apex of the head; 16 = medio-lateral and antero-posterior diameters of the proximal shaft end; 17 = smallest shaft width; 18 = greatest width of distal articulation; 19 = length from distal to proximal articulation surfaces; 20 = shaft length; 21 = greatest length; 22 = medio-lateral and antero-posterior diameters of the proximal end; 23 = medio-lateral and antero-posterior diameters of the distal end; 24 = shortest medio-lateral and antero-posterior diameters of shaft; 25 = shaft length; 26 = greatest length; 27 = greatest length; 28 = length till proximal articulation surface; 29 = shaft length; 30 = articulation length; 31 = width of lateral articulation facet; 32 = width of medial articulation facet; 33 = shortest medio-lateral and antero-posterior diameters; 34 = medio-lateral and antero-posterior diameters of distal shaft end; 35 = olecranon width; 36 = distance between the anterior edge of articulation facet and olecranon apex; 37 = ulnar notch length; 38 = neck longitudinal diameter; 39 = greatest length; 40 = shaft length; 41 = length from lateral condyle to the apex of the head; 42 = shortest medio-lateral and antero-posterior diameters of shaft; 43 = medio-lateral and antero-posterior diameters of the distal end; 44 = same, of the proximal end; 45 = distance between lateral edge of distal condyle to the lateral supracondylar tubercle. h, i: 1 = greatest width; 2 = upper neural arch apex width; 3, 4 = height and width of articulation surface; 5, 6 = greatest height and width of cerebrospinal canal; 7, 8 = greatest dimensions of transverse canal; 9 = greatest height; 10 = distance between exterior edges of articulations; 11 = length of transversal process; 12 = greatest width of body; 13 = transverse diameter of vertebra. j, k: 1 = width of spinous process; 2 = greatest height; 3 = height of vertebral body; 4 = combined height of neural arch and transverse process; 5, 6 = as in h, i: 5, 6; 7 = greatest width; 8 = as in h, i: 12; 9, 10 = as in h, i: 7, 8; 11- distance between distal articulations; 12, 13 - height and length of spinous process; 14 = greatest antero-posterior diameter; 15, 16 = height and widht of anterior articulation facets.

In fig. 3 wordt het meetschema gegeven van postcraniale beenderen van olifanten: a = schouderblad; b = dijbeen; c = opperarm; d = scheenbeen; e = spaakbeen; f = ellepijp; g = boveneind ellepijp, zijaanzicht; h = eerste nekwervel (atlas), vooraanzicht; i = atlas, bovenaanzicht; j = tweede nekwervel (draaier), vooraanzicht; k = draaier, bovenaanzicht. a-g: 1 = grootste lengte; 2 = lengte tot midden van de gewrichtskom; 3 = breedte van de bovenrand; 4 = breedte van de achterrand; 5 = grootste breedte gewrichtskop; 6 = nekbreedte; 7 = breedte katrol; 8 =breedte rollers; 9 = midden-zij- en voor-achter-middellijnen door onderuiteinde schacht; 10 = grootste lengte; 11 = middellijnen door dijbeenkop; 12 = schachtlengte; 13 - grootste breedte; 14 = kleinste schachtbreedte; 15 = afstand tussen zijroller en hoogste punt dijbeenkop; 16 = midden-zij- en voor-achter-middellijnen door bovenuiteinde schacht; 17 = kleinste breedte schacht; 18 = grootste breedte onderuiteinde; 19 = lengte van onderste tot bovenste gewrichtsvlaktes; 20 = schachtlengte; 21 = grootste lengte; 22 = midden-zij- en voor-achter-middellijnen door bovenuiteinde spaakbeen; 23 = midden-zij- en voor-achter-middellijnen door onderuiteinde spaakbeen; 24 = kleinste midden-zij- en voor-achter-middellijnen door schacht; 25 = schachtlengte; 26, 27 = grootste lengte; 28 = lengte tot aan bovenste gewrichtsvlakte; 29 = schachtlengte; 30 = lengte gewrichtsvlakte; 31 = breedte van zijfacet; 32 = breedte van middenfacet; 33 = kleinste midden-zij- en voor-achter-middellijnen; 34 = midden-zij- en voor-achter-middellijnen door onderuiteinde schacht; 35 = breedte olecranon; 36 = afstand tussen voorrand van gewrichtsvlakte en top van het olecranon; 37 = lengte gewrichtsinkeping; 38 =overlangse middellijn door nek; 39 = grootste lengte; 40 = lengte schacht; 41 = lengte van zijroller tot hoogste punt gewrichtskop; 42 = kleinste midden-zij- en voor-achter-middellijnen door schacht; 43 = midden-zij- en voor-achter middellijnen door onderuiteinde; 44 = midden-zij- en voor-achter-middellijnen door bovenuiteinde; 45 = afstand tussen de zijkant van zijroller tot supracondylare knobbel. h, i: 1 = grootste breedte; 2 = breedte bovenkant wervelboog; 3, 4 = hoogte en breedte gewrichtsvlak (fovea articulated atlantis); 5, 6 = grootste hoogte en breedte van ruggemergskanaal (foramen vertebrale); 7, 8 = grootste afmetingen van het dwarskanaal (foramen transversarium); 9 = hoogte wervel; 10 = afstand tussen buitenranden van gewrichtsvlakken; 11 = lengte van dwarsuitsteeksel; 12, 13 = breedte en hoogte van het wervellichaam. j, k: 1 = breedte doornuitsteeksel; 2 = wervelhoogte; 3 = hoogte wervellichaam (corpus vertebrae); 4 = gecombineerde hoogte van wervelboog en dwarsuitsteeksel; 5, 6 = grootste verticale en horizontale middellijnen door ruggemergskanaal (foramen vertebrae); 7 = wervelbreedte; 8 = breedte wervellichaam; 9, 10 = grootste afmetingen van het dwarskanaal; 11 - afstand tussen achterste gewrichtsvlakken; 12, 13 - hoogte en lengte doornuitsteeksel; 14 = grootste voor-achter-middellijn; 15, 16 = verticale en horizontale middellijnen door voorste gewrichtsvlakken.

enamel plates (usually five in the upper and four in the lower teeth).

Individual age

Owing to the good preservation of several complete skeletons of mammoth calves from the Sevsk locality, their individual age could be reliably determined at the basis of a complex of morphological features that characterizes age differences. These skeletons were used as reference material in further analysis of isolated teeth and bones of mammoth calves. Data from mammoth calf cadavers from the Magadan region and the Yamal peninsula (see above) constituted the second significant body of material used in the construction of a reference scale of age variability. All data on age related morphology was compared with data on morphology and skeletal dimensions of extant elephant calves of similar ages, which allowed us to develop a rather strict framework of size variability related to age as determined by teeth.

Data on the degree of formation and wear of teeth in *M. primigenius* was compared with similar data on *E. maximus* (McKay, 1973; Roth & Shoshani, 1988; Sukumar *et al.*, 1988) and *L. africana* (Sikes, 1966; Johnson & Buss, 1965; Jachmann, 1988). Data on the correlation between age determined by teeth and by corresponding stage of fusion of epiphyses in *M. primigenius* is scarce and rather contradictory (Lister, 1999). Researchers emphasize a common sequence of long bone epiphyseal fusion in modern elephants and mammoths and a considerably longer period of growth in mammoth males than in females. However, the individual age at which complete epiphyseal fusion occurs and the termination of growth are interpreted different by different authors (V. Garutt, A. Tikhonov, pers. comm.). As this process is already complex, heterochronous, and usually accompanied with individual deviations, in extant elephants, the reliability of the interpretation of data on mammoths may be better judged when new and more complete data is available (Baryshnikov *et al.*, 1977; Rensch & Harde, 1956; Roth, 1984).

The scale based on the reference series of the Sevsk juvenile skeletons was used to subdivide all the material into age groups with fixed borders of size variability and stages of tooth formation. Morphological peculiarities specific for each group were determined. The method of delimiting the borders between age groups was based on a combination of the following data: the stage of formation of the functional tooth generation, the linear dimensions of the skull, the lower jaw and the postcranial skeleton.

The conclusion on the duration of gestation in mammoths was based on their biological peculiarities, the seasonal restrictions of reproduction and the dimensions of newborns. It was taken into account that the gestation period in the woolly mammoth was slightly shorter than in modern elephants, owing to the differences in biology of these two species. Data on the dimensions and sizes of foetal bones and bodies at different stages of prenatal development in modern elephants was extrapolated to *M. primigenius*, with a necessary correction owing to the shorter gestation in the latter, as well as the smaller size of woolly mammoth females.

Systematics

The systematic biology of the family Elephantidae and the genus *Mammuthus* is described at the basis of data supplied by Osborn (1942), Maglio (1973), Garutt (1986), Baigusheva & Garutt (1987) and Lister (1996). In the revision of the genus *Mammuthus* made by the author, some features of the diagnosis were judged from the point of view of their expression during the individual development (ontogeny) of *M. primigenius*.

The relation between the morphology of mammoth calves and features that characterize the phylogeny of the mammoth-like elephants is analysed on the basis of selected morphological features of *M. primigenius* during ontogenesis in comparison with some relevant features of the phylogenetic development of the group. The analysis was not aimed at the revision of the family Elephantidae, for the biological system of the family is based on more general features that characterize the family as a whole. The analysis covers especially the stages of plate formation (the duration of mineralization of plate-constituents is estimated), and the formation of deciduous and permanent tusks. In some cases, morphological homologies were compared not only to representatives of the genus *Mammuthus*, but also between these and other representatives of the proboscideans.

The estimation of the taxonomic weight of the features used to discriminate between species or genera, subsuming close relatives under a single taxon, or their distribution among different taxa, are the most complicated problems of any study dedicated to a biological system. Considerable differences exists in the way different authors conceive homology of biological structures that are used for the construction of biological systems. However, ontogenetic studies of these biological structures may cast new light on the nature of their homology and, consequently, provide new opportunities for a more reliable use of the features bound up with them. In a number of works on the phylogeny of Proboscidea and Elephantidae, methods of parsimony analysis and extensive comparison of homological morphological structures among different proboscidean groups are used for the systematic discrimination within the order and the family (Tassy & Darlu, 1986; Tassy, 1987; Tassy & Shoshani, 1988). This work is an attempt to apply this strategy, which had previously only been used on the level of the family and higher, to the level of a single genus.

Teeth and skeleton of *M. primigenius* during ontogenesis

Introduction

Although woolly mammoths are relatively well studied, transformations in skeletal morphology during ontogenesis remain understudied because calf remains are rare finds (Vereshchagin, 1981; Vereshchagin & Tikhonov, 1986, 1999; Kerkhoff, 1993; Garutt, 1999; Lazarev, 1999; Kuzmina, 1999; Kuzmina & Maschenko, 1999). This is particularly true of the formation and fusion of skull bones, the formation of epiphyses of long bones, and the ossification of vetebral parts. Data on skeletal morphology of other proboscideans is also relatively scarce (Eagles, 1926; Morrison-Scott, 1938; Hooijer, 1953, 1954; Ambrosetti, 1968; Tassy, 1987; Roth & Shoshani, 1988; Raubenheimer, 1991). In this chapter a first attempt is made to analyse new data and generalize the material on mammoth calf osteology that was already published.

The skull during early stages of development

Studies of skull morphology in relation to individual ages reveal a number of considerable changes during ontogenesis. The most important changes connected with morphology and non-linear growth of bones as well as of cranial parts occur in the facial region of the skull at the time the permanent tusks start to replace the di [deciduous incisors] and when dp^4 are formed and become functional. Qualitative transformations in the cerebral region of the skull occur when the cartilage between the bones of the cerebral region begins to ossify, when the parts of the bones start to fuse and when bone-to-bone fusion comes about as well. Skull measurements, represented according to increasing individual age (table 1) illustrate the growth of mammoth calves during the first years of their life with some individual and population related peculiarities.

The distorted foetal skull of *M. primigenius* from Kostionki 12 (ZIN 34416; fig. 4a, b; photo 1) differs significantly in proportions from adults. To judge by the dp^2 that had already been formed, the specimen represents the last stage of prenatal development , supposedly the 19th to 20th month of gestation. The skull is shallow and elongated. Its maximal height is at the level of the mid-parietals. The distal parts of the parietal and occipital bones are inclined backward. The occipital condyl is far displaced toward the rear end of the skull. The alveolar part of the skull is relatively short and the premaxillar bones almost follow the direction of the parietal bones (they are not curved forward). The nasal opening is situated above the level of the orbits. The post-orbital narrowing of the skull is only slightly expressed. The reconstructed parietal length is about 252 mm. As most of the maxillar and premaxillar bones are absent, the degree of development of the alveoli and the peculiarities of their structure at this stage cannot be determined precisely. However, to judge by the fragment preserved, the transverse diameters of the alveolar part are small.

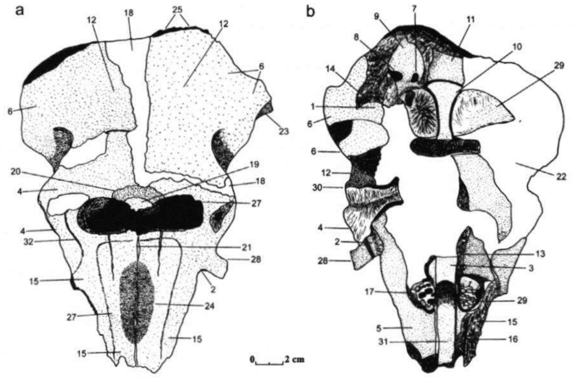

Fig. 4. Skull of a *M. primigenius* foetus (ZIN 34416; ca. 19-20 months of prenatal development; Kostionki 12, Voronezh region), upper view (a) and lower view (b). After Zalenskiy (1903). 1 = foramen acusticus externus; 2 = canalis infraorbitalis; 3 = vomer; 4 = frontale; 5 = maxillare; 6 = squamosum; 7 = foramen rotundum; 8 = fenestra rotunda; 9 = exoccipitale; 10 = basisphenoideum; 11 = basioccipitale; 12 = parietale; 13 = pterygoideum; 14 = ala temporalis; 15 = premaxillare; 16 = apertura jakobsoni; 17 = upper tooth of first generation (dp^2); 18 = reconstructed parts; 19 = nasale; 20 = sutura frontalis; 21 = sutura intermaxillaris; 22 = destroyed parts of cranium base; 23 = processus zygomaticus squamosi; 24 = depression in premaxillaries for trunk base musculature attachment; 25 = posterior edge of parietal bones (coincides with the occipito-parietal suture); 26 = sutura fronto-parietalis; 27 = cavum nasi; 28 = processus zygomaticus maxillae; 29 = alveolus of the upper jaw tooth; 30 = processus postorbitalis; 31 = intermaxillary gap; 32 = sutura frontomaxillaris.

Schedel van een ongeboren *M. primigenius* vrucht (ZIN 34416; ca. 19-20 maanden dracht; Kostionki 12, Voronezh), bovenaanzicht (a) en onderaanzicht (b). Naar Zalenskiy (1903). 1 = uitwendige gehooropening; 2 = kanaal onder de oogkassen (canalis infraorbitalis); 3 = vomer; 4 = voorhoofdsbeen; 5 = bovenkaaksbeen; 6 = schoep van het slaapbeen; 7 = het ronde gat (foramen rotundum, toegang tot canalis alaris vanuit hersenholte); 8 = het ronde venster (fenestra rotunda); 9 = exoccipitale (deel van het latere achterhoofdsbeen met achterhoofdsknobbel); 10 = basisphenoid (wiggebeen); 11 = basioccipitale (deel van het latere achterhoofdsbeen aan schedelbasis); 12 = wandbeen; 13 = vleugelbeen; 14 = rotsbeen; 15 = tussenkaaksbeen; 16 = kanaal van Jakobson; 17 = bovenkies van eerste generatie (dp^2); 18 = gereconstrueerde delen; 19 = neusbeen; 20 = voorhoofdsnaad; 21 = tussenkaaksnaad; 22 = vernielde delen van schedelbasis; 23 = jukbooguitsteeksel van het slaapbeen; 24 = del in tussenkaaksbeen voor spieraanhechtingen voor slurfbasis; 25 = achterrand wandbeenderen (valt samen met naad tussen achterhoofd en wandbeenderen); 26 = naad tussen voorhoofd en wandbeenderen; 27 = neusholte; 28 = jukbooguitsteeksel van het kaakbeen; 29 = tandkas voor bovenkaakskies; 30 = uitsteeksel achter de oogkas (processus postorbitalis); 31 = ruimte tussen bovenkaakshelften; 32 = naad tussen voorhoofd en bovenkaak.

The interior of the remaining premaxillar fragment is completely filled with cancellate bone. The part of the skull where the tusk alveoli would be situated is small (figs. 4b: 5), and the di would occupy practically all the space inside the alveolar part of the skull. In *E. maximus* and *L. africana* embryos the di head is calcified at the beginning of the second year of gestation. The tusk head projects beyond the edge of the premaxillar bone, yet remains covered by soft tissue (Eales, 1928; Deraniyagala, 1953). The small size of the alveolar part in ZIN 34416, as well as its internal structure, suggests that at this ontogenetic stage the di was not yet formed completely. Otherwise, the tusk root would not have had enough space within the alveolar part.

The diameter of the intraorbital foramen is about fourteen mm. The suture between the right and left premaxillar bones extends along the midline of the alveolar part (fig. 4a: 21), almost as far as the lower edge of the nasal opening. The oval depression for attachment of the trunk base muscles is well expressed (fig. 4a: 24). The suture between premaxillar and frontal bones is clearly seen (fig. 4a: 32). A similar development of the suture is preserved during the first months after birth.

The process of the nasal bone that supports the nasal cartilage at the base of the trunk is evidently not yet ossified at this stage. The edges of the frontal bones that border the fragments that are most probably just badly preserved nasalia are not well defined (fig. 4a: 19). In a *L. africana* foetus at the beginning of the second year of gestation, the entire area of the nasal bones consists of cartilage (Eales, 1925). In other skulls of mammoth calves, younger than three years of age, the nasal bones are never preserved, which suggests that ossification is incomplete at this age. Most probably, the nasal process is the last part to ossify.

The suture between the frontal and nasal bone is not seen in the specimen of Kostionki 12, while it can be discerned in the skull of a newborn (PIN 4353-2614). The sagittal suture is not seen, because of the reconstruction of the central part of the frontal and parietal bone (photo 1). The preserved fragments of these bones suggest that the left and right parts were not adjoining and were divided by cartilaginous tissue. The remaining cartilage in the skull of specimen PIN 4353-2614 is smaller and both parts of the frontal and parietal bone were mostly in contact. In the Kostionki 12 specimen the suture between the parietal and squamose bone cannot be seen. To judge by the posterior edge of the parietal bone, the occipital and parietal bones must have been in contact, although the occipital bone is missing here. Eales (1925) notes the presence of cartilage in the suture between these bones in a *L. africana* embryo at an earlier developmental stage. The maximal thickness of the parietal bone in the area of the suture between the occipital and temporal bone is eight mm (fig. 4a: 25).

When seen from its lower part, the skull shows a wide gap between the maxillar bones that reaches thirty mm (fig. 4b: 31). The maxillaries themselves run almost parallel. At later ontogenetic stages they gradually fuse: their posterior edges approach, and their longitudinal axes are at a small angle with each other. The final stage of this process may be illustrated by specimen ZIN 34378. The individual age of this calf must be five years, as nine plates of dp^4 are in wear. The distance between the left and right maxillary at the alveolar end is about twelve mm, at mid-length ten mm, and even less at the level of the tooth alveoli. In other words, fusion begins at the level of the tooth alveoli and is directed toward the end of the tusk alveoli. By the age of five to six years, the maxillaries are closely set, as in adults.

In specimen ZIN 34416 the upper part of the alveolus of dp^2 is approximately at the level of the crown. The tooth is not completely formed, mineralization of the plates is not complete and the tooth has not erupted from the alveolus. The vertical enamel columns that compose the five plates of the dp^2 crown are separated almost from their bases to the ends and form irregular groups, not regular rows transversely to the longitudinal axis of the crown (fig. 4b: 17). The crown base and the roots are not formed, which indicates the incomplete formation of the dp^2 at this ontogenetic stage. In the African elephant, dp^2 has not completely erupted from the gum by the time of birth, yet the plate mineralization is completed. In about 5% of the newborn Indian elephants, the dp^2 is in wear, but usually wear starts during the first month of life (Roth & Shoshani, 1988). To judge by the degree of formation of the dp^2 in specimen ZIN 34416, eruption of this tooth in mammoths took place within a similar time range.

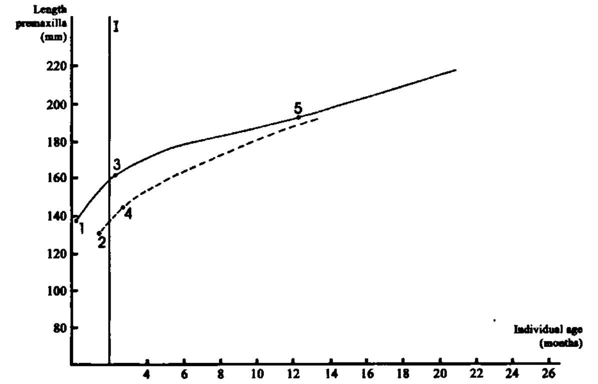

Fig. 5. Differences in premaxillar length in *M. primigenius* calves of ca. one-month from Western Siberia and East Europe: rows = individual age (months), columns = length of premaxillary (in mm). 1 = ZIN 34416; 2 = ZIN 31661; 3 = PIN 4353-2614; 4 = GIN 77; 5 = PIN 4353-933; 6 = ZIN 31837-1

Verschil in lengte van tussenkaaksbeenderen tussen *M. primigenius* kalveren van ongeveer een maand oud, afkomstig van West Siberië en Oost Europa: rijen = individuele leeftijd (in maanden), kolommen = tussenkaakslengte (in mm). Voor nummers, zie Engelstalig onderschrift

Towards the end of the prenatal period of *M. primigenius*, the alveoli of the di and the deciduous tusks are formed, which remain within the alveoli till after birth. In specimen ZIN 31611 (Mal'ta locality) the di is preserved in the left alveolus. The prenatal developmental age as estimated by the right dp^2 is about 20-21 months (photo 2). The dp^2 crown consists of five plates. The enamel columns that constitute it are completely fused. No cement is present. The dp^2 apex is above the level of the edge of the alveolar wall (photo 2: 3). At least three anterior plates of dp^3 are formed.

The linear dimensions of sp. ZIN 31611 are larger than those of sp. ZIN 34416 (table 1). The dimensions of the left dp^2 alveolus are 20x16 mm, the depth is 22 mm. The wall between the alveoli of dp^2-dp^3, absent in the preceeding stage, is completely formed.

The left di is preserved. Its head does not project beyond the edge of the premaxillary. The interior of the alveolus is completely occupied by the tusk root. The opening of the root canal is large. This position of the di leaves no space for the permanent tusk (I) inside the alveolus. The permanent tusk formation has therefore not begun. The alveolus of the di is formed by the premaxillar bone. There is a depression in the medial wall inside the alveolus which is partly separated from the rest of the alveolar cavity by an incomplete septum (photo 2: 4). About nine mm thick cartilage still remains between the supraoccipital and the exoccipital bone. Within the frontal and the parietal bone no cellular air cavities have yet been formed.

Specimen PIN 4353-2614 (Sevsk, a skull of an almost complete skeleton of a two-weeks-old calf; photo 3: 1, 2) is illustrative of this ontogenetic stage. The reconstructed height of this individual is 80-82 cm, which correlates to the minimal size of newborn *E. maximus*: 76-94.7 cm (Stanley, 1943). Another illustration of this developmental stage is specimen GIN 77, Yamal Peninsula.

In specimen PIN 4323-2614 the premaxillary bones are not curved upward as in sp. ZIN 31661. This is probably due to the populational differences between the Siberian (ZIN 31661) and the Central Russian (ZIN 34416, ZIN 4353-2614) populations (fig. 5). The diagram illustrates dimensional differences, i.e., specimen PIN 4353-2614 (no. 4 in the diagram) exceeds specimen GIN 77 in the length of the premaxillar bones (no. 4 in the diagram). Similar differences may be observed between embryo skulls from Siberia and Central Russia: ZIN 34416(1) and ZIN 31661(2), respectively. The length of the palatal bone is comparable with its width, and these proportions persist until the age of ten to eleven months. Later the length of the palatal bone becomes notably greater than its width because of the greater dimensions of the functional teeth.

The dp^2 are not in wear. The left one consists of four plates, the right one of five plates. Cement formation is beginning on the crown, but the tooth most likely has

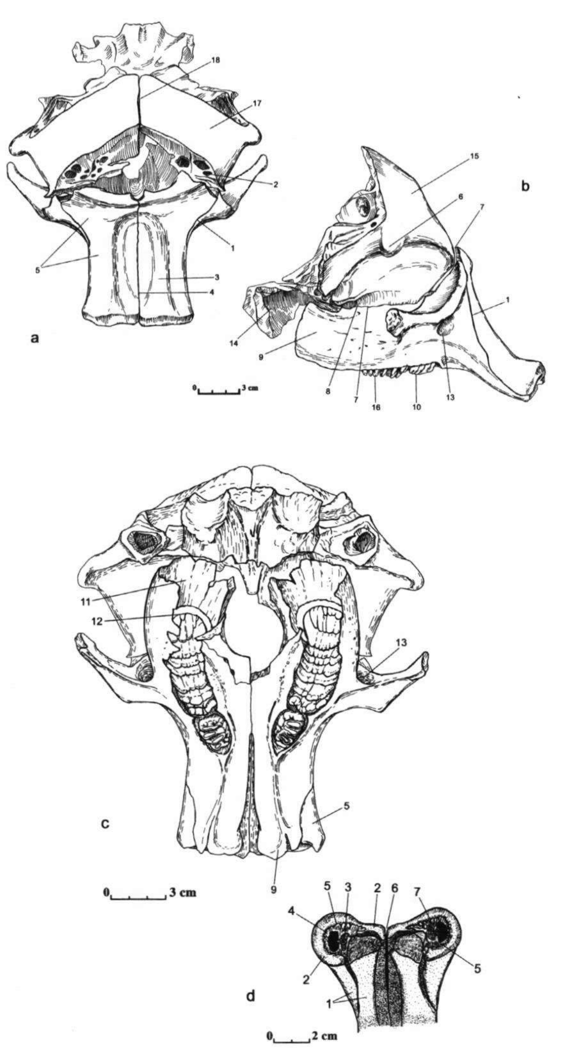

Fig. 6. Fragment of skull of ca. one-month calf of *M. primigenius* (GIN 77, Yamal Peninsula): a = upper view; b = side view; c = bottom view; d = structure of the alveolus. Scale bar 3 cm (a, b, c) and 2 cm (d). In a, b, c: 1 = suture between premaxillar and maxillar bone; 2 = air cells in frontal bone; 3 = depression on the anterior part of the premaxillary for trunk base muscle attachment; 4 = intermaxillar suture; 5 = premaxillary; 6 = postorbital process; 7 = maxillofrontal suture; 8 = sphenoidal fissure; 9 = maxillary; 10 = dp^2; 11 = dp^4 alveolus; 12 = interalveolar wall between dp^2 and dp^3; 13 = infraorbital foramen; 14 = posterior wall of dp^4 alveolus; 15, 17 = frontal bone; 16 = dp^3; 18 = suture between right and left parts of the frontal bone. In d: 1 = maxilla; 2 = premaxilla; 3 = internal depression; 4 = external canal; 5 = di alveolus; 6 = intermaxillar suture; 7 = incomplete wall separating internal depression from external canal inside alveolus

Schedelfragment van een *M. primigenius* kalf van circa 1 maand oud (GIN 77, Yamal schiereiland): a = bovenaanzicht; b = zijaanzicht; c = onderaanzicht; d = tandkasstructuur. Maatstreep 3 cm (a, b, c) en 2 cm (d). In a, b, c: 1 = naad tussen bovenkaaks- en tussenkaaksbeenderen; 2 = luchtkamers in voorhoofdsbeen; 3 = del in voorste deel van de tussenkaak voor spieraanhechting van slurfbasis; 4 = tussenkaaksnaad; 5 = tussenkaaksbeen; 6 = uitsteeksel achter oogkas; 7 = naad tussen bovenkaak en voorhoofd; 8 = wigvormige spleet; 9 = bovenkaak; 10 = eerste generatie kies (dp^2); 11 = tandkas voor derde generatie kies (dp^4); 12 = wand tussen tandkassen voor dp^2 en dp^3; 13 = opening onder oogkas; 14 = achterwand van tandkas voor dp^4; 15, 17 = voorhoofdsbeen; 16 = tweede generatie kies (dp^3); 18 = naad tussen rechter en linker voorhoofdsbeenderen. In d: 1 = bovenkaaksbeen; 2 = tussenkaaksbeen; 3 = interne groeve; 4 = extern kanaal; 5 = tandkas voor di; 6 = tussenkaaksnaad; 7 = onvolledige scheidingswand tussen centrale groeve en perifeer kanaal binnen de tandkas

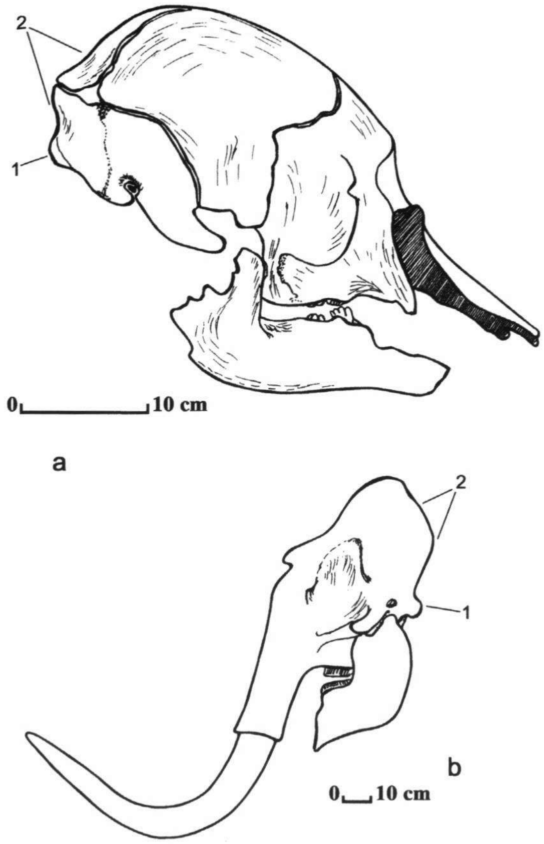

Fig. 7. Comparison of skull shape in newborn (a) and adult (b) *M. primigenius*, side view. a = PIN 4353-2614, Sevsk locality, Bryansk region; b = ZIN 5316, Beriozovka river, Yakutia; 1 = occipital condyle; 2 = occipital bone. Scale bar: 10 cm

Vergelijking van schedelvorm tussen een pasgeboren (a) en volwassen (b) *M. primigenius*, zijaanzicht. a = PIN 4353-2614, vindplaats Sevsk, district Bryansk; b = ZIN 5316, Beriozovka rivier, Yakutië; 1 = achterhoofdsknobbel; 2 = achterhoofd. Maatstreep 10 cm

not erupted completely from the alveolus. The dp^{3} are in the process of formation: nine plates are mineralized but not fused at the bases. The roots are absent. The wall that separates the dp^{2} from the dp^{3} is formed completely. The preserved part of the right premaxillary has a canal for the root of the first generation tusk. Inside the premaxillary the canal is displaced laterally. Its cross section is oval, with the axes 8 x 4.5 mm most likely corresponding to the cross section of the middle part of the di root. The canal noticeably narrows from the anterior end of the alveolus to its posterior end. The position of the root canal suggests that the tusk alveolus was also formed only by the premaxillary at this stage. The anterior part of the premaxillary adjacent to the maxillary is not preserved. The structure of the di root canal and its size suggest that permanent tusk formation begins at a later stage. The depression for the muscles for the attachment of the trunk base to the frontal surface of the premaxillary bones is large. The dimensions of the infraorbital foramen are 20 x 20.5 mm. The length and width of the jugal bone are 17 and 10 mm respectively. The nasal opening is above the level of the orbits.

The specimen GIN 77 from the Yamal Peninsula is a fragment of the facial part of the skull of an approximately one-month-old mammoth calf (fig. 6; photo 4: 1-3). The teeth are dp^{2}. The crown consists of five plates. All plates are functional, for they exhibit traces of wear. The dp^{3} consists of nine completely mineralized plates that are not coated with cement and whose bases are not fused. The roots have not been formed either.

The specimen differs from the Central Russian specimens ZIN 34416 and PIN 4353-2614 in proportions and shape of the alveolar part of the skull (table 1; fig. 5). This part is notably shorter in the Yamal specimen and the premaxillary is considerably curved (photo 4: 2) as in the specimen ZIN 31661 from West Siberia. To judge by the reconstructed dimensions of sp. GIN 77, the skull was smaller than in the Sevsk newborn sp. PIN 4353-2614. This makes a contrast with the greater individual age of sp. GIN 77, determined by the degree of wear of the dp^{2}. This discrepancy is probably also due to populational differences.

The nasal bones are not preserved. To judge by the suture formed between the frontal bones and the nonpreserved nasal bones (fig. 5a: 17), the nasal bones at this stage were at least partially formed by ossified tissue. The suture between the left and right halves of the frontal bone is well expressed (fig. 5a: 18). The air cells in the frontal bones of this individual have formed along the lateral edges of the bones (fig. 5a: 2).

The alveolar part of the skull is formed by two bones, each of which makes a different contribution. The upper and external part is formed by the premaxillar bone only (figs. 6a: 5, 6c; photo 4: 2). The lower and internal part is formed by the maxillar bone (photo 4: 1). The alveolus itself is formed only by the premaxillar bone (fig. 6d, 2). The depression for the attachment of the trunk base muscles to the anterior surface of the premaxillary bones is well expressed (fig. 6a: 3). The tusk alveolus is well preserved. Its internal wall surface is cellular (fig. 6d: 5). The thickness of the alveolar wall at the opening is about 6 mm, the diameter of the opening is about 16 mm. The diameter diminishes from the anterior edges of the premaxillar bones to the nasal opening. It reaches a minimum of 9 mm at a level situated 10 mm from the lower edge of the premaxillar bone. In this part of the alveolus, the di root and the neck of the tusk head were most probably situated.

The inside of the alveolus is subdivided into two parts (as in sp. ZIN 31661). The larger part (which is lateral in relation to the intermaxillary suture) is the alveolus of the di proper, or the external canal (fig. 6d: 4). This is more clearly visible in the right alveolus on photo 4: 2. The smaller (medial) part of the alveolus is a depression (internal depression) separated from the external canal by an incomplete wall (fig. 6d: 7). The depth of this internal depression is 26 mm. It has an oval cross section with axes of 7.5 and 5.0 mm. The bed of this depression has a porous structure but there are no large openings for big blood vessels or nerves. The part of the di alveolus that is seen is curved to follow the shape of the premaxillary. The dimensions of the alveolar cavity correspond exactly to the dimensions of the di root, which suggests that the I is not mineralized at this ontogenetic stage.

In the Yamal Peninsula calf cadaver (ZIN 34201), first generation tusks have erupted from the soft tissues (Vereshchagin & Tikhonov, 1999). The individual age of this calf as determined by the dp^2 is about one month. The extent of wear of the dp2 is the same as that in specimen GIN 77, which is close in individual age, so that one may suggest that the di was probably formed to an extent similar to that in GIN 77. It is evident that the di formation was completed by the age of one month.

The extant material allows the description of some peculiarities of skull morphology regarding the period between ten or eleven months to one year and two or two and a half to three and a half years. This interval is characterized by the end of the functionality of dp^2, the substitution of the I for the di, a change of the skull proportions (the facial part becomes relatively larger), and the obliteration of some cranial sutures (viz., the sutura sagittalis, and the suture between the exoccipital and supraoccipital bone). The suture between the parietal and occipital bone persists, the bones being in close contact, with no traces of cartilage between them. In addition, air cells under the internal surface of the nasal and frontal bone are no longer aligned in one row and form also under the internal surface of the parietal bone by the age of three years.

The specimen ZIN 31771(1) from Kostionki-1 is a fragment of a mammoth calf skull, with an individual age of ten to eleven months (photo 5). The dp^2 and dp^3 are functional, the former is heavily worn. All plates are in wear, the first one is completely worn down. Six anterior plates of the dp^3 are in wear. All plates of the dp^3 are completely formed and coated with cement. Specimen ZIN 31771(1) is close to the mammoth calf from the Magadan region (ZIN C 70188) in the extent to which the functional teeth have been formed (Vereshchagin, 1981).

The next stage in mammoth ontogenesis, well exemplified by the extant cranial material, coincides with the age of eleven to fourteen months, estimated on the basis of dentitional data. In the dentition, the end of the first year of postnatal development in mammoths is signalled by the substitution of dp^3 for dp^2. In specimen ZIN 31771(1), from Kostionki 1, a skull fragment of a juvenile aged ten to eleven months (photo 5), the dp^2 and dp^3 are functional. All dp^2 plates are heavily worn, the anteriormost plate is worn totally. In the dp^3, the six anterior plates are in wear. All dp^3 plates are completely formed and covered with cement. In regard to the level of formation of the functional teeth sp. ZIN 31771(1) is close to the mammoth calf from the Magadan region, ZIN C 70188 (Vereschagin, 1981).

The specimens PIN 4353 from Sevsk (photo 6), and ZIN 31277(1), 31689, and Kostionki 1 (table 1), represent a later stage of ontogenesis, viz. twelve to fourteen months. Specimen PIN 4353 is a skull of a complete skeleton of a one-year-old calf with a functional dp^3. All plates are in wear. The anterior plates of dp^4 are mineralized, but the basis of the crown and roots have not been yet. The alveolus of the posterior root of the dp^2 still remains (photo 6, fig. 2). Four anterior plates of the dp^4 emerge from the opening in the maxillar bone behind the alveolus of the dp^3. Only the apex of the anteriormost plate of the dp^4 is covered with cement. Other plates lack cement totally. The dp^3 of the specimens ZIN 31277(1) and 31689 show somewhat more advanced wear, which suggests that these individuals were older than one year.

It is only the maxillar bone that forms the tusk alveolus in sp. PIN 4353-933. This well-preserved specimen provides a good example of the changing overall proportions of the skull owing to elongation of the alveolar part. In the alveolar part, the diameter of the alveolus increases (table 1), the premaxillar bones become X-shaped, and the main axes of the alveolar openings become slightly divergent. Both tusks, di and I, remain in the left alveolus (photo 6: 3). The di does not project beyond the edge of the premaxillar bone and is situated lateral to the I, while the root of the di is in touch with the apex of the I. The head of the root of di shows traces of resorption. There is no enamel on the head end, the enamel remains only at its basis. The root of the di has no canal and is approximately twice as short as in younger animals. This structure of the di suggests that substitution of the I for the di in *M. primigenius* took place in calves with an age of approximately one year.

The length of the palate is considerably greater than its width. In specimen PIN 4353-933, the palate length is 90 mm, its width up to 27 mm. The alveolar wall between dp^3 and dp^4 is incomplete. The posterior and the upper walls of the dp^4 alveolus are formed by the pterygoid processes. Nasal and frontal bones are not preserved. The suture between the right and left parietal bones is clearly seen (photo 6: 1). The suture between the squama temporalis and the pterygoid bone is also seen. The external ear opening is oval, its dimensions are 20,5 x 23 mm. This opening is situated at the level of the jugal process of the squama temporalis. All sutures between the bones in the brain region, i.e., between the frontal and parietal bone, and between the supraorbital and parietal bone and the squama temporalis, remain well expressed in sp. PIN 4353-933 and other specimens of the same age. The cartilage between the supraorbital and parietal bone and squama temporalis most evidently disappears.

The occipital bone is still subdivided. The upper part (supraoccipital bone) has a paired fossa, the fossa sphenoperiotica. The lower part (exoccipital bone) bears the occipital condyles. With respect to their situation and orientation, these bones are similar to those in specimen PIN 4353-2614, whereas their orientation differs significantly from that of the same bones in adults (fig. 7). Air cavities are well developed in the frontal bone and in some areas of the basicranial bones. In the frontal bone they form one row.

During the next ontogenetic period (one and a half to two years), the proportions of the facial and cerebral parts of the skull in mammoth calves become similar to those in adults. The skull bones come into immediate contact with each other, and the sutures start being obliterated. In the zones of bone contact some sutures partly disappear. Cartilage disappears completely. The length of the alveolar part becomes equal to or even greater than the length of the cerebral region of the skull. During this period, dp^3 is replaced by dp^4. The I - its tip already in wear - starts emerging from its alveolus as the animal is two years old.

Specimen ZIN 31772(2), Kostionki 1, a fragment of the facial part of the skull (photo 7: 1), displays the dp^3-dp^4 replacement. In the dp^3 all plates are in wear. The anteriormost one is worn down completely. In the dp^4 four anterior plates are touched by wear. The dimensions of the skull are intermediate between those of a one-year-old calf (PIN 4353-933) and specimens with functional teeth of the second and third generations in more advanced wear (table 1). To judge by the tooth generation sutures on the skull, and overall dimensions, the individual age of this specimen should be about fourteen to eighteen months. Not only the premaxillar bone, but also the maxillar bone forms the alveolus in the preserved fragment of the alveolar part of the skull, where the alveolar diameter is 23 mm. It should definitely be greater at the opening of the alveolus.

The specimens ZIN 31837(1) (photo 7: 2) and ZIN 31773 from Kostionki 1, are fragments of facial parts of calf skulls with the remains of functional dp^3 (bases of five posterior plates) and functional dp^4. Six anterior plates of dp^4 are in wear. The teeth and the degree of formation of the skull bones suggest that their individual age was between one and a half and two years (table 1). The alveoli of I are formed by both premaxillar and maxillar bones. The nasal opening is situated above the level of the orbits. The dimensions of the infraorbital foramen in ZIN 31773 are 18 x 22 mm. The sutura sagittalis is obliterated, as well as the suture between the exoccipital and supraorbital bone, whereas the suture between the parietal and occipital bone still persists, but these bones fuse. Air cavities in nasal and frontal bone are well developed and form more than one row. There are air cavities in the parietal bone also.

It is evident that, from the age of one and a half to two and a half years, the size of tusks is not only influenced by individual variations, but also by sexual dimorphism. In ZIN 31773 the tusk diameter is 40 mm, and in sp. PIN 4353-2824 (three plates of dp^3 remaining, individual age 3-4 (?) years) it is 32 mm. In sp. PIN 4353-445, the individual age as determined by the functional dp^4 is about six to seven years, and the tusk diameter is 28 mm (table 1).

Thus, to judge by the material described, qualitative changes in morphology connected with growth during the first one to two and a half years of postnatal development are succeeded by quantitative changes at three to four years. The specimens PIN 4353-2824 and ZIN 31773 represent exactly this transitional stage of ontogenesis and are illustrative of these changes.

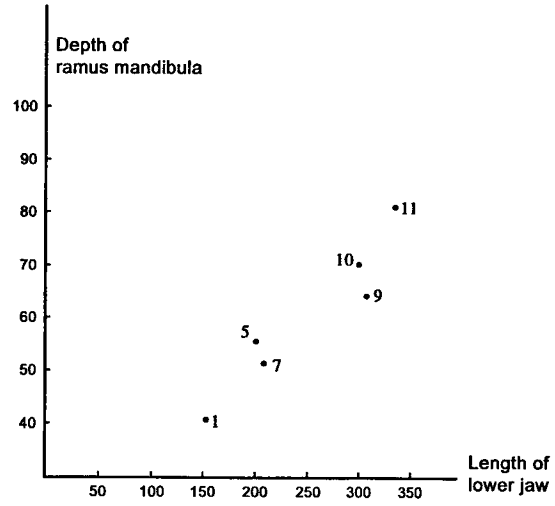

Fig. 8. Proportions (in mm) of lower jaws of *M. primigenius* calves from Central Russian and Siberian localities. The numbers in the diagram correspond to the order of specimens as given in table 2. Columns: height of the mandibular body at the posterior edge of the functional tooth; rows: length of lower jaw

Afmetingen (in mm) van onderkaken van *M. primigenius* kalveren uit Centraal Russische en Siberische vindplaatsen. De nummers komen overeen met de volgorde van exemplaren in tabel 2. Kolommen: hoogte van het kaaklichaam ter hoogte van de achterrand van de functionele kies; rijen: kaaklengte

The lower jaw in early stages of ontogenesis

Twenty four lower jaws were studied. Their measurements are presented in tables 2 and 3. The material embraces the time span between the end of prenatal ontogenesis and three to four years of age. The data shows that in early ontogenesis of *M. primigenius* the length of the symphyseal part diminishes relatively to the ramus of the mandible (table 3). The material studied displays a variability that is most probably connected with populational differences (fig. 8): in comparison with the individuals from Central Russia (nos. 5, 10, and 11), the individuals from Siberia (nos. 1, 7, and 9) have a relatively lower mandibular ramus. The wear of dp_2, dp_3, and dp_4 proceeds at a relatively slower rate than in the corresponding teeth of the upper jaw, and the speed of wear of dp_3 and dp_4 in different populations and different individuals is evidently slightly different. That is why a wider age range was selected for determing individual ages.

During the prenatal ontogenesis the compact layer of the body of the lower jaw is thin and differs in structure from what is observed during later periods. The left and right halves are not fused in the symphysis. The specimens ZIN 31661, Mal'ta (Western Siberia), ZIN 29843, Eliseevichi, ZIN 28392(4), Kostionki 14 (photo 8: 9), and ZIN 34419(24), are fragments of symphyseal parts of lower jaws and complete lower jaws of embryos of 20-28 months of gestation. The length of the symphyseal part (from the anterior end of the symphysis to the beginning of the interalveolar crest) in each of these is greater than the height of the mandibular body. A mental process has not yet formed in these specimens (table 2). In sp. ZIN 31661 the symphyseal part of the mandible (in this case from the end of mental process to the anterior edge of the dp$_2$ alveolus) is much shorter than the horizontal ramus (from the anterior edge of the dp$_2$ to the angle of the lower jaw): 50 mm and 90 mm respectively. This ratio (1.8) is the greatest of the whole sample (table 3). To judge by sp. ZIN 31661, the coronoid process is sharply inclined backward, its angle with the mandibular body less than 65° (photo 8: 3).

The materia compacta is thinner in the symphyseal part and thicker at the lower and upper surfaces of the horizontal branches. There are multiple small nutritional foramens in the symphysis. The mental foramen is either singular (ZIN 28392(4)) or paired, and opens only on the buccal surface of the horizontal ramus (mandibular body) as in ZIN 29843 (photo 8: 9). In sp. ZIN 29843, the mental foramens are divided (fig. 9c, d). A narrow anastomosis divides them at the lingual surface. At the buccal surface the anterior foramen is larger (55 x 4 mm), and the posterior one is smaller (2 x 1.5 mm). At the level of the bottom of the dp$_3$ alveolus the mandibular canal is seen. It fuses with the mental foramens and leads through them to the external and internal surfaces of the horizontal ramus. The diameter of the canal at the level of the dp$_3$ alveolus is 6 x 5 mm.

Age peculiarities in morphology are best expressed in the structures of dp$_2$ and its alveolus.In ontogenesis the formation of dp$_2$ proceeds parallel to the formation of its alveolus. Originally the crown of dp$_2$ does not go beyond the edge of the alveolus and the space between the alveolar wall and the root is filled with materia spongiosa as in ZIN 28392(4) (photo 8: 2; fig. 10a, b). In sp. ZIN 28392(4) part of the interorbital crest is destroyed and the root of dp$_2$ is open. The root is considerably deflected forward, and long. The opening of the root canal is large. Later (sp. ZIN 29843), the apex of the dp$_2$ crown stands out above the bony edge of the alveolus, but remains unworn, which suggests that the tooth did not erupt from the soft tissues. Between the crown base, the root and the wall of the alveolus there is a space not filled with materia spongiosa, and the alveolar walls are well formed (photo 8: 1; fig. 10c, d).

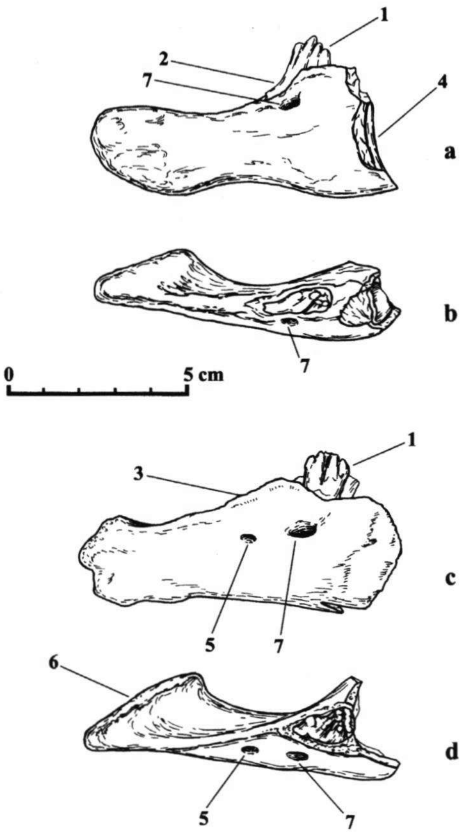

Fig. 9. Left part of symphyseal part of the lower jaw of *M. primigenius* foetuses during the last prenatal stage. a = ZIN 28392(4), Kostionki 14, Voronezh region, side view; b = same, upper view; c = ZIN 29843, Elisievichi, Bryansk region, side view; d = same, upper view. Scale bar: 5 cm. 1 = dp$_2$; 2 = root of dp$_2$; 3 = crista interalveolaris; 4 = anterior plate of dp$_3$; 5 = anterior mental foramen; 6 = symphyseal suture; 7 = posterior mental foramen.

Linkerdeel van symphyseaal deel van de onderkaak van *M. primigenius* foeten tijdens laatste stadium van de dracht. a = ZIN 28392(4), Kostionki 14, district Voronezh, zijaanzicht; b = idem, bovenaanzicht; c = ZIN 29843, Elisievichi, district Bryansk, zijaanzicht; d = idem, bovenaanzicht. Maatstreep 5 cm. 1 = dp$_2$; 2 = wortel van dp$_2$; 3 = kam tussen de tandkassen (crista interalveolaris); 4 = voorste plaat van dp$_3$; 5, 7 = voorste en achterste opening tot onderkaakskanaal (foramina mentalia); 6 = versmeltingsnaad tussen de kaakhelften.

No dp$_2$ crowns are preserved in specimen ZIN 31661. The depth of the left dp$_2$ alveolus is 18 mm, the other dimensions are 11 x 8 mm. On the bottom of the dp$_2$ alveolus an opening is preserved that most probably united the dp$_2$ root canal and the mandibular canal. The latter opens with a separate foramen onto the inner surface of the mandibular body at the level of the anterior edge of the dp$_2$ alveolus, twelve mm beneath its upper edge (photo 8: 3, 4).

Near the end of prenatal ontogenesis, changes in dp$_3$ morphology and the structure of its alveolus are observed. In sp. ZIN 28392(4) the anterior plate of dp$_3$ is preserved. The plate is formed by mineralized enamel columns that are grouped together. The base of the crown and the roots are not yet mineralized. The positions of the first and the base of the second plate

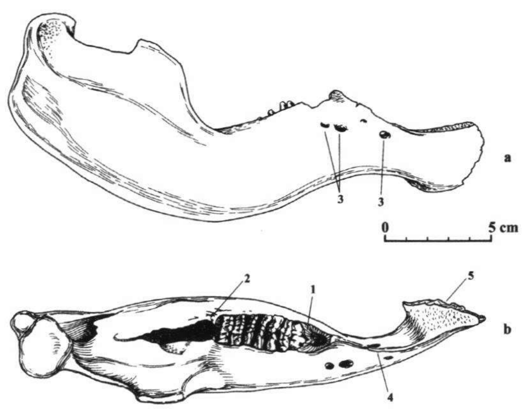

Fig. 10. Right ramus of lower jaw of ca. one-month-old calf of *M. primigenius*, GIN 77, Yamal Peninsula; a = side view; b = upper view. Scale bar: 5 cm. 1 = dp$_2$ alveolus; 2 = incomplete wall between dp$_2$ and dp$_3$ alveoli; 3 = mental foramen; 4 = interalveolar crest; 5 = symphyseal suture

Opgaand deel van de rechter onderkaak van een *M. primigenius* kalf van ca. 1 maand oud (GIN 77, Yamal schiereiland); a = zijaanzicht; b = bovenaanzicht. Maatstreep: 5 cm. 1 = dp$_2$ tandkas; 2 = onvolledige wand tussen tandkassen van dp$_2$ en dp$_3$; 3 = gat voor zenuwen; 4 = kam tussen de tandkassen; 5 = vergroeiingsnaad tussen de kaakhelften

suggest that the dp$_3$ is still completely inside the alveolus. In sp. ZIN 31661 (photo 8: 3, 4) the anterior three plates of the right dp$_3$ are similar in structure and position. The interalveolar wall between dp$_2$ and dp$_3$ is complete in all specimens. The opening of the mandibular canal is situated under its lower edge at the lingual surface of the mandibular body. An incomplete wall remains between the dp$_3$ and the dp$_4$ alveoli of the left ramus. The length of the dp$_3$ alveolus is about 51 mm, its greatest width about 27 mm. The thickness of the dp$_3$ alveolar walls is about 2 mm.

No significant qualitative transformations of the lower jaw take place in the beginning of postnatal ontogenesis (from birth to one or two months). The superficial layer (materia compacta) is formed everywhere, but for the head of the lower jaw. Nutritive foramens situated at the inner surface of the symphyseal part during the preceding ontogenetic stages, are absent. The symphyseal suture between the right and left ramus of the jaw is well developed (fig. 10). The formation of dp$_2$ is completed and wear begins. Mineralization of all plates of dp$_3$ occurs. In the sample studied the following specimens illustrate this stage: PIN 4353-2615, a lower jaw of a complete skeleton from Sevsk, ZIN 34201(1), a lower jaw of a calf cadaver from Yamal (photo 9, figs. 1, 2) and GIN 77 (fig. 10).

The proportions of the lower jaw are similar to those related to the previous ontogenetic stage (tables 2 and 3): in specimen PIN 4353-2615 the length of the symphyseal part is 75 mm, the length of the mandibular body from the dp$_2$ alveolus to the posterior end of the mandibular ramus is 140 mm (134 mm in ZIN 3420(1)). The ratio of these lengths is 1.86. It is 1.80 in ZIN 31661 (a foetus). In specimen PIN 4353-2615 the mandibular body is relatively shallow, the anterior part of the ascending ramus is directed upward vertically and the posterior part, together with the condylar process, is inclined backward. The height to length ratio of the lower jaw is 0.54 in PIN 4353-2615, and the height to thickness ratio of the mandibular body 1.31. In ZIN 3420(1) the latter ratio is 1.19 as the specimen is less lengthy and more robust. The data in table 3 illustrates the relative reduction of symphysis length during later ontogenetic stages.

At this stage of ontogenesis some differences emerge that depend on individual and populational peculiarities. In a one-month-old calf of *M. primigenius* from the Bensheim locality (Germany) the epiphyseal part is significantly inclined downward. The length of the interalveolar crest is about 80 mm, while the symphyseal part measures 65 mm (Döbert, 1992). The distance from the base of the mandibular body to the lower edge of the symphyseal part is about 32 mm. In the specimens from localities of the Russian Plain and Siberia the symphyseal part is shorter and directed forward. The length ratio between the symphyseal part and the mandibular body (partly reconstructed) is 2.07 (table 3).

The formation of the mental foramina nears completion. There are usually two foramina and their formation correlates with the formation of the interalveolar crest. In sp. PIN 4353-2615 the posterior foramen is situated under dp$_2$, whereas the anterior one is closer to the interalveolar crest. A similar position of the mental foramina is observed during later stages. In sp. PIN 4353-2615 and specimens of later ontogenetic stages the anterior mental foramen is no longer separated from the mandibular canal at the internal surface of the symphyseal part. In addition, the anterior mental foramen passes through the interalveolar crest. The dimensions of the anterior mental foramen are 7 x 5.5 mm; those of the posterior one are 7 x 3.5 mm.

The structure of the mandibular head is illustrated with the specimens ZIN 34201(1), PIN 4353-2615, and GIN 77. The articular surface of the head is flattened, the neck is not expressed. The head is slightly inclined forward, the coronoid process is shallow. The head is much elongated rostro-caudally. Its medial edge is lower than the lateral one, and the anterior edge is lower than the posterior one.

The mandibular incisura is shallow (fig. 10). In sp. PIN 4353-2615 the difference in height between the apex of the coronoid process and the lowermost point of the mandibular incisura is ca. six mm. The mandibular head is ten mm higher than the top of the coronoid process. The lower jaw angle (angulus mandibulae) on the rear edge of the ascending ramus is situated 28 mm beneath the lower edge of the jaw head. In sp. ZIN 34201(1) the mandibular angle is the hindmost part of the jaw. It is situated ca. 33 mm beneath the posterior edge of the mandibular head. Such a high position of the mandibular angle is usual before the age of three to four years. The posterior edge of the mandibular ramus is strongly rounded (photo 9: 1).

The ascending ramus remains relatively wide and shallow during the first postnatal period, at the expense of proliferation of the mandibular angle (tables 2 and 3). The posterior edge of the ascending ramus is sharply inclined backward. In sp. GIN 77 the mandibular incisura is elongated rostro-caudally and its posterior edge is situated at the level of the coronoid process. The top of the coronoid process is 18 mm lower than the highest point of the mandibular head.

In sp. ZIN 34201(1) the apexes of plates one to three of dp_3 emerge 3-4 mm above the level of the upper edge of the tooth alveolus (photo 9: 2). During this stage of ontogenesis dp_3 remains inside the soft tissues of the gum. The structure of the anterior plates in sp. GIN 77 is similar. In both specimens the interalveolar wall between dp_2 and dp_3 is incomplete and occupies only the lower third of the alveolus. Behind the posterior edge of dp_3 there is an incomplete wall that separates the tooth from dp_4. In specimen ZIN 34201(1) there is an oval opening in the upper surface of the mandibular body above the dp_3. The opening narrows from the anterior to the posterior edge of the tooth crown. Distal from dp_3, above the dp_4 germ, the opening becomes a fissure that still narrows towards the posterior end of the jaw. In both specimens (ZIN 34201(1) and GIN 77) the bony tissue around the fissure is very thin, with many large nutritive foramens that indicate the zone of active growth.

The lower jaw morphology at the next stage of postnatal ontogenesis (eight to twelve months) may be characterized with a number of transformations connected with linear growth. The functional teeth during this stage are dp_2 and dp_3. If the former is still functional, it is represented by the base of the posterior part of the crown. In dp_3 two posterior plates begin to wear (ZIN 28284(2), photo 9: 3; ZIN 34426, photo 9: 4; ZIN 34427, photo 9: 5; ZIN, Kostionki 14 IV P 40; PIN 2323-12, photo 10: 1). The symphyseal suture is obliterated and both halves of the lower jaw fuse. Simultaneously, the formation of the mental process begins. In connection with the formation of the massive dp_4 and M_1, the mandibular body becomes more robust. In the specimens ZIN 34426 and PIN 2323-12, the height-to-width ratio of the mandibular body 1.09 and 1.03 respectively and signals an increase in the robustness of the jaw (table 3). In specimen PIN 2323-12, the dimensions of the alveolus are 46 x 32 mm; the depth of the posterior root pit is 39 mm.

In comparison with the preceding ontogenetic stage, the proportions of the symphyseal part and the mandibular body change insignificantly. In specimen PIN 2323-12 the length of the symphyseal part, from the tip of the mental process to the anterior edge of the dp_2 alveolus is ca. 63 mm (table 3). Three mental foramina are usual at this stage. In sp. PIN 2323-12 the two posterior mental foramina are situated under the anterior edge of the dp_2 alveolus, 24 mm below the upper edge. Their dimensions are 3.5 x 3 and 3 x 2.5 mm. The anterior mental foramen goes through the interalveolar crest and opens onto the inner surface of the symphysis. The mandibular canal also opens onto the inner surface of the symphysis. It forms a separate foramen that is connected with the mental foramen.

The specimen ZIN field mark Kostionki 1, 1994, to judge by the tooth generation, is the eldest in this series: this is a lower jaw of a one-year-old calf (photo 10: 2). The functional tooth is dp_3 with all plates in wear and the anterior plate worn down completely. The horizontal ramus of the lower jaw in this specimen is relatively shallow and elongated. Its height-to-width ratio is 1.12 (table 2). The ratio of length between the symphyseal part (76.5 mm) and the mandibular body (229 mm?) is 2.9, which signals the relative shortening of the symphyseal part and the beginning of the transformation of the proportions of the lower jaw. To judge by the base of the left ascending ramus, its posterior edge was oriented upward and the mandibular angle probably was in a comparatively elevated position. The individual peculiarity of sp. ZIN Kostionki 1, 1994, is the presence of only one mental foramen that is situated under the medial edge of the dp_3.

The morphology of the lower jaw in the interval between one and one and a half years can be characterized with the rapid formation of morphological traits of adult individuals. The functional teeth during this period are dp_3 - dp_4. Three to five posterior plates persist in dp_3. Three to five anterior plates of dp_4 are in wear. The crown of dp_4 is completely mineralized and covered with cement (posterior plates may not yet be covered with cement, as in PIN 4353-678).

The most significant transformations in symphyseal structure are the growth of its height (as well as of the mandibular body) and the completion of the formation of the mental process. The latter is practically the same as those in adult individuals. The data in tables 2 and 3 shows that sp. PIN 778-1 differs from specimens that represent even later ontogenetic stages in a more lengthy interalveolar crest (117 mm, similar to PIN 4353-678). The angle between the crest and the horizontal surface is much greater in comparison with the preceding ontogenetic stage (photo 10: 3), and approaches the angle of inclination of the interalveolar crest in sp. PIN 4353-678 (photo 11). The reconstructed length of the mandibular body from the anterior edge of the dp_3 alveolus to the posterior edge of the jaw is ca. 205 mm (in PIN 4353-678 it is 250 mm). The length of the symphysis from the anterior edge of the dp_3 alveolus to the anterior edge of the mental process is 37 mm (in PIN 4353-678 it is 93 mm). The ratio between the two lengths is 2.80. The height-to-width ratio of the mandibular body is 1.0 (in PIN 4353-678 it is 1.05). It is worth mentioning here that these ratios vary relatively little even in lower jaws of different linear sizes.

In all specimens at this ontogenetic stage the anterior edge of the ascendent ramus is almost upright and its posterior edge is less inclined distally than at the previous stage. The mandibular angle is the most posterior point of the lower jaw: in sp. PIN 4531-12 it is situated 38 mm below the posterior edge of the mandibular head, i.e., relatively far down. The neck of the mandible forms the condylar process. The mandibular incisura transforms its shape. Its maximal depth is in the area of the anterior edge; in the direction of the head of the mandible its outline gradually rises.

From the beginning of this ontogenetic stage the positions of the mental foramina practically do not change. However, many variations are observed in their relative positions and connections with the mandibular canal. It is possible that these variations are determined by the growth intensity of the lower jaw and by continuous transformations connected with tooth formation and changes of tooth generations. Indirectly indicative of this is the different number of additional nutritive foramina located around the mandibular canal that open onto the inner surface of the symphysis.

There are two mental foramina in sp. PIN 778-1. The anterior one is 35 mm below the anterior edge of the dp_3 alveolus. Its dimensions are 7 x 4.5 mm. The anterior mental foramen is situated 67 mm below the anterior edge of the dp_3 alveolus. It goes through the interalveolar crest and connects with the mandibular canal that opens onto the internal surface of the symphysis with a common depression. In sp. PIN 4353-678 the anterior and the posterior mental foramen are situated under the dp_3 alveolus and are separated from each other by twelve mm (photo 11). Their distance from the anterior edge of the alveolus is 44 mm. The dimensions of the anterior mental foramen are 5 x 4.5 mm; those of the posterior one 5.5 x 4 mm. The anterior mental foramen does not perforate the interalveolar crest, so that only the mandibular canal (2 x 1.5 mm) opens onto the internal surface of the symphysis. In sp. PIN 4531-12 there are three mental foramina in the left mandibular ramus and four in the right (photo 10, 4). In the right ramus the distal mental foramen is situated below the centre of dp_3. The two middle foramina are under the anterior edge of dp_3. The medial mental foramen is situated below the other three. It goes through the interalveolar crest and opens onto the same depression as the mandibular canal. The dimensions of the four mental foramina are: 4 x 3.5 mm, 3.5 x 2 mm, 3.5 x 2.5 mm, and 4 x 2.5 mm. The opening of the mandibular canal is oval and large (12 x 8 mm).

The next ontogenetic stage (two and a half to five years) is characterized by changes in linear dimensions without significant transformations in the lower jaw morphology. From two and a half to three and a half years, substitution of dp_4 for dp_3 occurs. The anterior six to eight plates of dp_4 may be in wear, and the dp_4 crown is completely covered with cement. This ontogenetic period is illustrated with the specimens ZIN 31836(1) (photo 12: 1) and PIN 4353-591.

The specimen ZIN 31836(1) is the only known lower jaw of a representative of the family Elephantidae with dp_2, dp_3 and dp_4 simultaneously in function. The distal part of the dp_2 crown base as well as bases of the two posterior plates of dp_3 persist. Six anterior plates of dp_4 are in wear. The retardation in change of not only dp_3, but also dp_2 is probably due to peculiar occlusion of teeth caused by individual and weak pressure exerted by subsequent tooth generations on the preceding ones. In PIN 4353-591, wear of the functional dp_4 suggests the individual was older than sp. ZIN 31836 as eight anterior plates are worn.

The mandibular ramus in sp. PIN 4353-591 is short and high. The posterior edge of the ascending ramus is inclined backward. The mandibular angle is situated 40 mm below the posterior edge of the mandibular head. Together with the distad inclination of the whole posterior edge of the ascending ramus, this determines the relatively low position of the mandibular angle, which is the posteriormost point of the lower jaw. The mandibular head is slightly inclined forward. The posterior edge of the mandibular head is at the same level as the anterior edge. The coronoid process lies approximately 30 mm below the articular surface of the mandibular head. The mandibular incisura is shallow, the distance between its lowermost point and the top of the coronoid process is about 9 mm.

The ratio between the lengths of the symphyseal part and the horizontal ramus (3.67) is indicative of a relative reduction of the symphyseal length in comparison with the preceding ontogenetic stage. The height-to-width ratio of the mandibular body is 0.9, which means that at the age of three and a half years the lower jaw becomes relatively shorter and deeper.

There are three mental foramina. The posterior one (9.5 x 5.5 mm) is situated under the medial edge of dp_4. The distance between the middle (5 x 3 mm) and the anterior (5.5 x 5 mm) ones is 10 mm. The middle mental foramen goes through the interalveolar crest and opens onto the same depression in the inner symphyseal surface as the mandibular canal.

All morphological transformations stop during the next ontogenetic stage, between three and a half and five years. After this stage, all age-related differences are determined by linear growth of the lower jaw and transformations caused by the formation and substitution of teeth of the dp_4 - M_1 generation (greater depth of the mandibular body). During this period dp_4 completely loses several anterior plates. This ontogenetic stage is represented by the specimens ZIN 31278(1), 31236(1), and PIN 4531-14 (photo 12: 2). In sp. PIN 4531-14 the distal part of the dp_3 crown persists.

The lower jaw finally acquires the proportions typical of adult individuals. The angle between the interalveolar crest and the horizontal plane increases, the crest becomes more upright. The length of the crest increases together with the increasing depth of the horizontal ramus. In sp. ZIN 31278(1) the length of the interalveolar crest is 145 mm, in PIN 4531-14 it is 120 mm. The height-to-width ratio of the mandibular body is less than 1. The ratio between the length of the symphyseal part and the horizontal ramus is 3.75 - 3.95.

The deciduous (di) and permanent (I) tusks of *M. primigenius* during early stages of formation

The morphology of the deciduous tusks (di) of the calves of *M. primigenius* is regular and typical of non-specialised incisors as found in other mammals (fig. 11). Deciduous tusks have a well-developed root with a root cavity. The root surface is covered with cement that tightens the attachment of the tooth to the alveolus. The tusk head is homologous with the tooth crown of other mammals, and has a regular dental neck. The root is curved to follow the alveolus, so that its medial surface is convex, and its lateral surface concave. Both root and head are oval in cross section. According to the position of the tusk in the alveolus, the longer diameter appears to be vertical and the shorter horizontal (fig. 11a; photo 13: 1, 5; photo 14: 1-4). Until three to four months after birth, the root canal remains open, and later fuses (fig. 11c; photo 13: 5). The root cavity volumes reduce simultaneously at the expense of the dentine filling. The replacement of the di by the I is followed by resorption of the major part of the root (fig. 11d; photo 13: 6). The formation of deciduous tusks and their substitution takes place during the first postnatal year (table 4). In the mammoth a deciduous tusk has no functional load and is a completely rudimentary element of the dentition.

The homology of the head of the deciduous tusk with the tooth crown in other mammals is illustrated by its enamel structure. Enamel covers the entire head of the deciduous tusk and the basis of the tusk root. During the first stages of its formation, cement is formed on the surface of the deciduous tusk. To judge by its location, the homogeneous cement layer is present on the head and on the basis of the tusk root (fig. 11 a-c; photo 13: 1, 2). During the first three months after birth, the first generation tusk head erupted from under the soft tissues while progressively loosing its cement cover (Vereshchagin & Tikhonov, 1990). The cement was preserved longer on the tusk root base.

Changes in morphology connected with the stages of tooth formation take place gradually. Some of them are illustrated by table 4. The cement covering the head of the tusk is lost within one month after birth. Some lumps of cement persist on different parts of the head, mainly near the basis (table 4, ZIN 31661). Wear of tusk head enamel is observed after the first month following birth. Loss of cement is most probably accounted for by mechanical load on the tusk tip, but also by its resorption when the tusk changes its position in the alveolus.

At the age of six to eight months the root canal fuses and resorption of the root end begins. This process is preceded by the reduction of the dimensions of the root and pulp cavities of the tusk head. Sometimes the fusion of a root canal occurs at earlier stages when the cement on the tusk head is still preserved (PIN 4353-3240) (fig. 11c). Immediately before replacement no less than 50% of the tusk root are resorbed, and an even greater part of the enamel on the head may be absent. The root cavity is either completely fused, or reduced drastically. In *M. primigenius*, the eruption of the tusks of the first generation from the soft tissues may occur at the age of one month, and their replacement at twelve months.

There was only one deciduous tusk of *A. meridionalis* (ZIN N 25094(1)) at the author's disposal (Vereshchagin, 1957). Its length is 75 mm. It is considerably greater than the first generation tusks of *M. primigenius*, which are not longer than 53 mm (table 1). The length of the di head in *A. meridionalis* is 20 mm; its cross section diameters are 18 x 8 mm. There is no cement on the head, whereas it is present on the root basis, where it causes a considerable thickening of this part of the tusk. The cross section of the head is almost triangular, not oval as in *M. primigenius*. The enamel crests that

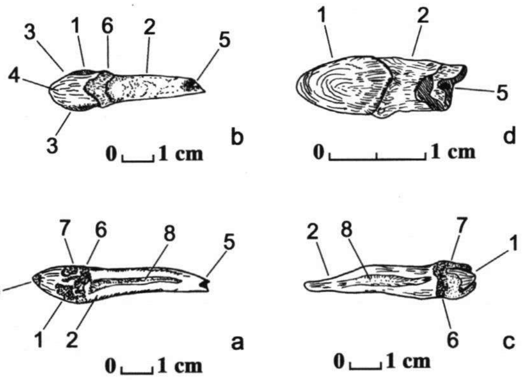

Fig. 11. Deciduous tusks (di) of *M. primigenius* calves: a = ZIN 31372-1, Kostionki 1, Voronezh Region, 2-4 month of age, medial surface; b = ZIN 32572(3), Kostionki 21, Voronezh Region, 6-9 month of age, lateral surface; c = ZIN 32572(6), Kostionki 21, Voronezh Region, 11-12 month of age, lateral surface; d = PIN 4353-3240, Sevsk, Bryansk Region, ca. 6-9 months of age, medial surface. Scale bar: 1 cm. 1 = tusk head; 2 = root; 3 = enamel thickenings on the edges shaping crests on the tusk head; 4 = longitudinal enamel folds on the tusk neck; 7 = cement on the head enamel; 8 = longitudinal depression on medial surface of the root; 9 = damaged enamel on the head tip.

Melkslagtanden (di) van *M. primigenius* kalveren: a = ZIN 31372-1, Kostionki 1, district Voronezh, leeftijd 2-4 maanden, binnenzijde; b = ZIN 32572(3), Kostionki 21, district Voronezh, leeftijd 6-9 maanden, buitenzijde; c = ZIN 32572(6), Kostionki 21, district Voronezh, leeftijd 11-12 maanden, buitenzijde; d = PIN 4353-3240, Sevsk, district Bryansk, leeftijd ca. 6-9 maanden, binnenzijde. Maatstreep 1 cm. 1 = slagtandtop; 2 = wortel; 3 = glazuurverdikkingen op de randen in de vorm van richels op slagtandtop; 4 = overlangse glazuurplooien op slagtandnek; 5 = breukvlak; 6 = overgang wortel-nek; 7 = cement op het glazuur aan de top; 8 = overlangse groeve aan binnenzijde van de wortel; 9 = beschadigd glazuur op slagtandtop.

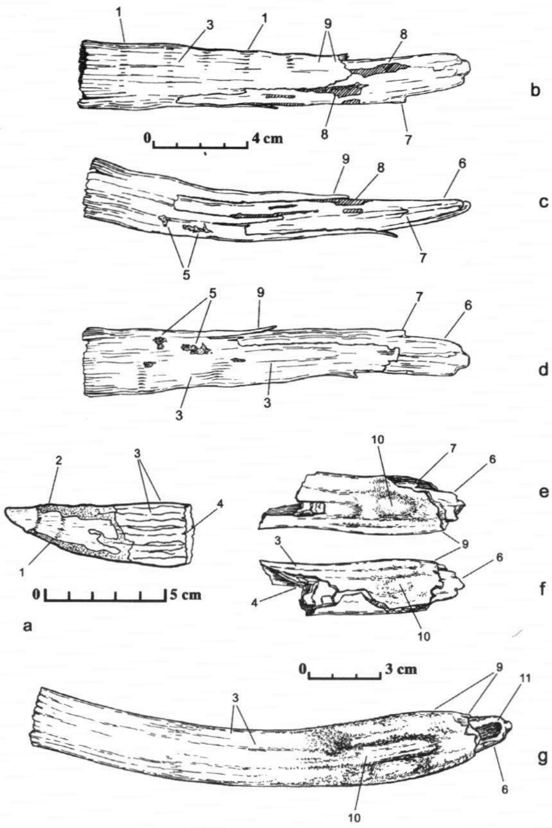

Fig. 12. Permanent tusks (I) of calves of *M. primigenius* (b, c, d, e, f, g) and *E. maximus*: a = DSM 421-1, ca. 2-year-old, lateral view; b = PIN 4531-24, Yakutia, 1.5-year-old, lateral view; c = same, ventral view; d = same, medial view; e = PIN 4353-1008, Sevsk locality, Bryansk region, 2- to 2.5 year-old, medial view; f = same, lateral view; g = PIN 4531-25, Yakutia, 2.5-year-old, medial view. Scale bar 5 cm. 1 = ring-shaped uneven and thickened relief; 2 = cement layer on tusk end; 3 = longitudinal trough relief; 4 = pulp cavity; 5 = spongy bone tissue of the inner layer of alveolus preserved on the tusk surface; 6 = flattened tusk end; 7 = additional dentine process on the lower surface of the tusk; 8 = cement; 9 = superficial layer of the alveolar part of the tusk; 10 = longitudinal depressions on lateral surfaces of the tusk; 11 = layer of enamel-like substance.

Fig. 12. Blijvende slagtanden (I) van kalveren van *M. primigenius* (b, c, d, e, f, g) en *E. maximus* (a): a = DSM 421-1, leeftijd ca. 2 jaar, buitenzijde; b = PIN 4531-24, Yakutië, leeftijd 1,5 jaar, buitenzijde; c = idem, onderaanzicht; d = idem, binnenzijde; e = PIN 4353-1008, vindplaats Sevsk, district Bryansk, leeftijd 2-2,5 jaar, binnenzijde; f = idem, buitenzijde; g = PIN 4531-25, Yakutië, leeftijd 2,5 jaar, binnenzijde. Maatstreep 5 cm. 1 = ringvormige oneffen en verdikt relief; 2 = cementlaag op het uiteinde; 3 = overlangs gegroefd relief; 4 = pulpholte; 5 = sponzig beenweefsel van de binnenste laag van de tandkas, achtergebleven op tandoppervlak; 6 = afgeplat tanduiteinde; 7 = extra tandbeenvorming aan onderzijde; 8 = cement; 9 = oppervlakkige laag van het tandgedeelte binnen de tandkas; 10 = overlangse groeves op zijkant van de tand; 11 = laag glazuurachtige substantie.

form the sides of the triangle are well developed. The horizontal and vertical diameters of the head differ by more than a factor two, whereas in *M. primigenius* this factor is no greater than one fourth (table 1). One surface of the head is concave, the two others are convex, which makes the head look spade-like. The enamel has a relief in the shape of longitudinal folds. Regardless of the lack of cement on surface of the head, the presence of relief on the enamel testifies to a rather early stage of tusk formation. The root is slightly curved. Its medial and lateral surfaces are smooth, without such longitudinal grooves and depressions as occur on the root of the di in *M. primigenius*. The root is curved in the vertical plane only. The root canal is open. The opening of the canal is 4 x 3 mm. The root is oval in cross section. The greatest diameters are 14 x 12 mm. The widest part of the root is at its base, immediately behind the head.

The presence of a big root canal testifies to the incomplete formation of the tusk. The head of the specimen ZIN 25097(1) has no cement and, by analogy with the di of *M. primigenius*, allows the supposition that it does not necessarily represent an early stage of formation. The proportions of the head and the root in *M. primigenius* and *A. meridionalis* differ: in *M. primigenius* the length of the head ranges from 18.5 to 24.6% of the total length, and in specimen ZIN 25097(1) up to 27%. The ratio between the longest transverse diameter of the root and that of the crown in *M. primigenius* is 1.05-1.25, and 1.28 in *A. meridionalis* .

A. meridionalis and *M. primigenius* differ in the structure of the crown basis. In *A. meridionalis* it is thickened, without a developed neck, which is usually present in first generation tusks of *M. primigenius*. The cross section of the first generation tusk head in *A. meridionalis* is triangular, with one concave and two convex surfaces. In *A. meridionalis* , the formation of the di most probably went through similar stages as in *M. primigenius*. The greater dimensions of the di and the different proportions of the tusk head and root in *A. meridionalis* may indicate that *A. meridionalis* calves were larger in comparison with those of *M. primigenius* of similar age.

Some peculiar features of the formation of tusks of the second generation (I) in *M. primigenius* have been understudied until now. The material studied is a series of specimens that represent various stages in the formation of permanent tusks, from the replacement of the di by the I to the eruption of the I from its alveolus.

The specimen PIN 4353-933 is the right permanent tusk from the skull of a mammoth calf of approximately one year of age (photo 6: 2, 3; table 5). The tusk has a dentine cone. Its lateral surface is slightly convex, medially it is slightly concave. The cross section is oval. Its position within the alveolus is such that the greater diameter is vertical, and the smaller horizontal in relation to the alveolar cross section. The tusk end is oval and gradually forms a cone. It is covered with a discontinuous cement layer. On the tip of the tusk the cement layer is thicker (1.5 mm) than on the lateral surfaces (0.5 mm). The cement layer becomes thinner from the tip towards the tusk base and covers the entire tusk end (ca. 48 mm; the total length of the tusk is 64 mm).

The pulp cavity is oval in cross section. Its depth is about 43 mm (ca. 67% of the tusk length). The greatest diameter of the tusk is at the basal level. The greatest diameter of the pulp cavity is 16 x 11 mm. The thickness of the walls of the pulp cavity increases evenly from the base to the end. At 21 mm from the tusk end the lower surface of the tusk bears a protrusion in the shape of a dentine denticle.

The end of the tusk lies 35 mm away from the lower frontal edge of the maxillary. In the left alveolus of the same skull the end of the permanent tusk makes contact with the internal surface of the end of the di root. The depth of the alveolus is about 100 mm, the length of the premaxillary (from the frontal edge to the lower edge of the nasal cavity) is 151 mm. The tusk length is 64 mm. Approximately 50% of the total length of the premaxillary is covered by the cavernous tissue of the rear wall of the tusk alveolus.

A comparison with modern elephants was made using the I of a one-year-old male calf of *E. maximus*, from the skull of specimen DSM 421-1 (fig. 12a). Many similarities in the I structure of the Indian elephant and the mammoth may be observed. The tusk is oval in cross-section. Its diameters are 21 and 25 mm (table 5). The end of the tusk is cone-shaped, and oval in cross section. The depth of the pulp cavity is ca. 61 mm, which makes 83.5% of the total length of the tusk.

Specimen PIN 4531-24 is a right tusk of a mammoth calf (fig. 12b-d). The tooth generation is dp^3 (the last four plates remain). The first three plates of dp^4 are slightly worn. The tip of the tusk projects 10 to 11 mm beyond its alveolus. The larger part of the tusk (ca. 150 mm of its total length) is inside the alveolus. The length of the the premaxillar bone from the lower edge of the nasal cavity to the anterior edge of the alveolus is about 185 mm. The length of the alveolus is ca. 150 mm.

The basis of the tusk (the posterior third of its length) is covered with a discontinuous layer of cavernous bone tissue tightly connected with the tusk surface (fig. 12:b-d). Approximately two thirds of the surface of the tusk, also within the alveolus, are are not covered. The cross section is ellipsoid. The tusk length from end to base, measured along a chord, is 160 mm. Along the convex surface it is 170 mm. One fourth of the tusk end is considerably flattened (the diameters of this part are 14 and 7 mm respectively). The end of the tusk is spear-shaped, consists of three segments, and bears traces of wear (fig. 12c, d). The central segment of the tusk end is longer than the lateral ones.

In the specimens PIN 4353-320 and PIN 4353-1213, which represent older individuals, the ends of the tusks are oval and not subdivided into three segments (photo 14: 5-6). The ends of the tusks project from under the surface layer, which forms a sort of cover. At later stages of individual development the tusk end remains oval in cross section and cone-shaped, and it does not project from under the 'cover' of the surface layer, which is totally reduced. At this stage, the tusk is formed exclusively of dentine.

The lower surface of specimen PIN 4531-24, like PIN 4353-933, has an additional dentine protrusion that is fused with it along the longitudinal axis of the tusk (fig. 12b-d: 7). The distance between the end of the tusk and the protrusion is 27 mm. The length of the protrusion is about 30 mm. The end of the tusk is not covered with cement, but cement is present on the end of the lateral and medial surfaces inside the alveolus. Cement and cavernous tissue of the alveolar surface of the tusk combine to fix the tusk in the alveolus. Differences in the structure of the combination as observed in different individuals indicate that these tissues dissolve to form new structures from the moment the eruption starts and while the tusk is moving out of the alveolus.

The maximal diameter of specimen PIN 4531-24 is found at the tusk base. The opening of the pulp cavity is oval, its size is 30 x 24 mm. The depth of the pulp cavity is about 94 mm, which makes 58.7% of the tusk length. Compared with the preceding stage, the pulp cavity is relatively short, while the dimensions of the tusk are greater. In adults, and especially old individuals of *M. primigenius*, the depth of the pulp cavity is even smaller. In large individuals, with tusks about 3.5 m long (along the greater curve), the cavity may be 35-40 cm, which makes 10% of the total length (Maschenko *et al.*, in press). Haynes (1992) reports similar changes in the depth of pulp cavities in tusks of *L. africana*.

The specimens PIN 4353-1000 and -1008 are damaged, but the end parts preserved show the same structure as in specimen PIN 4531-24 (fig. 12e, f). It is probable that the specimens PIN 4353-1000 and -1008 belong to one individual of the same age as specimen PIN 4531-24 (over two years) (fig. 11g). The medial and lateral surfaces have a relief formed by longitudinal depressions. The depressions are greater on the medial than on the lateral side.

The tusk end is flattened and has a three-segmented structure (fig. 12g: 6). As in the specimen PIN 4531-24, the central segment is longer than the lateral ones. At the medial and lateral surface of the lower segment of PIN 4353-1000, an area covered with enamel is preserved. Enamel is also present on the lateral and medial surface of the three-segmented dentine end of the tusk. The lower surface of sp. PIN 4353-1000 has an additional dentine protrusion (fig. 12e: 7). It is 8 mm long and aligned with the longitudinal axis of the tusk, with its end 19 mm away from the end of the tusk.

The individual ages of the specimens PIN 4531-25 and 4531-26 are most probably similar and over 2.5 years. The diameter of the tusk and the considerable wear at the ends (fig. 12g) are indicative of this. The greatest diameter at the front equals one fourth of the length (table 5). Thickening in the anterior part of the tusk is due to the outgrowth of the surface layer of the tusk. It spreads inside the alveolus along its edge, so its functional purpose is fastening the tusk inside the alveolus. The diameter of the pulp cavity of sp. PIN 4531-25 is 24

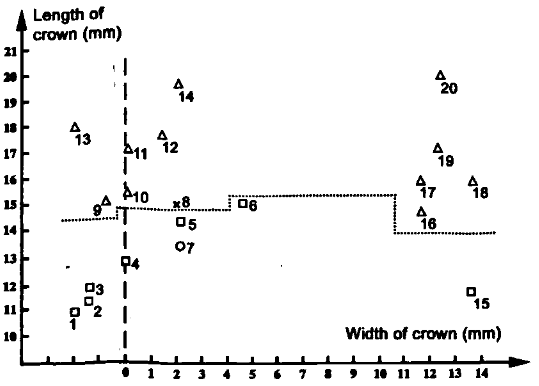

Fig. 13. Dimensions of dp2 in calves of *M. primigenius*. Vertical scale: crown length (mm); horizontal scale: individual age (weeks). Horizontal hatched line divides dimensional areas of upper and lower dp2; Δ = dp^2; □ = dp_2; + = dp^2, Sevsk locality, Bryansk region; O = dp_2, Sevsk locality, Bryansk region. 1 = ZIN 34421; 2 = ZIN 28392-4; 3 = ZIN 34419-25; 4 = ZIN 29843; 5 = ZIN 34419-31; 6 = ZIN 29842; 7 = PIN 4353-2615; 8 = 4353-2614; 9 = ZIN 31517-1; 10 = ZIN 34419-29; 11 = ZIN 28392-1; 12 = ZIN 32572-9; 13 = ZIN 34416; 14 = ZIN 31836-1; 15 = ZIN 31517-1; 16 = ZIN 31541-13; 17 = ZIN 29070; 18 = ZIN 29841-255; 19 = ZIN 32572-7; 20 = ZIN 30932

Afmetingen van boven- en onderkaaks-dp2 *M. primigenius* kalveren. Verticaal: kroonlengte (in mm); horizontaal: individuele leeftijd (in weken). Horizontale stippellijn scheidt boven- en onderkiezen; Δ = dp^2; □ = dp_2; + = dp^2, vindplaats Sevsk; O = dp_2, vindplaats Sevsk. Voor de nummers, zie Engelstalig onderschrift

× 25 mm. The depth of the pulp cavity is about 73 mm, which makes about 34% of the tusk length. So the pulp cavity depth is reduced after the previous formation stage.

To sum up the morphological transformations observed in the specimens studied, one can conclude that they are due to stages of formation and growth of the tusk and to the change of its position in the alveolus. The morphology of the second generation tusks differs greatly from that of non-specialised incisors of other mammals. No root, crown or neck is formed. The growth of the tusk is accompanied with a continuously open pulp cavity. It has not been observed before that the end of the tusk's primordial bud has a three-segmented structure which is lost later, after the tusk has erupted and was started to wear. It is the presence of enamel on the tusk end only that allows one to speak about homology of the tusk end and the crown of the other mammals' incisors. Various layers observed on the tusk in the process of formation and eruption are connected with changes of its position in the alveolus. These superficial layers fix the tusk inside the alveolus, which makes them functionally equivalent to the dentine and ligaments on the neck and root base of non-specialised incisors of other mammals. While the tusk moves out of the alveolus, the fixation area moves from the end of the tusk to its base and the superficial layers on its end lose their function, though they remain preserved until the age of six to seven years. The three-segmented end and the additional dentine protrusion on the lower surface of the tusk in the process of formation are probably indicative of the presence of several different centres of mineralization. First generation tusks do not exhibit such centres, not even at very early stages of the tooth plate primordium, which was demonstrated on a foetus of modern *L. africana* (Lucert, 1996).

The data of this study allows the establishment of approximate time intervals for several formative stages of second generation tusks in mammoth calves. Mineralization of odontoblasts around the primordial cusp does not begin earlier than at the age of four to six months. Between the sixth and the twelfth month, the first as well as the second tusk generation are simultaneously present in the alveolus. Complete eruption of the permanent tusk does not occur earlier than at the age of twelve months, but most probably between one and two years. Before eruption the end of the tusk is covered by a cement layer. By the age of two years the cement is covered by a superficial layer that most probably consists of mineralized ligaments that fasten the tusk to the alveolus.

At the age of one and a half to two years the tusk end structure preserves traces of three longitudinal dentine denticles. Besides these, the lower surface of the tusk has an additional dentine segment which is fused with the tusk surface. By four to six years the tusk end loses its flattened shape and three-segmented structure in the course of wear, its cross section becomes oval and the end of the tusk acquires the shape of a cone. Simultaneously, the superficial layer on the tusk end is lost and tusk morphology by this time does not differ from that of adult individuals. During the most intensive formative period (one to two years) the pulp cavity length makes up no less than 70% of the total length of the tusk. By two and a half to three years it is no more than 35-40%.

In *M. primigenius* the root of the di during the final stages of its existence has immediate contact with the end of the second generation tusk. Within the alveolus, the latter is situated on the medial side of the di.

The first generation tooth (dp2)

In *M. primigenius*, dp^2 usually consists of five plates (dp_2 of four to five plates) and is longer and wider than the dp_2 (tables 6, 7; fig. 13). Before their formation is completed, the plates are composed of vertical enamel columns. These fuse from base to top in the process of plate formation (fig. 14a, d, e; photo 15: 1-3). The number of the columns in a dp^2 plate is usually greater than in a dp_2 plate. The mineralization of the plate columns in dp^2 of the mammoth foetus ZIN 34416 is incomplete, and the crown base is not formed completely (photo 1). The columns are separated from base to top and form an irregular group, not lined up along the transverse axis of the crown. First the bases of the columns of one row fuse, and later, when the plates are almost formed, the bases of the plates fuse and the bases of crown and roots are formed (ZIN 31661).

In the process of crown formation the number of enamel columns in the plate becomes greater and their transverse diameter diminishes (ZIN 28392(1), 34419(29) (fig. 14; photo 15: 1-3). The height of the plates in the process of formation varies insignificantly. The plates become transversely orientated with respect to the longitudinal axis of the crown. A tripartite division (one medial and two lateral parts) - as it is found in the completely formed plates of later tooth generations (Garutt & Foronova, 1976) - is not observed once the plates have been formed. The enamel thickness of the first generation teeth varies between 0.5 and 0.8 mm (table 7).

All crown plates are formed simultaneously, accompanied by cement formation. Cement is formed on the base of the crown and fills in the interplate gaps. Cement formation begins simultaneously at the crown surface and the root bases. Crown wear begins before the cement formation is completed (PIN 4353-2614, ZIN 30932) (fig. 14a, b; photo 15: 4, 5). There are no significant differences in the formation between upper and lower dp2, however, the speed of formation is higher in dp^2 than in dp_2.

The teeth in the upper jaw have two or three roots, those in the lower jaw two or one. Before the crown formation is completed, the root canal remains open. Later it closes and the root cavity is greatly reduced. Before tooth substitution takes place, the roots are resorbed and their length is reduced by 50-60% (fig. 14c; photo 15: 6-7).

The dp^2 material studied allows a reconstruction of the process of formation of the crown, from the last prenatal stage to eleven and twelve months of postnatal ontogenesis. The specimens ZIN 34416, ZIN 28392(1) (photo 15: 1); ZIN 34419(29) (photo 15: 2, 3), and ZIN 31661 represent the final stage of prenatal development. At this stage dp^2 have not been formed completely, have not erupted, have no roots, and lack cement. The crown bases are much wider than the crown top. The tooth ZIN 34416 is the least formed. Its plates are narrow in comparison with the crown base. They are composed of vertical columns of enamel fused only at the bases. The columns are densely packed. A plate comprises five to six columns only, not seven to ten as in dp^2 of later ontogenetic stages. Eales (1926) indicates that a foetus of *L. africana* of the beginning of the second year of gestation has more dispersed enamel segments and that the number of segments in a plate may be three to four.

The specimens ZIN 28392(1), 34419(29), and 31661 evidently represent later ontogenetic stages, viz. a foetus in the end of the prenatal period or a newborn calf. The crown comprises five plates and is not in wear. The medial end is wider than the distal end. The base of the anterior plate is situated higher than the bases of the other plates. The enamel segments are transversely aligned with respect to the longitudinal axis of the crown. Each plate consists of four to five segments. The segments are fused completely, only their tops are slightly separated. The plates are rather tightly grouped and the crowns look much more condensed than in ZIN 34416. The specimens ZIN 28392(1) and 34419(29) have three root bases with spacious root cavities and thin walls.

During this postnatal period plate formation finishes, and cement formation begins. Crown wear begins approximately at one month (cement formation is still in progress). The dp^2 crowns are usually larger than during the preceding prenatal stage. In particular the height of the crown is greater (tables 6 and 7). The specimens ZIN 32572(9) and PIN 4353-2614 represent dp^2 of newborn calves, the latter from a calf skull from Sevsk (photo 15: 4). At this stage dp^2 emerges from the soft tissues of the gum, but is not yet in wear. Cement begins to form between the plate bases. The three

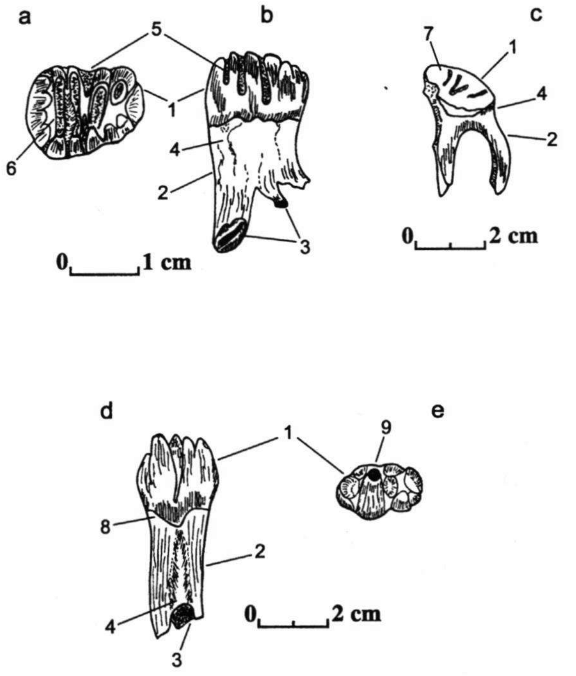

Fig. 14. Structure of dp2 of *M. primigenius* calves: a = ZIN 32572-8, Kostionki 21, Voronezh region, dp^2, 1-2 months of age, upper view; b = same, side view; c = ZIN 34420-2, Kostionki 19, Voronezh region, dp_2, 10-16 months of age, side view; d = ZIN 34421, Kostionki 19, Voronezh region, dp_2, newborn, side view; e = same, bottom view. 1 = crown; 2 = root; 3 = root canal opening; 4 = cement on root base; 5 = cement between plates; 6 = worn plate; 7 = worn crown with bases of three posterior plates; 8 = root base; 9 = enamel column affected by resorption. Scale bar 1 cm (a, b) and 2 cm (c, d, e).

Structuur van een eerste generatie kies (dp2) van *M. primigenius* kalveren: a = ZIN 32572-8, Kostionki 21, district Voronezh, dp^2, leeftijd 1-2 maanden, bovenaanzicht; b = idem, zijaanzicht; c = ZIN 34420-2, Kostionki 19, district Voronezh, dp_2, leeftijd 10-16 maanden, zijaanzicht; d = ZIN 34421, Kostionki 19, district Voronezh, dp_2, pasgeboren, zijaanzicht; e = idem, onderaanzicht. 1 = kroon; 2 = wortel; 3 = wortelkanaalopening; 4 = cement op wortelbasis; 5 = cement tussen de platen; 6 = afgesleten plaat; 7 = afgesleten kroon met bases van drie achterste platen; 8 = wortelbasis; 9 = door resorptie aangetaste glazuurkolom. Maatstreep 1 cm (a, b) en 2 cm (c, d, e).

widest plates in the middle have eleven cusps each, the narrow anterior and posterior plates have seven cusps.

The specimens ZIN 32572(8) and 29841(255) (fig. 14a, b) represent dp^2 with two anterior plates in wear (approximately two months). All plates are transversely situated with respect to the longitudinal axis of the crown. Cement fills in the interplate gaps but does not spread on the masticatory surface. In sp. ZIN 32572(8) the fragment of the root base has a small root cavity, which suggests that the root canals were open (fig. 14b: 3). Crown and root base are covered with a thin layer of cement. To judge by the distribution of cement it is first formed on the crown base and then fills in the interplate gaps.

By approximately the middle of the first postnatal year all dp^2 plates are in wear and the crown is completely covered with cement. This ontogenetic period is illustrated by the specimens ZIN 30932 (photo 15: 5) and ZIN 32572(7), whose individual ages are four to eight months. In the dp^3 of sp. ZIN 30932 two anterior plates are in wear. Patches of cement are preserved on the roots. The root canals, however, are less open than at the previous stage. To judge by an X-ray photo of a mammoth calf from the Magadan region (ZIN C 70188), and by the wear stage of the dp2, its individual age is seven to eight months.

At the end of the first postnatal year resorption of roots takes place (sp. ZIN 31541(13); photo 15: 7). The dp^2 crown loses its parts in the process of substitution. The posterior part of the crown and the posterior root remain functional longer (ZIN 29070; 31541(13); photo 15: 7; ZIN 31771; photo 5: 1). By that time the distal part of the crown is obliterated (PIN 4353-933; photo 6: 2).

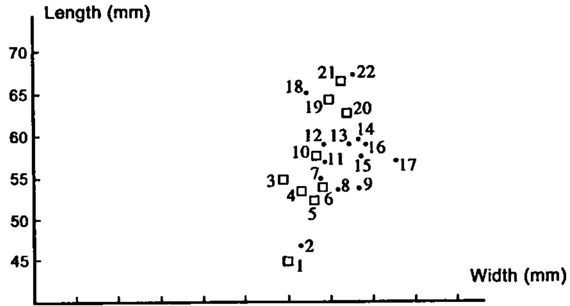

Fig. 15. Dimensions of dp^3 and dp_3 of *M. primigenius* calves from Central Russia and the Urals. Vertical scale: crown length (mm); horizontal scale: crown width; •- dp^3; □ - dp_3. 1. ZIN field mark: Kostionki 1, 1994; 2. ZIN 25550-1; 3. ZIN 25860-1; 4. ZIN 28284-1; 5. ZIN 30924; 6. ZIN 29875; 7. PIN 4353-933; 8. ZIN 30934; 9. ZIN 30928; 10. ZIN 30927-1; 11. ZIN 29070; 12. ZIN 31540-21; 13. ZIN 30932-1; 14. ZIN 30925; 15. ZIN 30926-1; 16. ZIN 29880; 17. ZIN 31773; 18. ZIN 31771-1; 19. ZIN field mark: Bliznetsov Cave 1968 D/1, 2; 20. ZIN 34419-27; 21. ZIN field mark: Bliznetsov Cave 1968 D/1.

Afmetingen van dp^3 en dp_3 van *M. primigenius* kalveren uit Centraal Rusland en de Oeral. Verticaal: kroonlengte (in mm); horizontaal: kroonbreedte (in mm). • = dp^3; □ = dp_3. Voor de nummers, zie Engelstalig onderschrift.

Peculiarities of the dp2 crown and root formation near the end of the prenatal period and during the first postnatal year include the final bifurcation of the root (fig. 14d). In comparison with those of dp^2, the dp_2 plates consist of a smaller number of enamel columns. In the process of plate formation, one to two additional columns emerge. It is possible that the eruption of dp_2 takes place somewhat later than that of dp^2, inasmuch as dp^2 and dp_2 of the skull and lower jaw of the Sevsk mammoth calf PIN 4353-2615 slightly differ in the degree of formation. The data on dp_2 are given in tables 6 and 7 and illustrated by fig. 13. As in dp^2, the dimensions of the dp_2 crown do not depend directly on individual age. In comparison with dp^2, the dp_2 crown is relatively shorter: the length of dp_2 is not greater than (sometimes equal to) the length of dp^2 (fig. 13).

In the end of the prenatal and at an early postnatal stage (newborn calves), the segments that compose the dp_2 plates are grouped more closely than those in dp^2 at the same stage of individual development (ZIN 28392(4); ZIN 29843; ZIN 34421, photo 16: 1-2; ZIN 34419(3); photo 16: 3-4). In sp. ZIN 34421 (fig. 14d, e) the top of the largest segment is destroyed by resorption. To judge by the preserved part of the root, the root cavity was rather spacious and the root walls were thin, ca. 1 mm (fig. 14d: 3). In the specimens ZIN 28392(4) and 29843 the crowns evidently had emerged into the soft tissues of the gum. Both dp_2 have two roots. The anterior root is curved forward (fig. 9; photo 8: 1-2). Its length is about 14 mm (ZIN 28392(4)). The root canal is closed. The beginning of the cement formation on dp_2 coincides with the beginning of the postnatal stage (PIN 4353-933; photo 6: 2).

The substitution of dp_3 for dp_2 in mammoths is completed by the tenth to fourteenth month, somewhat later than the dp^3 for dp^2 substitution. Specimen ZIN 31836(1) illustrates that the subsitution of dp3 for dp2 could have been retarded (photo 12: 1). The base of the distal part of the dp^2 crown persists in this specimen. The root canal is closed and, to judge by the part of the root that has emerged from the alveolus, is partly resorbed. To judge by the wear stage of dp_3 and dp_4, the individual age of the animal was two and a half years or more. However, this case of retardation is not typical of *M. primigenius*.

The second generation tooth (dp3)

The dp^3 crown usually consists of eight plates, sometimes of seven (tables 8, 9). The dp_3 consists of eight to nine plates, occasionally of seven (ZIN 25860(1), 34419(27); tables 9, 10). The dimensions of dp^3 and dp_3 crowns are given in fig. 15. This diagram suggests a lack of correlation between the crown dimensions and the position of dp3 in either upper or lower jaw. The basis of the first plate is situated considerably above

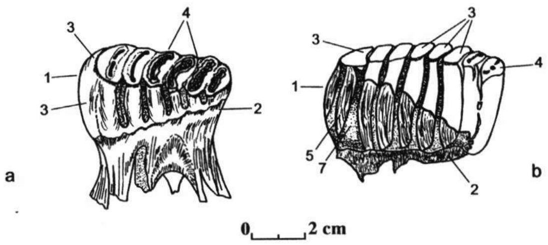

Fig. 16. Structure of dp^3 and dp_3 of *M. primigenius* calves: a = ZIN 30926-1, Kostionki 1, Voronezh region, dp^3, ca. 1-year-old, side view; b = ZIN 25860-1, Kostionki 19, Voronezh region, dp_3, ca. 4 months of age, side view. Scale bar: 2 cm. 1 = talon; 2 = cement on root base; 3 = cement on crown plates; 4 = anterior plate touched by wear; 5 = part of plate uncovered by cement; 6 = posterior plate and talon covered with cement only on top; 7 = interplate gap.

Structuur van dp^3 (a) en dp_3 (b) van *M. primigenius* kalveren: a = ZIN 30926-1, Kostionki 1, district Voronezh, leeftijd ca. 1 jaar, zijaanzicht; b = ZIN 25860-1, Kostionki 19, district Voronezh, leeftijd ca. 4 maanden, zijaanzicht. Maatstreep 2 cm. 1 = talon; 2 = cement op wortelbasis; 3 = cement op kroonplaten; 4 = voorste plaat aangetast door slijtage; 5 = niet door cement bedekt deel van de plaat; 6 = achterste plaat en talon alleen aan top bedekt door cement; 7 = ruimte tussen de platen.

the basal level of the subsequent plates. The last plate equals the first one in height. However, its basis is situated much below the level of the preceding plates (fig. 16a, b; photo 17: 1, 5). The plates consist of numerous enamel columns that fuse when the process of plate formation is completed. During the early stages the plates two to seven are subdivided into three lobes - one median and two lateral - which has been noted by other authors describing the formation process of the teeth of *M. primigenius* (Garutt & Foronova, 1976). When wear begins, the occlusal surface displays wear figures in the shape of a complete enamel loop (fig. 16a, b; photo 17: 1, 5). The enamel thickness is 0.6 - 1 mm (tables 8, 9).

From dp3 onward, tooth formation in *M. primigenius* radically differs from the formation of dp2. Plates and crown cement are formed in sequence, first in the anterior, then in the posterior part of the crown. Cement fills in the interplate gaps and covers the crown base and roots with a thin layer (fig. 16). Cement begins to develop on the top of the anteriormost plate and toward the crown basis, then the process repeats itself on the next plates. After a plate has been covered by cement from top to basis, it fills in the interplate gaps and covers the lateral surface of the crown, as may be observed in specimen ZIN 30932(1), which represents dp2 in the process of formation (photo 15: 5).

By the time all plates have completely been formed, cement covers two to five anterior plates and the crown begins to wear. Roots function in the same sequence. When the anterior is being resorbed, the posterior one is still functional.

The dp^3 always has well-developed anterior and posterior roots, with one to three smaller roots in between. The intermediate roots may form an irregular group or a row at square angles to the longitudinal axis of the crown (ZIN 30926(1)). The anterior root is situated under the base of the plates one to three. The intermediate roots are under the fourth plate (sometimes under the plates four or five). The posterior root is situated under the bases of the posteriormost three to four plates. The dp_3 always has two roots. The root canals of a completely formed tooth are filled with dentine and closed, the root cavities absent or small. The root openings close first in the anterior root, then in the posterior ones. The roots are formed following the completion of the mineralization of all crown plates. The formation coincides with the fusion of the plate bases. The dimensions of a root canal and a root cavity are the direct indication of metabolism intensity.

The material studied allows the conclusion that the dp3 eruption in *M. primigenius* occurred earlier than in modern *E. maximus*. The beginning of wear of dp3 in *M. primigenius* took place at the age of four to five months, and its substitution by dp4 most probably at two to two and a half years, in any case not later than at three years (ZIN 30925, 31771(1), 31837) (photo 7: 1).

In the dp3 of a mammoth calf from the Kirgiliakh river in Magadan region (ZIN 70188), the plates one to four are in wear (Vereshchagin, 1981). Pollen from the stratum that embedded the frozen carcass indicated that the animal died in late autumn. Mammoth calves were born in spring or early summer, so that the biological age of this individual was no greater than eight months. To judge by its rather small dimensions it was probably six to seven months old. A one-year-old mammoth calf from Sevsk (PIN 4353-211 to -217, -507, -570 to -573, -709 to -716, -810, -817, -873 to -880, -884 to -887, -894 to -899, -900 to -907, -922 to -965) does not differ much from the Kirgiliakh calf in its dimensions (Maschenko, 1992). In the mammoth calf from Sevsk, the dp^3 is functional (all plates in wear). The dp^4 of this specimen has a completely formed anterior part and is ready for eruption (photo 6: 2).

The specimens ZIN 29070 and 30932 (1) belong to four- to eight-months-old calves and show dp^3 in the course of formation in the middle of the first postnatal year. The specimen ZIN 30932(1) comprises eight plates. The two anterior plates are completely covered with cement. The third plate is covered with cement for up to three quarters of its height, the fourth one only in its upper third, the fifth in the upper quarter. Only the top of the sixth plate is covered with cement, and there is no cement on the seventh and eighth plates. After the cement has covered a plate from top to base, cement formation is continued in interplate gaps and on lateral surfaces of the crown. Two anterior plates are in wear and the proximal end of the crown is still within the alveolus. At least three root bases with thin root walls are preserved.

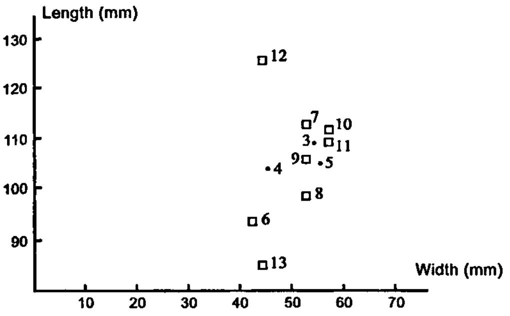

Fig. 17. Dimensions of dp^4 and dp_4 of *M. primigenius* calves from Kostionki locality, Voronezh region. Vertical scale: crown length; horizontal scale: crown width; • = dp^4; ☐ = dp_4. 1. ZIN 31252; 2. ZIN 30937; 3. 31773; 4. ZIN 31772; 5. ZIN 31837-1; 6. ZIN 31836-1; 7. ZIN 31278-1; 8. ZIN 28284-2; 9. ZIN 31250; 10. ZIN 30936; 11. ZIN 28284-2; 12. ZIN 30947.

Afmetingen van derde generatie kiezen (dp^4 en dp_4) van *M. primigenius* kalveren uit de vindplaats Kostionki, district Voronezh. Verticaal: kroonlengte; horizontaal: kroonbreedte. • = dp^4; ☐ = dp_4. Voor nummers, zie Engelstalig onderschrift.

By the end of the first postnatal year, cement formation on the crown of dp^3 stops. At this time, six anterior plates are in wear. This is illustrated by the specimens ZIN 31771(1) (photo 5) and ZIN 34321 (photo 17: 1), which represent calves aged ten to eleven months. The canals of the anterior and medial roots have become narrow. The opening of the canal of the posterior root is large, and the root walls are relatively thin. This structure reflects the gradual formation of the crown. A closed or narrowed canal is indicative of the absence of live pulp in the root cavity and of the end of the formation of the anterior part of the crown.

The beginning of the second year of postnatal development is illustrated by the dp3 series PIN 4353-933 (photo 6: 2), ZIN 30929(1) (photo 17: 2-3), and ZIN 31689, 30926(1), and 28284. These belong to calves aged eleven to fourteen months. By this time the tooth has formed completely, and all plates are in wear. The dp3 specimens differ in the degree to which their crowns are worn. ZIN 31689 and PIN 4353-933, of individuals aged eleven to twelve months, are the least worn. ZIN 30929(1) and ZIN 30926(1), of individuals aged twelve to fourteen (?) months, the most. Substitution of dp^3 for dp^2 takes place at this time. In sp. ZIN 31689 the dp_2 crown is worn to the base and almost shed; in sp. PIN 4353-933 it is already gone. In the specimens ZIN 30926(1) and 30929(1) the anterior root is still present under the first three plates, and the posterior root under three to four of the hindmost plates. One to three smaller medial roots are situated under the plates four to five. The medial roots may either form irregular groups or be aligned transversely to the longitudinal axis of the crown (fig. 16a). All root canals but that of the posterior root are closed at this stage.

The next stage is represented by the specimens ZIN 29880 (photo 17: 4), ZIN 30981(1), 30934, 31540(21), 31772(2) (photo 7: 1), ZIN 30925, 31773, and ZIN 31837 (photo 7: 2). These belong to mammoth calves aged one and a half or two years up to three years. The dp^3 crown is heavily worn, and the bases of three to six posterior plates persist. At this stage dp^4 begins to wear. The number of anterior plates in wear varies between one to two (as in ZIN 30928(1) and 30934) and five to six (as in ZIN 30925, 31773, and 31837). This wear stage immediately precedes substitution of dp^4 for dp^3. All root canals, including the posterior root, are closed, the root cavity is small, if preserved and not filled with dentine. This is direct evidence of the absence of pulp and the end of the tooth's functioning.

In modern *E. maximus*, dp^3 is functional at the age of three to five years. The crown preserves from three to five plates until the age of five years (Roth & Shoshani, 1988). In *L. africana* dp^3 erupts during the first weeks of life and is functional until the age of four to five years (Sikes, 1966). This data demonstrates that the dp3 of the mammoth erupted and was substituted earlier than in the calves of modern Indian and African elephants, but its functionality lasted about half as long as in these species.

The formation of the crown and roots of dp_3 takes place in the same sequence as in dp^3 and is illustrated by sp. ZIN 25860(1), whose individual age is four to six months (fig. 16b: 4). The dimensions of the teeth of this generation are represented in tables 9 and 10 and illustrated with a diagram (fig. 15). The crown is usually covered with cement before two posterior plates are in wear: ZIN 28284(1) (photo 17: 5); ZIN field mark: Bliznetsov Cave, 1968, E/1, 2; ZIN field mark: Bliznetsov Cave, 1968, D/1. Wear of dp_4 evidently takes place at the age of 16-20 months, when dp3 is in wear and its anterior plate is worn down: ZIN 34419(17), ZIN field mark: Kostionki 1, 1994 (photo 10: 2), ZIN 29875, 30924(1), 30927(1).

In some specimens deformation of enamel loops of two anterior plates is observed, as in ZIN 34427, whose individual age is eight to eleven months (photo 9: 4). On the whole, deformation of anterior plates is more typical of the dp4 - M3 generations and is caused by pressure of the anterior edge of the following tooth crown on the posterior end of the preceding one. This phenomenon was observed both in extinct and modern elephants (Sher & Garutt, 1995; Roth, 1989, 1992).

The substitution of dp3 for dp4 was preceded by the loss of the anterior part of the crown and a considerable resorption of the posterior roots. In specimen ZIN 31836(1), the complete lower jaw bears three tooth generations: dp_2, dp_3, and dp_4. These teeth were simultaneously functional. In dp_2 the posterior root and the basal part of the distal edge of the crown are present. The dp_3 crown is hardly worn: only the bases of three posterior plates and the posterior root remain. In dp_4, seven anterior plates are in wear. This stage very probably corresponds to an individual age of at least two and a half to three years. This specimen is an example of extremely prolonged functioning of dp_2 and dp_3.

The third generation tooth (dp4)

In *M. primigenius* there are no differences in the formation of dp4 and dp3 (the crown of dp4 is formed gradually in medio-distal direction). The morphological differences between the tooth generations dp3 and dp4, as well as between the generations dp4 and M1-M3, are expressed in terms of a greater number of plates and a longer period of crown formation for every following generation. The dp4 of *M. primigenius* consists of eleven to thirteen plates. The basis of the first plate is situated above and the basis of the posterior plate below the level of the intermediate plates. The enamel thickness ranges from 0.9 to 1.3 mm (tables 11 and 12). The dimensions of the upper and lower teeth are represented in a diagram (fig. 17).

When the individual has reached the age of two to two and a half years, wear starts in dp^4, and somewhat later in dp_4. The lower jaw specimen ZIN 30937 bears a dp_4 with eleven plates preserved, all of which are in wear. The plates 1 and 2 have been worn down completely. M_1 of the same specimen has only two plates touched by wear. In dp_4 the opening of the anterior root canal is closed. The root cavity of the posterior root is narrow and represents not more than 5% of the root volume. The rest of the root volume consists of very thick root walls. The individual age of specimen ZIN 30937 is over five years.

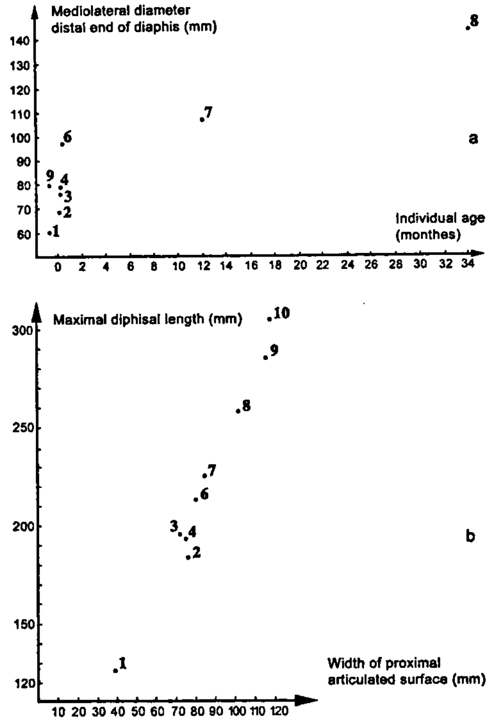

Fig. 18. Dimensions of humerus and ulna (mm) of *M. primigenius* calves: a = medio-lateral diameter of distal shaft end of the humerus depending on individual age (specimen numbers as in table 13); b = medio-lateral diameter of proximal end of ulna depending on individual age (specimen numbers as in table 14).

Maten van opperarm en ellepijp (in mm) van *M. primigenius* kalveren naar leeftijd. a = midden- zij-middellijn door onderste uiteinde van de opperarm (exemplaarnummers in tabel 13); b = midden- zij-middellijn door bovenste uiteinde van ellepijp (exemplaarnummers in tabel 14).

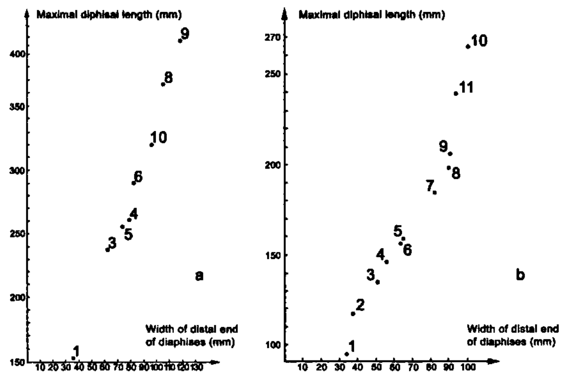

Fig. 19. Dimensions of femur and tibia (mm) of *M. primigenius* calves from Central Russia and Siberia: a = greatest length of the shaft (vertical scale) and medio-lateral diameter of distal end of the femur (horizontal scale), specimen numbers as in Table 16; b = greatest length of the shaft (vertical scale) and medio-lateral diameter of proximal end of tibia (horizontal scale), specimen numbers as in table 17.

Maten van dijbeen en scheenbeen (mm) van *M. primigenius* kalveren uit Centraal Rusland en Siberië: a = grootste lengte schacht (vertikaal) en midden-zij-middellijn van onderuiteinde van het dijbeen (horizontaal), exemplaarnummers in tabel 16; b = grootste lengte schacht (vertikaal) en midden-zij-middellijn van bovenuiteinde van het scheenbeen (horizontaal), exemplaarnummers in tabel 17.

The long limb bones

Skeletons of mammoth calves from Sevsk provided a first opportunity in the history of *M. primigenius* studies to investigate the formation and growth of long bones. Almost complete and well-preserved skeletons of a newborn calf and individuals aged one year, three to four, and six to seven years made it possible to subdivide the sample into age groups. These are based upon shaft dimensions (length and transverse diameters) and formation stages observed in shaft and epiphyseal ossification centres. This new data supports earlier observations, according to which two types of growth zones were functional in the shaft extremities during early ontogenetic stages in mammoths as well as in modern elephants. The growth zones with ossification centres surrounded by cartilage were functional until the age of six to seven years, after which the growth zones remained between completely ossified epiphyses. The formation process of shaft and epiphyses suggests the existence of multiple primordial ossification centres in both shaft and epiphyses of the long bones. The speed

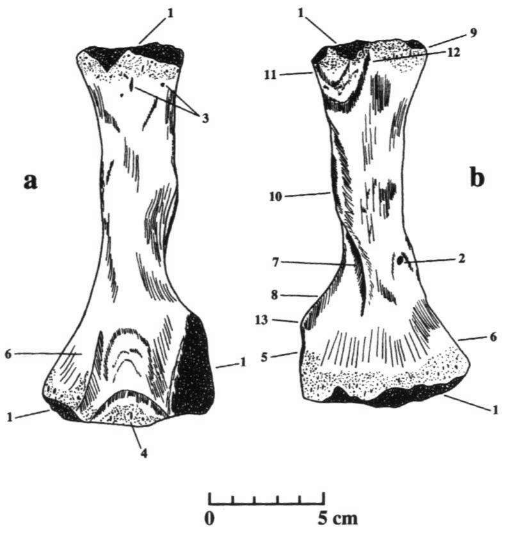

Fig. 20. Right humerus of an incomplete skeleton of a *M. primigenius* foetus during last prenatal stage (ca. 20-21 months of pregnancy), field mark IAE Sh-77 4c, Shestakovo locality, Chebula district, Kemerovo region. a = posterior surface; b = anterior surface. Scale bar: 5 cm. 1 = damaged areas of the shaft; 2 = nutritive foramen ; 3 = small nutritive foramina of the proximal shaft end; 4 = olecraneal groove; 5 = lateral epicondyle; 6 = medial epicondyle; 7 = delta-shaped crest (crista tuberculi majoris); 8 = crest of lateral epicondyle; 9 = smaller tubercle; 10 = deltoid tuberosity; 11 = greater tubercle; 12 = intertubercular groove; 13 = tuber localized in proximal part of lateral epicondyle.

Rechter opperarm van een onvolledig skelet van een *M. primigenius* foetus gedurende laatste prenatale stadium (ca. 20-21 maanden dracht), veldnummer IAE Sh-77 4c, vindplaats Shestakovo, district Chebula, regio Kemerovo. a = achterzijde; b = voorzijde. Maatstreep 5 cm. 1 = beschadigde delen van de schacht; 2 = voedingskanaal; 3 = kleine voedingskanalen in bovenuiteinde schacht; 4 = groeve voor olecranon; 5 = buitenste epicondyl; 6 = binnenste epicondyl; 7 = delta-vormige kam; 8 = kam op buitenste epicondyl; 9 = kleine tuberculum; 10 = delta-vormig ruw gebied; 11 = grote tuberculum; 12 = groeve tussen de tuberculi; 13 = knobbel op bovenste deel van buitenste epicondyl.

of ossification is higher in shafts than in epiphyses. All main transformations of the proportions of the long bones in *M. primigenius* are expressed in terms of a relative reduction of epiphyseal lengths in comparison with shaft lengths, and of a relative reduction of transverse diameters of shafts in comparison with their lengths.
The dimensions of the long bones of the legs are given in tables 13-17 and illustrated by diagrams (figs. 18 and 19).

The humerus

The dimensions of the humerus in relation to individual age are shown in a diagram (fig. 18a) and table 13. It is demonstrated there that mammoth foetuses near the end of the prenatal period are very variable, probably because of individual peculiarities and a relatively high speed of growth.

At early ontogenetic stages (until six to seven years after birth), the humerus comprises a shaft and non-fused proximal and distal epiphyses. In their turn, the epiphyses comprise two ossification centres each. In the course of ontogenesis - and simultaneously with the overall growth of shaft and epiphyses - these centres fuse with each other. The fusion of the epiphyses follows later. The head of the humerus-to-be ossifies before birth, whereas the smaller (lateral) centre does so later. The ossification centres of the proximal epiphysis are situated within the growth zone of cartilage and are separated from the proximal surface of the shaft. The distal epiphysis of the humerus also comprises two ossification centres (lateral and medial) which on average are ossified simultaneously. The centres lie within the cartilage of the distal growth zone and are primordial lateral and medial condyls. It is possible that the larger (medial) centre of the distal epiphysis is ossified before birth.

Near the end of the prenatal period and during the first postnatal years an additional nutritive opening exists besides the permanent ones at the proximal and distal extremities of the shaft as well as in its middle. The compact layer in the middle part of the shaft has already formed by the end of the prenatal ontogenesis. It is thinner at the ends of the shaft and its formation process goes on during the first postnatal year.

The specimens ZIN 32572(1) (photo 18: 2), ZIN 31744(1), 31740(1) (photo 8: 1), and ZIN 34386(2) (photo 18: 3) exemplify the prenatal period from the beginning of the second prenatal year to the age of 15-18(?) months. The shaft of the humerus shows reliefs for the insertion of the large muscles (tuberositas deltoidea, crista epicondyli lateralis) and, on the posterior surface, the crests of the lateral and medial epicondyles and the depression between them. The fossa olecrani has not yet formed. The materia compacta is very thin. It becomes noticeably thicker near the end of the prenatal ontogenesis, when the number of nutritive foramina in the growth zones at the shaft extremities becomes significantly smaller, as in the foetal specimen IAE Sh-77 4c, whose stage of development indicates the 20th or 21st month of gestation (fig. 20a: 3). The permanent nutritive foramen (4 x 2 mm) is present in all age groups (fig. 20b: 2). A large nutritive foramen (1 x 1 mm) is situated on the lateral surface, 28 mm away from the proximal edge of the shaft.

New elements appear in the surface relief of the humerus: an about 2.5 mm deep depression in the intertubercular groove (fig. 20b: 12) and in the fossa olecrani on the posterior surface of the distal end of the shaft (fig. 20a: 4). The materia compacta reaches a thickness of about 1.5 mm. Its surface relief in the middle part of the shaft shows vertical lines which are oriented along the longitudinal axis of the shaft. This kind of microrelief is absent in specimens that relate to the postnatal period.

The distal part of the shaft becomes narrower from the level of the lateral ectocondyl, and its antero-medial diameter becomes greater than the shaft width. The shaft is twisted by ca. 80° (fig. 20b). The change of proportions is accounted for by the position of the tubercle in the proximal part of the lateral epicondyl, which is closer to the end of the shaft than in the postnatal period, and the relatively higher position of the narrowest part of the shaft (the area where the lateral epicondylar crest ends), so far as this part is situated much lower in the postnatal period. Some zones of the crest of the greater tubercle have an uneven relief. The deltoid tuberosity originates from the apex of the crest of the greater tubercle and spreads onto the anterior shaft surface, whereas the crest itself extends onto the lateral surface (fig. 20b: 10). The lower edges of the lateral and medial epicondyles are situated at different levels (the former is always lower), as in the postnatal period.

At the beginning of the postnatal ontogenesis the ossification centres of the shaft are already formed, as in ZIN 31744(1), 20564(54), 34419(17) (photo 18: 4), and PIN 4353-2658, which belongs to a newborn calf skeleton from Sevsk (photo 18: 6; photo 19: 1, 5). In the distal epiphysis of specimen PIN 4353-2658, the larger (lateral) as well as the smaller (medial) centre are ossified. Their measurements are 49 x 36 and 33 x 24 mm respectively. The height at the lateral edge of the larger centre is 27 mm (photo 19: 1-3). The lateral centre is sub-rectangular, the medial one is oval. The centre surfaces that face the articular surface of the ulna are convex and possess a thin layer of materia compacta. The other surfaces lack materia compacta and show a relief that suggests the former presence of cartilaginous tissue between the surfaces. The centres are not fused with the shaft and remain embedded in the cartilage of the growth zone. In sp. ZIN C 70188, a *M. primigenius* calf from the Magadan region, the thickness of the cartilaginous layer between the epiphyseal ossification centres and the distal surface of the shaft reaches 12 mm (Vereshchagin, 1981). In a two-months-old calf of *E. maximus* (PIN 4353-264) the thickness of this layer is the same.

The distal surface of the shaft shows a relief formed in contact with the cartilage of the growth zone (PIN 4353-2658). It is eight-shaped in cross section, and is medially significantly more widened than laterally (photo 19: 1). The shortest medio-lateral diameter of the distal surface is 22 mm. The materia compacta is evenly developed over almost the entire shaft surface, and becomes noticeably thinner only along the distal end of the shaft. The cubital fossa (34 x 20 mm) is clearly outlined.

The proximal surface of the shaft has a lateral and a medial part, separated by the intertubercular sulcus. The lateral part has a big tuber in its base. The medial part is situated under the humeral head. The latter is oval (56 x 48 mm, height 33 mm) (photo 19: 5). The convex proximal surface of the head is covered with materia compacta, the less convex surface, which faces the shaft, lacks materia compacta. The relief of the entire head suggests formation in contact with the cartilage of the growth zone.

At the end of the first postnatal year the shape of the distal end of the shaft changes: the major tuber becomes greater and the lateral epicondylar crest meets the shaft at an angle of 70°, as in sp. PIN 4353-713, which belongs to a one-year-old calf skeleton from Sevsk (photo 19: 2, 6; photo 21: 1). In sp. PIN 4353-2658 this angle is about 50°. The part of the shaft with the smallest medio-lateral diameter is situated 112 mm above the distal end of humerus. In comparison with the situation at the end of the prenatal period (sp. IAE Sh-77 4c), this part has been lowered and the proximal part of the shaft has become relatively longer.

The proximal end of the shaft is robust (at the expense of the formation of the tuberculum majus) and twisted 90° with respect to the distal end. The crest of the greater tubercle is large, and the deltoid tuberosity is transformed into the relief of the greater tubercle and becomes crest-like in shape. This enlarges the transverse diameter of the proximal end of the shaft. The permanent nutritive foramen (5 x 3 mm) is situated laterally from the middle part of the crest of the greater tubercle, 84 mm above the distal end of the shaft. There are no additional nutritive foramina at the proximal end of the shaft. A large fossa for the insertion of the musculus latissimus dorsi is situated at its antero-medial surface. Materia compacta is distributed evenly over the shaft's surface, but for the ends, where it is thinner.

At the end of the first year of postnatal ontogenesis the relief of the proximal surface of the shaft remains as in PIN 4353-2658. The proximal epiphysis of the humerus includes the humeral head and the lateral centre (not preserved in sp. PIN 4353-2658) (photo 19: 6). The surface of the head that faces the lateral centre has a relief that suggests contact of these two centres mediated by the cartilage of the growth zone between them (photo 19: 6). The lateral ossification centre of the humerus of a two-months-old calf of *E. maximus* (PIN 4353-264) is represented by a tiny plate enclosed in cartilage. This suggests that during the first postnatal year this centre was small in the mammoth as well.

In sp. PIN 4353-713 the lateral centre of ossification of the distal epiphysis (58 x 45 mm, height 30 mm) is preserved (photo 19: 2). Its lateral edge is oval and the edge that faces the medial centre is even. The surface that faces the ulna is convex and covered with a thin layer of materia compacta with numerous pores. The humeral head is oval (76 x 68 mm, height 44 mm). Its surface relief suggests that it remains embedded in the cartilage of the growth zone. If viewed from above, the lateral edge of the head looks flattened and the medial edge is more convex. The distal surface of the head is flattened, the proximal surface is hemispherical.

During the period between the third to fourth and the sixth to seventh postnatal year, no qualitative transformations occur in the structure of the ossification centres of the distal and proximal epiphyses. The centres remain incorporated in the cartilage of the growth zone, but their formation continues and their dimensions increase.

In sp. PIN 4353-496, a humerus of a skeleton of a three- to four-year-old calf from Sevsk (photo 19: 3, 7; photo 20: 3), the shaft length is 320 mm and the shaft mounted together with the epiphyses is 425 mm long (table 13). The possible cartilage thickness in the growth zones taken into consideration, the total length of the bone may have amounted to 445 mm. The epiphyses comprise about 29% of the total bone length (20% in a newborn calf, as in PIN 4353-2658). The ossification centres of the distal epiphysis are separated by a small growth zone (photo 19: 3). The lateral centre is subrectangular (70 x 51 mm, height at the lateral edge 45 mm, at the medial edge 24 mm). The surface of the lateral centre that faces the distal surface of the shaft is convex, the one that faces the proximal articular surface of the ulna is semicylindrical. The medial centre is oval, with a strongly convex surface that faces the articular surface of the ulna (photo 19: 3; photo 20: 3). The relief of practically the entire surface is determined by recesses with numerous foramina for small blood vessels.

In addition to the head (99 x 84 mm, height 61 mm), the second ossification centre of the proximal epiphysis is preserved (photo 19: 7). It is oval and much smaller than the head (62 x 41 mm, height 49 mm). The surface of this centre that faces the scapula is hemispherical, the opposite surface is flattened. The distal surface of the head is convex, and the proximal surface, which faces the glenoid fossa of the scapula is hemispherical (photo 19: 7).

On the whole, the relief for the insertion of the musculature does not differ much from that observed in specimens at the previous growth stage, but it is better developed. The crests and grooves of the greater tubercle extend over the lateral face of the humerus to form the relief of the proximal end of the shaft (photo 20: 3). The cubital fossa (55 x 34 mm) on the posterior surface of the shaft is well expressed. The permanent nutritive foramen (3 x 5 mm) is situated on the posterior surface of the shaft, whereas in all other specimens it is located on the anterior surface. Neither the anterior nor the posterior surface of this specimen has any other nutritive foramina in its middle and distal parts.The compact layer is developed evenly over the entire shaft.

In sp. PIN 4353-630, a humerus of a six- to seven-year-old individual from Sevsk, the medio-lateral and antero-posterior diameters of the proximal end of the shaft are almost equal (photo 19: 4, 8; photo 20: 4). At the preceding ontogenetic stages the antero-posterior diameter was greater than the medio-lateral one. The proportions of the distal end and the shaft change: the tubercle situated on the proximal end of the lateral epicondyle is situated 148 mm above the distal end of the bone. This distance is about equal to 34% of the shaft length. At the age of three to four years it was 46%, and in one-year-olds 45%. The distal centres of ossification fuse to form a consolidated epiphysis as in adults (transverse diameter 178 mm, width of lateral edge 89 mm, of medial edge 98 mm, height 69 mm). The proximal epiphyseal centres are incompletely fused.

The proximal epiphysis consists of two non-fused centres: the humeral head and the lateral centre. The head (140 x 105 mm, height 78 mm) has a rounded medial, and a flattened lateral edge. The length of the facet that is in contact with the medial surface of the lateral centre via the cartilage is 96 mm (photo 19: 8). The proximal surface of the head is hemispherical. Its materia compacta does not differ from that on the shaft. Evidently this is indicative of a transformation of the growth zone of the head, where two areas can be discerned: one between the shaft and the epiphysis, the other between the medial surface of the head and the lateral centre. The lateral centre is oval. Its medial edge, which faces the head, is flattened out to a facet (82 x 42 mm). Unlike the head, this centre remains embedded in cartilage, of which the relief on its upper and lateral surface is indicative. At this stage, the centres are ten to fifteen mm apart. They would have fused into a consolidated proximal humeral epiphysis later. The cartilage of the growth zone taken into consideration, the length of the epiphysis equals about 24% of the total bone length, which is less than at the previous stage.

The completion of the formation of ossified but still unfused epiphyses is indicative of a substantial transformation of processes of growth and physiology, and evidently coincides with the beginning of puberty.

It is worth mentioning that the distal epiphysis of the humerus is ossified before the proximal one. This corresponds with the fusion sequence of the humeral epiphyses in modern elephants (Roth, 1984). In *M. primigenius*, the distal epiphysis is fused first followed by the proximal one. Complete fusion of epiphyses and epiphyseal sutures takes place earlier in females (at the age of 25-30 years).

The ulna

During the early ontogenetic stages, the ulna of *M. primigenius* comprises the shaft, the distal epiphysis and the epiphysis of the olecranal process. In the period that comprises the end of the prenatal stage up to and including the first year of postnatal ontogenesis, the distal epiphysis is represented by an ossification centre that is embedded in the cartilage of the growth zone. The epiphysis of the olecranal process is ossified soon after birth, but the ulnar growth zones persist for a long time. The distal epiphysis fuses completely after thirty years. The epiphysis of the olecranal process fuses most probably by the age of ten to fifteen years. This data is in good agreement with the data on the functioning of the growth zones in *L. africana* (Roth, 1984). In this species, the proximal growth zones in ulna and tibia and the distal growth zones in humerus and femur are the first to cease active functioning, a sequence which is exactly the same as in *M. primigenius.* . One more zone of growth is situated on the articular surface of the lateral and medial coronoid processes and on the greater part of the surface of the ulnar notch. No epiphyses are formed here.

Additional nutritive foramina are situated along the growth zones at the ends of the shaft, and the materia compacta is thinner here than on their middle parts, as in other long bones. Once the growth intensity has decreased, the structure of the materia compacta becomes homogeneous throughout the entire shaft. During early ontogenetic stages materia compacta of the distal end of the shaft is formed at a slower rate than in other parts of the ulna and there are several additional nutritive foramina at the distal end until the end of the first postnatal year. The only permanent nutritive foramen is situated on the anterior surface of the shaft, closer to the proximal end of the bone. The shape of the ulnar shaft changes in the course of postnatal development. Before the end of the first postnatal year the shaft is curved backwards to a lesser degree than at later stages, and the olecranal process only slightly projects beyond the contour of the ulnar shaft.The shaft is short and robust, especially during prenatal ontogenesis. Later its length becomes greater in relation to its transverse diameters.

The data on size variability of the sample studied is represented in table 14 and illustrated by a diagram (fig. 18b). These cover the period from the end of prenatal ontogenesis to a postnatal age of six to seven years, and reflect a smooth increase in shaft length as well as in the width of the proximal articular surface. It may be assumed that after the first postnatal year the increase in shaft length leaves the width increase of the proximal articular surface behind.

At the end of the prenatal ontogenesis, the olecranon is underdeveloped, as in sp. ZIN 31740(3) (photo 21: 1). The olecranal process is incompletely formed, and small nutritive foramina are situated along its proximal extreme. The shaft is relatively robust (the mediolateral diameter of the distal shaft equals ca. 22% of its length). The olecranal process slightly projects beyond the contour of the shaft. The preserved parts of the compact layer suggest it was better developed on the middle part of the shaft than on its ends. The surface of the incisura semilunaris is slightly concave, uneven, with many pores. The length and the width of the medial coronoid process are much greater than those of the lateral coronoid process. This, however, is usual for all ontogenetic stages.

At the beginning of postnatal ontogenesis, the shaft remains relatively robust and slightly curved, as in specimen PIN 4353-2659, the ulna of a complete skeleton of a newborn calf from Sevsk (photo 21: 2). The medio-lateral diameter of the distal end of the shaft equals about 30% of its length (to the level of the incisura semilunaris). The cross section of the shaft in its middle part is subtriangular, and its distal part is oval. The olecranon is relatively short, its surface together with the surface of the incisura semilunaris has a relief that was formed in contact with the cartilage of the growth zone. In sp. PIN 4353-2659 the angle between the medial coronoid process (47 x 29 mm) and the lateral coronoid process (20 x 35 mm) equals ca. 90°. The incisura semilunaris is slightly concave. The surfaces of both processes are slightly inclined forward. The depth of the facies articularis radialis is 23 mm. The materia compacta on the distal part of the shaft is thin, with many small nutritive foramina. There is a vertical longitudinal groove (width 1 mm, length 28 mm) on the anterior surface of the distal end, which is surrounded with tiny nutritive foramina. The permanent nutritive foramen (diameter 1 mm) is situated in the upper part of the groove. The lower end of the groove is 14 mm apart from the distal end of the shaft. There are two similar grooves on the medial surface of the distal end. Such structures of the materia substantia on the distal end of the ulna are connected with the growth zone complex.

In sp. PIN 4353-2659, an oval distal epiphysis (38 x 30.5 mm, height 20 mm), the surface that faces the carpal bones is convex. The epiphysis represents a centre of ossification with numerous tiny nutritive foramina for blood vessels. Other specimens that exemplify early postnatal ontogenesis are ZIN 34201, 31740(5) (photo 21: 3), ZIN 31740(4), and GIN 77 (photo 22). These specimens have more gracile shafts and represent approximately one-month-old calves (table 14). In sp. GIN 77 the cross section of the distal end is ellipsoid (the long axis of the ellipsoid is oriented antero-posteriorly), and the anterior edge of the shaft is more rounded than the posterior one. The transverse diameter of the distal end of the shaft equals 32% of its length. The olecranon is inclined backward beyond the line of the posterior shaft surface. The angle between the medial coronoid process (39 x 25 mm) and the lateral coronoid process (29 x 15 mm) exceeds 90°. A depression for the proximal end of radius extends along the upper facies articularis radialis. Other peculiarities of the morphology are similar to those in sp. PIN 4353-2659.

At the end of the first year of postnatal ontogenesis, a relief for the insertion of ligaments that support the radius appears on the anterior surface of the shaft and on the articular facet for the radius. This is exemplified by the specimens ZIN 34419(13) and PIN 4353-878, an ulna from the skeleton of a one-year-old calf from Sevsk (photo 21: 4-5). In sp. PIN 4353-878 the shaft is still relatively robust (table 14). In the middle part its cross section is almost triangular. The antero-posterior diameter of the distal part of the shaft equals 26% of its length (less than at the beginning of postnatal ontogenesis). The surface of the olecranon (length from the upper edge of the incisura semilunaris to the distalmost point 50 mm, width 51 mm) and the entire surface of incisura semilunaris have the relief that signals the presence of the cartilage of the growth zone.

Another difference between the proximal end of the ulnar shaft at this stage and at the previous one is greater concavity of the incisura semilunaris. The articular surfaces of the medial and lateral coronoid processes are not inclined forward and the angle between the processes exceeds 100°. The articular facet for the radius is therefore very wide.

The ossification centre of the distal epiphysis of sp. PIN 4353-878 (photo 21: 8) is oval (55 x 42 mm, height 35 mm). The length of the distal epiphysis equals ca. 19% of the total length of the ulna. The surface that faces the distal surface of the shaft is flattened, the side surfaces are vertical. The surface that faces the carpal bones is inclined antero-posteriorly. The relief of all surfaces of the centre signals that the centre remained embedded in the cartilage of the growth zone.

Specimen PIN 4353-499, from Sevsk, is an ulna that belongs to a skeleton of a calf aged three to four years. The medio-lateral diameter of the distal part of the shaft equals 27.7% of its length, which is 285 mm (table 14). The total length of the bone - including the distal epiphysis and the cartilage of the growth zones - is an estimated 327 - 330 mm. The length of the distal epiphysis therefore equals about 14% of the total length of the ulna. Relatively speaking this is less than during the first postnatal year. The growth zones on the ends of the olecranon and the incisura semilunaris persist. The permanent nutritive foramen (4 x 3 mm) is situated on the medial surface of the proximal end of the shaft, at the level of the articular surface on the medial coronoid process.

The partially formed materia compacta on the distal end of sp. PIN 4353-499 occupies a small area: it is a band that lies ten to twelve mm above the distal border of the ulna. There are seven vertical grooves on the medial surface of the distal end. These are seven to twelve mm long and one to two mm wide. Small nutritive foramina (1 x 1 mm) are situated in the proximal parts of the grooves. There are no such grooves on the anterior and lateral surfaces of the shaft, so the small nutritive foramina immediately pass through the surface layer. Evidently, the growth zone is situated not only between the end of the shaft and the epiphysis, but also extends onto the distal end of the shaft. The nutritive foramina are the passways of relatively large blood vessels that mark the growth zones. After the bone was substituted for the cartilage, the smaller foramina disappear immediately. The greater ones disappear later, so that the nutritive foramina for some time persist in the already ossified shaft ends in the shape of grooves. The permanent nutritive foramen (usually one, sometimes two) is normally situated in the middle part of the shaft. In the ulna it lies closer to the proximal end.

In sp. PIN 4353-499 the distal epiphysis is partially formed (74 x 61 mm, height 39 mm). Its lateral surface is more sloping than the medial one. The epiphysis cross section is almost triangular. The longest side of the triangle is the medial one, which faces the radius. The surface that faces the carpal bones is slightly convex.

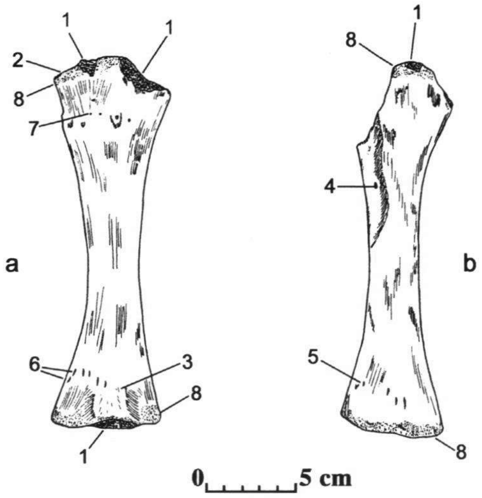

Fig. 21. Left femur of the same individual as figured in fig. 20. a = anterior surface; b = medial surface. Scale bar: 5 cm. 1 = damaged area of femur with substantia spongiosa; 2 = greater trochanter ; 3 = protrusion of the anterior surface of the distal shaft end over developing patellar groove; 4 = permanent nutritive foramen; 5 = grooves of small nutritive foramens on the posterior surface of the shaft; 6 = grooves of small nutritive foramens on antero-medial surface of the distal shaft end; 7 = small nutritive foramens on anterior surface of proximal shaft end; 8 = thin compact layer on shaft ends.

Linker dijbeen van hetzelfde individu als afgebeeld in fig. 20. a = voorzijde; b = binnenzijde. Maatstreep 5 cm. 1 = beschadigd gebied met sponzige substantie; 2 = grote trochanter; 3 = overlap van voorzijde van onderuiteinde van de schacht over de zich ontwikkelende knieschijfkatrol; 4 = blijvend voedingskanaal; 5 = groeves van kleine voedingskanalen op de achterzijde van de schacht; 6 = idem, op voor-binnenzijde van onderuiteinde van de schacht; 7 = kleine voedingskanalen op voorzijde van bovenuiteinde van de schacht; 8 = dunne compacte laag op schachtuiteinden.

At the age of six to seven years the surface of the growth zones on the proximal end of the shaft is drastically reduced, as in sp. ZIN 31744(4) (photo 21: 7) and PIN 4353-299, an ulna of a six- to seven-year-old individual from Sevsk. In specimen PIN 4353-299, the length of the shaft is 370 mm. When it is mounted together with the distal epiphysis, the combined length is 440 mm (table 14). The bone length including the cartilage of the growth zone would be 450 to 455 mm. The length of the distal epiphysis equals about 18% of the total length of the ulna. The cross section of the middle part of the shaft is subtriangular. There are two permanent nutritive foramina (3.5 x 3.5 mm) on the medial and proximal surfaces.

The distal epiphysis of PIN 4353-299 bears a its own number, PIN 4353-681, and has no longer a centre of ossification at this ontogenetic stage. Because it is a 'diminished copy' of the distal epiphysis as it is found in adult animals, it has a completely formed layer of materia compacta on the major part of its lateral surface. The growth zone remains only between the surface that faces the shaft and the distal surface of the shaft. It is almost triangular in cross section, with one angle directed backward. The distal, lateral and medial sides are vertical. The articular surface that faces the carpal bones is smooth. The width of the distal side is about 90 mm, that of the lateral and the medial side 77 and 83 mm respectively. The greatest height of the epiphysis is ca. 69 mm.

The early completion of the formation of the distal epiphysis of the ulna in *M. primigenius* is combined with protracted functioning of the growth zone between the shaft and the distal epiphysis. Among the epiphyses of the long bones it is one of the last to fuse, and this appears to be a peculiarity which is shared by the woolly mammoth and the two modern elephant species (Lister, 1999). The proximal epiphysis of the olecranon, though ossified later than the distal epiphysis of the ulna, is fused earlier. The growth zone on the surface of the proximal end of the ulna differs from all other ulnar growth zones in the absence of the centre of ossification.

The femur

The femur of *M. primigenius* at early stages of ontogenesis consists of the shaft and the proximal and distal epiphyses. Each of these comprises two ossification centres embedded in the cartilage of the growth zones at the shaft ends. After the completion of ossification of the epiphyses and the formation of consolidated proximal and distal epiphyses, two growth zones persist between the proximal end of the shaft and the proximal epiphysis and between the distal end of the shaft and the distal epiphysis. The epiphyses become fused at rather late stages of postnatal ontogenesis.

The proximal epiphyseal centres are ossified asynchronously. First a large femoral head is formed. The next ossification on the proximal surface is the greater trochanter. The ossification centres of the distal epiphysis evidently are formed synchronously (most probably during the final stage of prenatal development), and have similar dimensions. The centres correspond to the future medial and lateral condyles. Materia compacta is formed from the middle part of the shaft to its ends. There are additional nutritive foramina on the shaft ends during the later stages of prenatal and the earlier stages of postnatal ontogenesis. These foramina disappear by the beginning of the second year of postnatal ontogenesis. The only permanent nutritive foramen is situated in the middle part of the shaft and persists during the entire ontogenesis.

The femoral dimensions are given in table 15 and represented in fig. 19a, where a considerable variability in size is noticeable at the end of the prenatal stage and the beginning of the first postnatal year. In addition, length increase and width increase at the distal end of the shaft remain correlative until the end of the second postnatal year. In specimen ZIN 34201(4), a one-month-old calf cadaver from Yamal with two plates of dp^2 in wear, the dimensions of the femoral shaft are similar to those in a newborn from Sevsk. This discrepancy may be accounted for by individual developmental peculiarities of the former.

The shape and proportions of the femoral shaft change during ontogenesis. At the end of prenatal and the beginning of postnatal ontogenesis the proximal end of the shaft is curved antero-posteriorly (figs. 21, 22). At the beginning of the second postnatal year the shaft becomes straight. At this stage the transverse diameters of the epiphyses become reduced in relation to the epiphyseal lengths, but the relative robustness of the distal end of the shaft becomes greater. By the end of the seventh postnatal year the relative epiphyseal length diminishes in comparison with the shaft length (table 15). In addition, during the first postnatal year the angle between the base of the femoral head and the longitudinal axis of the shaft diminishes from 80° (ZIN 31760(6), 34419(10), 31744(5)) to 50°-60° (ZIN 31744(5), 34419(11), 34419(12)).

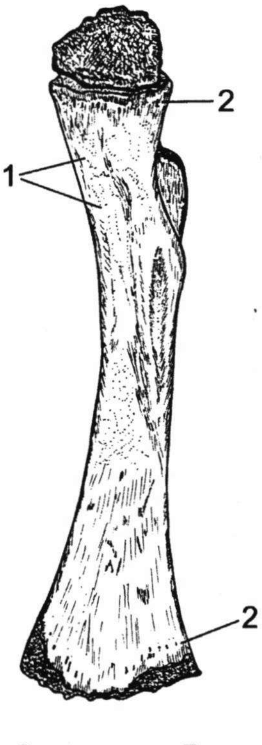

Fig. 22. Right femur of a *M. primigenius* foetus, sp. ZIN 34419(10), from Kostionki 1, Voronezh region, last stage of pregnancy (21-22 months), medial surface. Scale bar: 5 cm. 1 = curve of proximal quarter of the shaft; 2 = small nutritive foramina on the shaft ends.

Rechter dijbeen van een *M. primigenius* foetus, sp. ZIN 34419(10), vindplaats Kostionki 1, regio Voronezh, laatste stadium van de dracht (21-22 maanden), binnenzijde. Maatstreep 5 cm. 1 = curve van bovenste kwart van de schacht; 2 = kleine voedingskanalen op schachtuiteinden.

At the end of the prenatal ontogenetic period the proportions of the femur differ considerably from the femoral proportions in adult animals. In sp. ZIN 31740(6) (photo 23: 1) - which was in the middle of its second year (?) of prenatal ontogenesis by comparison with the dimensions of foetuses of modern elephants (Beyer *et al.*, 1990) - the shaft is relatively straight, and its proximal end curved antero-medially. The shortest transverse diameter of the shaft equals 12% its length. For the transverse diameter at the distal end the analogous percentage is 21. The materia compacta on the middle part of the shaft is better formed than on the ends. The relief for muscle insertions is absent. Several additional nutritive foramina are situated on the shaft ends. The permanent nutritive foramen (3 x 2 mm) is situated on the medial surface of the shaft, 42 mm below its upper edge.

From the end of prenatal ontogenesis (ZIN 32572(10), IAE Sh-77 5b) to the beginning of postnatal ontogenesis the proportions of the shaft do not change significantly (fig. 21, table 15). In sp. IAE Sh-77 5b the proximal part of the shaft is inclined antero-posteriorly. Near the distal edge of the anterior surface an expansion appears to form the base of the trochlea for the patella (fig. 21a: 3). The area with the smallest medio-lateral diameter is in the middle of the shaft, from where it becomes wider upward and downward. This shape of the shaft is similar to that in *E. maximus*. In *L. africana* the smallest diameter is in the lowest third of the shaft, whereas the middle and proximal parts have more or less similar transverse diameters (Zalensky, 1909). The trochanteric fossa and the greater trochanter are in the earliest stage of their formation. The permanent nutritive foramen (4 x 3 mm) is situated on the medial surface, 73 mm below the greater trochanter (fig. 22b: 4). At the distal end of the shaft, five additional nutritive foramina are situated in grooves that have a length of six to ten mm and lie twenty-one to thirty-one mm above the distal edge (fig 21a: 8). Six similar foramina are situated on the anterior surface of the proximal end of the shaft (fig. 22a: 7). The thickness of the materia compacta in the middle part of the shaft is 1 mm or less.

The structure of the shaft is similar in the newborn calves ZIN 34419(10) (fig. 22) and PIN 4353-2698. The latter specimen is a femur that belongs to a skeleton from Sevsk (photo 23: 4).

In sp. PIN 4353-2698 the smallest medio-lateral diameter of the shaft equals 13.6% of its length. For the medio-lateral diameter of the distal end this percentage is about 25. The medio-lateral diameter of the proximal end of the shaft under the base of the femoral head is 54 mm, the antero-posterior diameter of this part is 61 mm. The angle between the shaft surface under the base of the femoral head and the longitudinal axis of the shaft is slightly less than 90°. The head is oval (51 x 46 mm), its proximal surface is rounded and lacks materia compacta and relief that may be expected in an autonomous ossification centre embedded in the cartilage of the growth zone. The proximal end of the shaft is inclined antero-posteriorly, as in sp. ZIN 34419(10). The distal epiphysis comprises two autonomous ossification centres (photo 23, 2). The greater (medial) centre is oval (51 x 39 mm, height 38 mm), and its flattened surface faces the distal end of the shaft. The smaller (lateral) centre is almost spherical (39 x 30 x 29 mm). With the cartilage of the growth zones taken into consideration, the maximal length of the bone may have been 310 mm (the length of the shaft equals 80%, and the smallest medio-lateral diameter 16% of the total length). The medio-lateral diameter of the distal end of the shaft equals 32% of its length.

At the end of the first postnatal year (exemplified by PIN 4353-552, a femur of the skeleton of a one-year-old calf from Sevsk) and the beginning of the second postnatal year (ZIN 31744(5), 34419(1)), the relief for the insertion of the large muscles is formed in the areas of the greater trochanter, the small trochanter, and other parts of the shaft. It is then similar to the relief found in adult animals (photo 24, 1-3). If the cartilage of the growth zones is taken into consideration, the length of the femur is about 415 mm. The length of the shaft is about 15% of the total bone length. The smallest medio-lateral diameter equals 15% of the total bone length. For the medio-lateral diameter of the distal end the analogous percentage is 32. In the area of the bottom of the trochanteric fossa the antero-posterior diameter of the proximal end of the shaft is 22.5 mm. In the area of the base of the femoral head and the proximal end of the shaft the diameters are 70 and 75 mm. The proximal growth zone occupies the entire surface of the proximal end of the shaft and from the base of the head to its lateral edge. The permanent nutritive foramen (5 x 4 mm) is situated on the medial surface of the shaft, 111mm below its upper edge. The number of additional nutritive foramina on the shaft ends is small, the thickness of materia compacta on the middle part of the shaft is roughly equal to that on the ends.

The femoral head in sp. PIN 4353-552 is oval, drop-like in cross section, with the long axis medio-laterally oriented (photo 25: 4). The length of the femoral head is 73 mm. Its width and height are 67 and 45 mm respectively. Its medial edge is oval and laterally (opposite the greater trochanter) sharpened. The surface that faces the acetabulum is hemispherical. The surface opposite the proximal surface of the shaft is flattened, the relief formed in contact with the cartilage.

The distal shaft of sp. PIN 4353-552 comprised two ossification centres (the medial one is not preserved). The lateral centre is oval. Its surface opposite the shaft is flattened, and the surface that faces the tibia is convex. The height of the centre is 47 mm, its width 55 mm, and its length 44 mm. The surface that faces the medial centre of ossification has a process that proliferates at later stages and gradually fuses with the medial centre thus forming the base of the consolidated distal epiphysis.

During the third-to-fourth year of postnatal development, the shaft's proportions and morphology remain more or less the same as at the previous stage, as in sp. PIN 4353-479, a femur of a skeleton of a calf from Sevsk (photo 24: 5). The smallest medio-lateral diameter equals 14.5% of the shaft length. For the greatest medio-lateral diameter of the distal end the analogous percentage is 28. The permanent nutritive foramen (4 x 5 mm) is situated 130 mm below the proximal end of the shaft, in the middle part of a vertical groove that is 80 mm long and 6 mm wide. The smallest antero-posterior diameter of the proximal surface (at the level of the bottom of the trochanteric fossa) is 34 mm. The length of the head is 94 mm, its width 85 mm, and its height 63 mm. Its proximal surface is hemispherical. The surface that faces the proximal end of the shaft is flattened. In comparison with the situation at the previous stage, the lateral edge is much more elongated in the direction of the greater trochanter.

At the age of six to seven years, the ossification centres of the distal epiphysis have fused. The suture between them persist, as in PIN 4353-48, a femur of a six- to seven-year-old calf from Sevsk (photo 24: 6-8). Materia compacta is formed on the surface that faces the foot, which suggests that from this stage onward the growth zone was situated between the distal surface of the shaft and the epihysis. There are many small and large nutritive foramina in the area of the suture between the medial and lateral parts of the epiphysis. The fusion of the lateral and medial centres of the distal epiphysis proceded from the anterior end of the epiphysis toward the posterior end. The suture is already absent in the anterior part of the epiphysis, which forms the trochlea for the patella. The suture persists in the posterior part, where it extends along the notch between the lateral and medial condyles.

The proximal epiphysis at this stage, as at the previous one, consists of two ossification centres: the femoral head and the lateral centre, or the greater trochanter (photo 24, 8). Materia compacta that is formed on the head suggests that this part of the epiphysis is no longer embedded in the cartilage of the growth zone, where only the lateral centre remains. On the lateral surface of the head a process is formed and directed toward the lateral centre. The materia compacta on the lateral process is relatively thin, with numerous nutritive foramina.

The structure of specimen PIN 4353-48 suggests that during the prenatal as well as during the initial postnatal ontogenesis the femur develops a weak relief for muscle insertions, the formation of which takes place at relatively late ontogenetic stages. Besides, the speed of formation of the proximal femoral epiphysis is lower than that of the distal one, and by the age of six to seven years the proximal epiphysis still consists of two centres. This structure and the sequence of the formative stages of the femur - as in the cases of the humerus and the ulna - are indicative of the initial existence of several primordial ossification centres in the long bones of the mammoth.

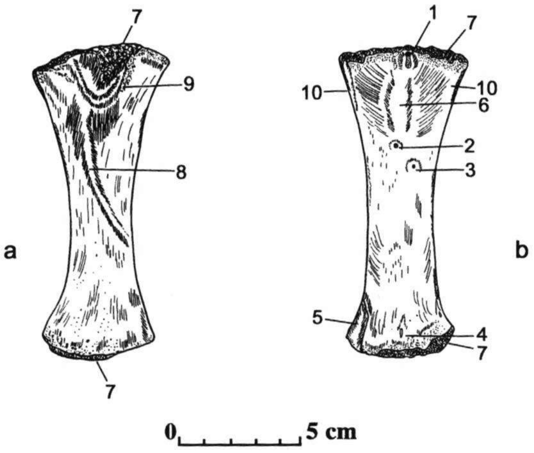

Fig. 23. Left tibia of a *M. primigenius* foetus of last prenatal stage (20-21 months of pregnancy), field nummer IAE Sh-77 3d, Shestakovo locality, Chabula district, Kemerovo region. a = anterior surface; b = posterior surface. Scale bar: 5 cm. 1 = proximal nutritive foramen ; 2 = middle nutritive foramen; 3 = distal nutritive foramen; 4 = depression near distal shaft end; 5 = sulcus malleolaris; 6 = concavity of posterior surface of the shaft; 7 = damaged areas of bone; 8 = tibial crest; 9 = tibial tuberosity; 10 = lateral and medial crests on posterior surface of the shaft (linea muscularis).

Linker scheenbeen van een *M. primigenius* foetus gedurende het laatste prenatale stadium (20-21 maanden dracht), veldnummer IAE Sh-77 3d, vindplaats Shestakovo, district Chabula, regio Kemerovo. a = voorzijde; b = achterzijde. Maatstreep 5 cm. 1 = bovenste voedingskanaal; 2 = idem, middelste; 3 = idem, onderste; 4 = del nabij onderuiteinde van de schacht; 5 = malleolare groeve; 6 = holte aan achterzijde van de schacht; 7 = beschadigde delen; 8 = scheenbeenkam; 9 = plaats van peesaanhechting; 10 = kammen aan binnen- en buitenzijde aan de achterzijde van de schacht (grenslijnen spieraanhechting).

The tibia

At early ontogenetic stages the tibia is represented by an ossified shaft and two epiphyseal ossification centres (proximal and distal) forming in the cartilage of the growth zones. The growth zones remain functional for a long time after the epiphyses have been ossified completely. A relative reduction of the transverse diameters of the epiphyses with respect to their lengths takes place heterochronously at different stages. In addition, development of relief in the middle part of the shaft causes a transformation of its shape in cross section. The materia compacta on the shaft of the tibia is formed earlier than on other long bones and the number of additional nutritive foramina is greatly reduced soon after birth. The formation of relief for musculature insertions takes place mostly at the end of the first postnatal year. The lateral edge of the proximal end of the shaft becomes much higher than the medial one in the course of ontogenetic development. Dimensions and proportions of the tibia at early ontogenetic stages are given in table 16 and illustrated with a diagram (fig.19b).

At the end of the prenatal period and the beginning of postnatal ontogenesis, materia compacta is practically not formed on the shaft ends, and the growth zones here are marked with numerous tiny nutritive foramina. This age group is exemplified by the specimens ZIN 31740(7), a foetus in the 14th to 16th month of development (photo 25: 1), and ZIN 31740(16), 31740(9) (photo 26: 3), ZIN 34419(16) (photo 26: 2), and IAE Sh-77 3d, which all represent foetuses in the 20th to 21st month of development (fig. 23). In sp. ZIN 31740 the medio-lateral diameter of the proximal end of the shaft equals 33% of its length. Consequently, the shaft looks short and robust. The proximal and distal ends of the shaft are damaged. The cross section of the shaft in the middle part is oval. The only relief is the rough surface in the area of tibial crest and the weakly-expressed tuberosity. The materia compacta is better formed in the middle than on the ends of the shaft, where many small nutritive foramina are situated.

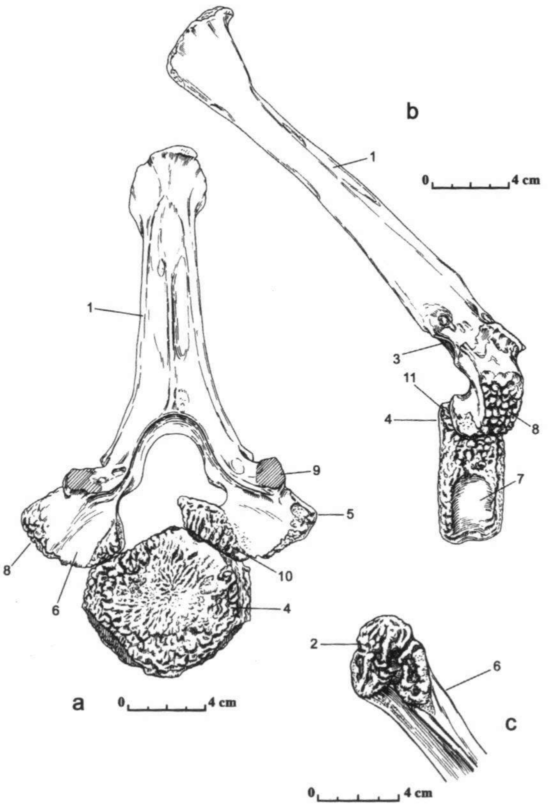

Fig. 24. First thoracic vertebra of a 3- to 4-year-old calf of *M. primigenius*, PIN 4353-512, Sevsk locality, Bryansk region. a = front view; b = side view; c = end of spinous process. Scale bar: 4 cm. 1 = spinous process; 2 = growth zone at end of spinous process; 3 = caudal articular facet; 4 = corpus vertebae; 5 = transverse process; 6 = end of spinous process; 7 = compact layer on ventral surface of vertebral body; 8 = apophysis articular facet on transverse process; 9 = cranial articular facet; 10 = proliferation of bases of neural arch legs; 11 = suture between neural arch base and dorsal surface of vertebral body, the latter with a relief indicating the presence of cartilage.

Eerste borstwervel van een *M. primigenius* kalf van 3-4 jaar oud, PIN 4353-512, vindplaats Sevsk, regio Bryansk. a = vooraanzicht; b = zijaanzicht; c = eind van doornuitsteeksel. Maatstreep 4 cm. 1 = doornuitsteeksel; 2 = groeizone aan eind van doornuitsteeksel; 3 = achterste gewrichtsvlak; 4 = wervellichaam; 5 = dwarsuitsteeksel; 6 = top van doornuitsteeksel; 7 = compact been aan onderzijde van wervellichaam; 8 = aanhechtingsplaats van gewrichtsvlak op dwarsuitsteeksel; 9 = voorste gewrichtsvlak; 10 = proliferatie van de basis van de benen van de wervelboog; 11 = naad tussen basis van wervelboog en bovenzijde van wervellichaam; de laatste heeft een relief dat duidt op de aanwezigheid van kraakbeen.

In sp. IAE Sh-77 3d, the shaft is relatively short and robust. The medio-lateral diameter of the proximal end of the shaft equals 34%, the smallest width 19.6% of the length of the shaft. The tibial crest is represented by a primordial tuberosity. It extends from the level of the distal end of the tibial tuberosity in the direction of the distal end of the shaft without reaching it (fig. 23: 8). The crest extends onto the medial surface as well, though only slightly. The transverse diameter of the tibial tuberosity is greater than the vertical one (32 and 21 mm respectively, fig. 23a: 9). The difference in inclination between the lateral and medial edges is insignificant. The posterior surface of the proximal end of the shaft, between the muscular lines (lineae musculares) that delimit it from the side surfaces, is concave. There are three nutritive foramina on the posterior surface of the proximal end of the shaft. The greater one is oval (5 x 2 mm) and is situated 4 mm below the proximal end (fig 23: 1). The medium-sized (2.5 x 2 mm) and the smaller one (2 x 1.5 mm) are situated underneath (fig. 23: 2-3) On the posterior surface of the distal end of the shaft there are several small nutritive foramina (1 x 1 mm) situated in grooves (fig. 23: 4). The relief of the posterior surface of the distal end is represented only by the malleolar sulcus (fig. 23: 5).

At the beginning of postnatal ontogenesis the robustness of the shaft diminishes, yet the robustness of its proximal end becomes relatively greater. Examples are PIN 4353-2703, a tibia of the skeleton of a newborn calf from Sevsk (photo 25: 6), ZIN 31740(8) (photo 25: 4), and ZIN 34201(2). In specimen PIN 4353-2703 the medio-lateral diameter of the proximal end of the shaft equals 43%, and the smallest medio-lateral diameter 17% of the length of the shaft (in specimen ZIN 34201(2) these ratios are 42% and 16.6% respectively). The transverse diameter of the tibial tuberosity becomes smaller than its vertical diameter (22 mm and 28 mm respectively). A permanent nutritive foramen (2 x 1 mm) and two smaller ones underneath it are situated on the posterior surface, near the proximal end of the shaft. The width of malleolar sulcus is ca. 12 mm. There is no other relief on the distal end of the shaft.

At the end of the first postnatal year the cross section of the shaft is hemispherical, not oval (PIN 4353-1709, a tibia of the skeleton of a one-year-old calf (photo 25: 7), ZIN 34419(14), and 34419(15)). The robustness of the shaft is practically the same as at the previous stage. In sp. PIN 4353-1709 the smallest medio-lateral diameter equals 19% and the medio-lateral diameter of the proximal end 34% of the length of the shaft. The posterior surface of the proximal end of the shaft of this specimen is slightly concave and delimited by well-expressed muscular lines. In the area of the smallest shaft width its posterior surface is straight. In the direction of the distal end the transverse shaft diameter becomes

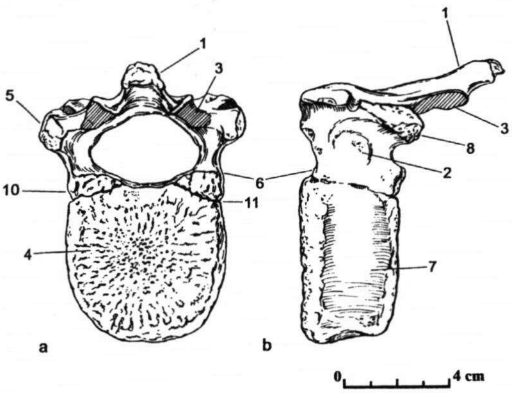

Fig. 25. Thoracic vertebra of a 3 to 4-year-old calf of *M. primigenius* of the Sevsk locality, Bryansk region, PIN 4353-526, front view (a) and side view (b). 1 = spinous process; 2 = articular fossa for rib head on neural arch base; 3 = caudal articular facet; 4 = vertebral body; 5 = transverse process; 6 and 10 = neural arch leg; 7 = materia compacta on the lateral part of the vertebral body; 8 = place for apophysis of transverse process; 11 = sutura between neural arch leg and vertebral body.

Borstwervel van een *M. primigenius* kalf van 3-4 jaar oud, vindplaats Sevsk, regio Bryansk, PIN 4353-526, voor- (a) en zijaanzicht (b). 1 = doornuitsteeksel; 2 = gewrichtsvlak voor rib op basis van wervelboog; 3 = achterste gewrichtsvlak; 4 = wervellichaam; 5 = dwarsuitsteeksel; 6 en 10 = been van wervelboog; 7 = compact been aan zijkant van wervellichaam; 8 = plaats voor aanhechting van dwarsuitsteeksel; 11 = naad tussen been van wervelboog en wervellichaam.

gradually greater and its posterior surface more prominent. The relief of the proximal and distal surfaces is typical of the growth zones. The vertical and transverse diameters of the tuberosity are 48 mm and 39 mm respectively. From its base the tibial crest extends toward the distal end. The permanent nutritive foramen is situated on the posterior surface, 82 mm below the proximal end. The materia compacta on the distal and proximal ends extends almost to the edges of the shaft.

The ossification centres of the proximal and distal epiphyses are probably formed during the third to fourth year of postnatal ontogenesis, which range is exemplified by the specimens ZIN 31744(6) and PIN 4353-873, a tibia of a calf skeleton (photo 25: 5, 8). The ossification centres are not preserved in these specimens, but indirect evidence is provided by the homogeneous structure of the materia compacta over the entire shaft. In sp. 4353-873 the medio-lateral diameter of the shaft is 21% and the transverse diameter of the proximal end equals 35% of its length. The cross section of the middle part of the shaft is hemispherical. The cross sections of the proximal and distal parts of the shaft are oval. The vertical and transverse diameters of the tuberosity are 38 and 67 mm respectively. The tibial crest almost reaches the distal edge of the shaft.

The cross section of the middle part of the shaft radically changes by the sixth to seventh year of postnatal ontogenesis. The relief of the tibia at this stage is also well developed. In sp. PIN 4353-625, a tibia of an incomplete skeleton from Sevsk, both non-fused epiphyses are preserved (photo 25: 9). The cross section of the shaft is subtriangular in the middle part and oval in the proximal and distal parts. The smallest medio-lateral diameter equals 19%, and that of the distal end 32% of the shaft length. The relief for large muscle insertions is present in several areas of the shaft. The vertical and transverse diameters of the tuberosity are 67 mm and 94 mm respectively. The development of the robust tibial crest determines the subtriangular shape of the cross section of the middle part of the shaft. The crest and the surrounding surface have the relief for muscle insertions. The posterior surface of the proximal end is noticeably concave. Both muscular lines are well expressed. There are three nutritive foramina on the posterior surface. These are almost vertically aligned (4 x 1.5 mm, 3 x 1 mm and 6 x 2 mm). The malleolar sulcus is shallow.

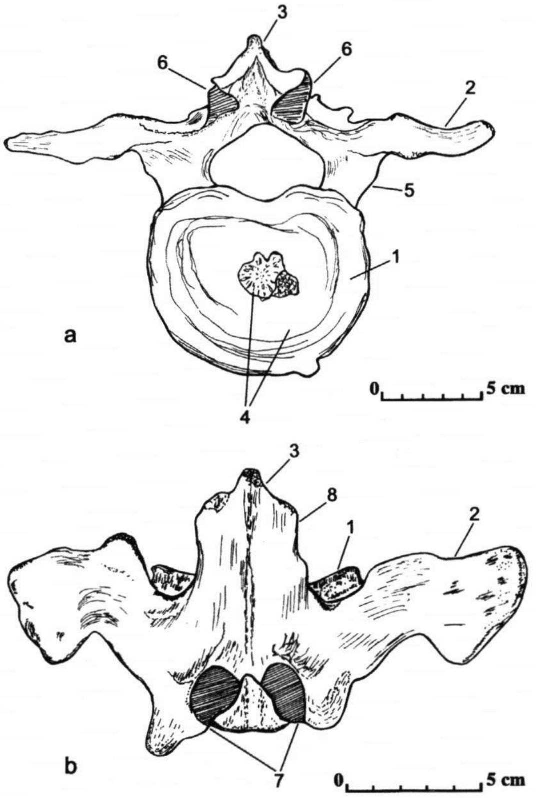

Fig. 26. Formation of bony epiphyses and apophyses on a lumbar vertebra of an adult *M. primigenius*, PIN 4353-2856, Sevsk locality, Bryansk region, front view (a), upper view (b). 1 = vertebral body; 2 = transverse process; 3 = spinous process; 4 = incompletely formed epiphysis of vertebral body with an opening with a non-ossified part in the centre of the epiphysis; 5 = neural arch leg; 6 = caudal articular facets; 7 = cranial articular facets.

Vorming van benige vergroeiingen op een lendenwervel van een volwassen *M. primigenius*, PIN 4353-2856, vindplaats Sevsk, regio Bryansk, vooraanzicht (a), bovenaanzicht (b). 1 = wervellichaam; 2 = dwarsuitsteeksel; 3 = doornuitsteeksel; 4 = onvolledig gevormde vergroeiing van wervellichaam met een opening met niet-verbeend deel in het centrum van de epiphyse; 5 = been van wervelboog; 6 = achterste gewrichtsvlakken; 7 = voorste gewrichtsvlakken.

The proximal epiphysis is oval, its dimensions are 125 x 100 mm. The height from base to top of the intercondylar eminence is 37 mm, and in this respect practically does not differ from the proximal epiphyses of adults. The lateral edge of the epiphysis is elongated and sharpened similarly to the sharpened lateral edge of the shaft. The dimensions of the medial articular facies are 84 x 70 mm, those of the lateral articular facies 62 x 54 mm. The surface of the latter is slightly inclined laterally (photo 25: 9). The structure of the materia compacta on the articular surface of the epiphysis is similar to that on the shaft. It is thinner on the side surfaces and more nutritive foramina are situated here. The distal epiphysis is oval (114 x 82 mm, height across the medial eminence 40 mm). The dimensions of the distal articular facies are 88 x 62 mm. Its surface is almost parallel to the distal surface of shaft. The relief formed by the cartilage of the distal growth zone on the proximal surface of the distal epiphysis (opposite the shaft) is well expressed.

The morphology of sp. PIN 4353-625 and other specimens studied suggests that on the whole the formation of this bone proceeds in a similar way as in other long bones, i.e. with two growth zones on the shaft ends and at least three autonomous centres of ossification: the shaft and the two epiphyses. In particular, the structure of the proximal and distal epiphyses in sp. PIN 4353-625 suggests that initially they are ossification centres embedded in the cartilage of the growth zones, and by the sixth to seventh postnatal year become ossified to an extent that makes the growth zones move into the region between the epiphyses and the distal and proximal ends of the tibial shaft.

The vertebras

A vertebra is formed of two autonomous ossification centres: the neural arch (arcus neuralis) and the vertebral body (corpus vertebrae). The formation (ossification in the growth zones in vertebral parts) continues until the age of eighteen to twenty. The neural arc conjoins the dorsal surface of the vertebral body after seven to ten postnatal years in females, and after forty in males. Before the beginning of postnatal ontogenesis the vertebral body is represented by an ossification centre embedded in cartilage (figs. 24, 25).

During ontogenesis the structures of the transverse dorsal processes and spinous processes are changed at the expense of the formation and fusion of their apophyses. The main zones of growth are situated between the epiphyses and the vertebral body and between the bases of the neural arches and the vertebral body. The fusion of autonomously ossified epiphyses of vertebral bodies takes place at late ontogenetic stages, i.e., after the age of seventeen in females and after forty in males. The apophyses fuse with the processes of the neural arches earlier. During ontogenesis the absolute length of the vertebral column becomes greater, whereas the relative lengths of its regions remain constant. The number of vertebrae in the cervical and sacral regions remains constant (seven and four). The total number of vertebrae in the thoracic and lumbar regions is also constant (23), but the number in each region varies with the incorporation (or non-incorporation) of vertebrae of the lumbar region into the thoracic region. Thus, in different individuals the number of vertebrae in the thoracic and lumbar regions may be nineteen to twenty and four to three, respectively. In some adult individuals - e.g., in PIN 4454, a skeleton of *M. primigenius* from the Novopetrovskoe locality in the Moscow region - a facet for a rib head is formed on the upper edge of the lateral surface of the first lumbar vertebra. The description of the morphological transformations of cervical, thoracic, lumbar and sacral vertebra in mammoth calves that is to follow is based on vertebrae of skeletons that belong to a newborn and to calves aged three to four and six to seven years, all from Sevsk (PIN 4353).

In the skeleton of a newborn calf the first to sixth cervical vertebrae are preserved (PIN 4353-2614, 2461, 2321, 2615, 2623, 2556). The sum of the lengths of the ossified vertebral bodies is 42.6 mm. At this ontogenetic stage, there are no ossified epiphyses of vertebral bodies on the vertebrae of the cervical and all other regions. The vertebral body is itself an ossification centre in the process of formation. The neural arch is not fused with the proximal surface of vertebral body. The thoracic region comprises eighteen vertebrae. Evidently, either the first or the second vertebra of the region is missing (PIN 4353-1625, -1621, -2623, -2624, -2629 to -2640, -2644, -2645). The sum of the lengths of the vertebral bodies is about 313 mm. The lumbar and sacral regions comprise four vertebras each. (PIN 4353-2640 to -2643 and PIN 4353-2646 to -2649, respectively). The sums of the lengths of the vertebral bodies in these regions are 72 mm and 73 mm respectively. If the absence of one or two vertebral bodies is taken into account, the length of the vertebral column (from the cervical up to and including the sacral region) may have been ca. 530 mm. The cervical region takes up 13.6% of the total length of the column, the thoracic region 59%, and the lumbar as well as the sacral region 13.6%. The estimated length of the vertebral column including the non-preserved cartilaginous parts of the vertebral bodies is twenty to thirty percent greater and would be about 670 to 770 mm (Vereshchagin, 1981; Kuzmina, 1999; Kuzmina & Maschenko, 1999). This estimate is based on X-ray photos of mammoth calf cadavers younger than one year.

In the skeleton of a one-year-old calf, all seven cervical vertebrae are preserved (PIN 4353-923 to -926, -929). The sum of their lengths is 121 mm. The thoracic region (PIN 4353-934 to -951, -955, -956) comprises of nineteen 19 vertebrae. To judge by complete skeletons of adult mammoths, all thoracic vertebrae are preserved (Zalensky, 1903). The sum of their lengths is ca. 530 mm. The lumbar and sacral regions consist of four vertebrae each (PIN 4353-952 to -954, -957, and PIN

4353-958 to -961). The lengths of these regions are 103 mm and 106 mm respectively. The length of the vertebral column (from the cervical up to and including the sacral region) is 860 mm. The cervical region takes up 14% of the total length of the vertebral column, the thoracic region 61.8%, the lumbar region 12%, and the sacral region 12.2%. The estimated total length including cartilage is 1100 to 1120 mm.

In the three- to four-year-old calf, the epiphyses of the vertebral bodies were evidently not ossified, as was the case at the two previous stages. All seven cervical vertebras are preserved (PIN 4353-505 to -509). The sum of the lengths of their ossified bodies is ca. 148 mm. There are twenty vertebras in the thoracic region (PIN 4353-510 to -530); the sum of their lengths is 623 mm. All vertebras have facets for rib heads (either on the lateral surfaces of the neural arch pedicles, or on the vertebral bodies), so their pertinence to the thoracic region may be established reliably (figs. 24, 25). There are twenty rib pairs that correspond to them. The four lumbar vertebras without facets for ribs (PIN 4353-531 to -533, -527) add up to a length of 132 mm. The sum of the lengths of the four sacral vertebrae (PIN 4353-534 to -537) is 29 mm. The total length of the vertebral column is 1032 mm, of which the cervical region constitutes 14.3%, the thoracic 59.7%, and the lumbar and sacral regions 13% each. The non-ossified parts of the vertebras taken into account, the estimated length of the vertebral column of this individual is 1330 to 1340 mm.

In the skeleton of a six- to seven-year-old individual six cervical vertebras are preserved (PIN 4353-633, -664, -671, -668, -130, -661). The sum of the lengths in this region (including the length of the missing sixth vertebra) is ca. 190 mm. In the thoracic region eighteen vertebras are preserved (PIN 4353-235, -240, -646, -261, -289, -632, -633, -635, -641, -643 to -645, -647, -650, -776, -1061, -1062, -1071). The sum of the lengths of these vertebras is 760 mm. Together with one or two missing vertebras, this sum would have been 800-820 mm. The lumbar and sacral regions consist of four vertebras each (PIN 4353-634, -642, -752, -649 and PIN 4353-1028, -651 to -653 respectively). The length of each of these regions is approximately 160 mm. The total length of the vertebral column is 1310 to 1330 mm, 14.4% of which is taken up by the cervical region, 61.6% by the thoracic region, and 12% by the lumbar as well as by the sacral region. The estimated length of the vertebral column of this individual, the non-preserved cartilage of the vertebral bodies taken into account, is about 1600 mm.

Changes in area and position of the vertebral growth zones and sequences of morphological transformations are well expressed at all four stages of postnatal ontogenesis described in this work (newborn, one year, three to four years, six to seven years). The process of ossification of the epiphysis may be illustrated by vertebrae with fused apophyses (PIN 4353-2856, -2734). The epiphysis (initially ring-shaped) ossifies from lateral parts toward the center (fig. 25a: 4; fig.

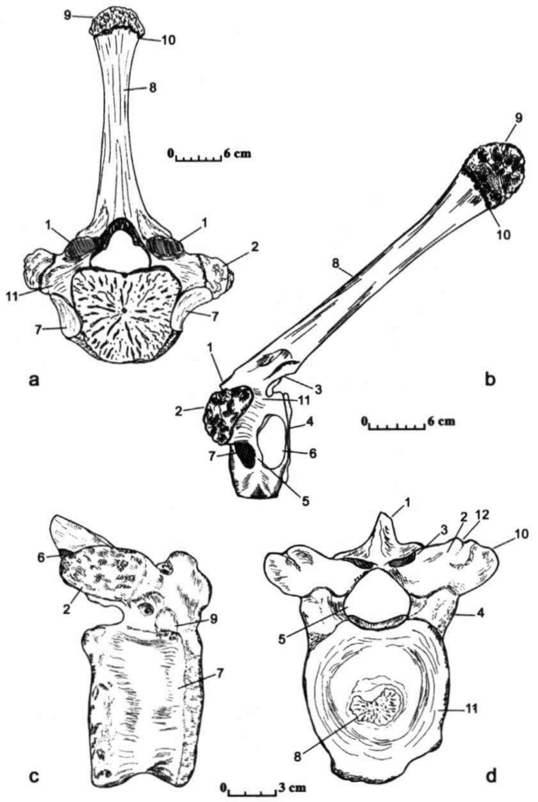

Fig. 27. The formation of the thoracic vertebra of an adult *M. primigenius*: PIN 4353-3690 (second thoracic vertebra) and PIN 4353-2734 (thoracic vertebra), Sevsk locality, Bryansk Region, front view (a, d) and side view (b, c). In the first, the ossified apophysis is formed though not yet fused to spinous process; in the latter, the ossified apophysis of the transverse process is formed, but the suture between the process and the apophysis still persists. a, b: 1 = cranial articular facet; 2 = ossified apophysis of transverse process; 3 = caudal articular facet; 4 = epiphysis of vertebral body; 5 = articular crest for rib head between cranial and caudal fossae; 6 = caudal articular fossa for rib head; 7 = cranial articular fossa for rib head; 8 = spinous process; 9 = apophysis of spinous process; 10 = suture between the spinous process and its apophysis; 11 = transverse process. c, d: 1 = spinous process; 2 = transverse process; 3 = cranial articular facet; 4 = neural arch leg; 5 = opening to cerebrospinal canal; 6 = caudal articular facet; 7 = vertebral body; 8 = opening in the centre of incompletely formed epiphysis of vertebral body; 9 = articular fossa for rib head on base of neural arch base; 10 = apophysis of transverse process; 11 = epiphysis of vertebral body; 12 = suture between transverse process and apophysis.

De vorming van borstwervels bij een volwassen M. primigenius: PIN 4353-3690 (tweede borstwervel) en PIN 4353-2734 (borstwervel), *vindplaats Sevsk*, regio Bryansk, vooraanzicht (a, d) en zijaanzicht (b, c). In de eerste is de benige apophyse gevormd, maar nog niet gefuseerd met het doornuitsteeksel; in de tweede is de benige apophyse van het dwarsuitsteeksel gevormd, maar de naad tussen het uitsteeksel en zijn apophyse is nog zichtbaar. a, b: 1 = voorste gewrichtsvlak; 2 = benige apophyse van het dwarsuitsteeksel; 3 = achterste gewrichtsvlak; 4 = epiphyse van wervellichaam; 5 = gewrichtskam voor ribhoofd tussen voorste en achterste groeves; 6 = achterste gewrichtskom voor ribhoofd; 7 = idem, voorste; 8 = doornuitsteeksel; 9 = apophyse van doornuitsteeksel; 10 = naad tussen doornuitsteeksel en zijn apophyse; 11 = dwarsuitsteeksel. c, d: 1 = doornuitsteeksel; 2 = dwarsuitsteeksel; 3 = voorste gewrichtsvlak; 4 = been van wervelboog; 5 = opening naar ruggemergskanaal; 6 = achterste gewrichtsvlak; 7 = wervellichaam; 8 = opening in het centrum van onvolledig gevormde epiphyse van wervellichaam; 9 = gewrichtskom voor ribhoofd aan de basis van de wervelboog; 10 = apophyse van dwarsuitsteeksel; 11 = epiphyse van wervellichaam; 12 = naad tussen dwarsuitsteeksel en zijn apophyse.

27d: 8). During the early postnatal ontogenesis the growth zones on the cranial and caudal surfaces of the vertebral bodies leave behind a relief in the shape of tubercles and a tuberosity with numerous foramina for small blood vessels (fig. 24a: 4; fig. 25a: 4; figs. 27a, 28a, 29a and 29c).

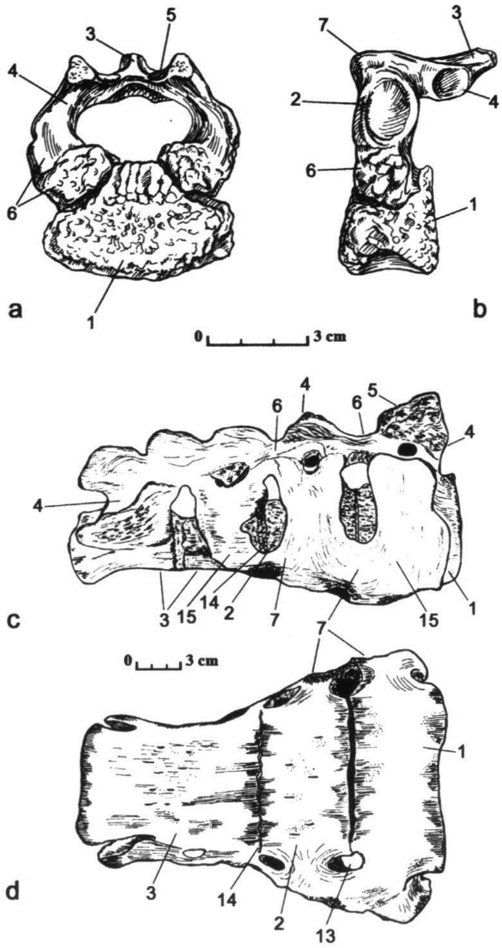

Fig. 28. Formation of vertebras of *M. primigenius*, Sevsk locality, Bryansk region: fourth sacral vertebra of a 1-year-old calf (PIN 4353-959, side view (a) and front view (b)) and sacrum of an adult individual (PIN 4353-3722, side view (c) and ventral view (d)). 1 = body of first sacral vertebra; 2 = body of second sacral vertebra; 3 = completely fused bodies of third and fourth sacral vertebrae; 4 = neural arch; 5 = spinous process of first sacral vertebra; 6 = completely fused caudal and cranial articular processes; 7 = proliferated bases of neural arch legs of adjacent vertebrae; 8 = spinous process; 9 = cranial articular facet; 10 = caudal articular facet; 11 = cranial articular processes; 12 = opening of cerebrospinal canal; 13 = opening between vertebral bodies and fused bases of neural arch legs; 14 = intervertebral sutures; 15 = transverse process.

Vorming van heiligbeenwervels bij *M. primigenius*, vindplaats Sevsk, regio Bryansk: vierde heiligbeenwervel bij een 1 jaar oud kalf (PIN 4353-959, zijaanzicht (a) en vooraanzicht (b)) en heiligbeen van een volwassen individu (PIN 4353-3722, zijaanzicht (c) en onderaanzicht (d)). 1 = lichaam van eerste heiligbeenwervel; 2 = idem, van tweede; 3 = volledig vergroeide lichamen van derde en vierde heiligbeenwervels; 4 = wervelboog; 5 = doornuitsteeksel van eerste heiligbeenwervel; 6 = volledig vergroeide achterste en voorste gewrichtsuitsteeksels; 7 = vergrote bases van wortels van wervelbogen van naastgelegen wervels; 8 = doornuitsteeksel; 9 = voorste gewrichtsvlak; 10 = achterste gewrichtsvlak; 11 = voorste gewrichtsuitsteeksel; 12 = ruggemergskanaalopening; 13 = opening tussen wervellichamen en vergroeide wortels van wervelboog; 14 = tussenwervelnaden; 15 = dwarsuitsteeksel.

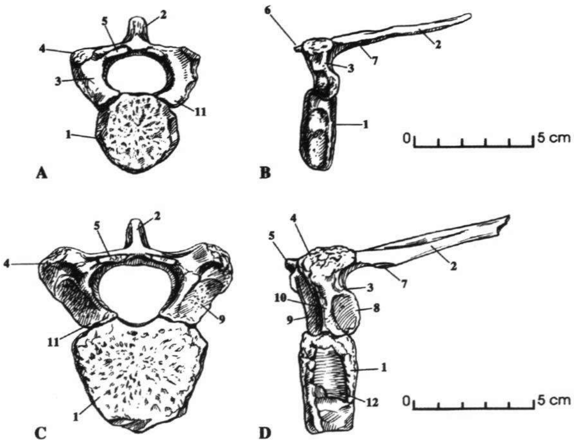

Fig. 29. Structure of *M. primigenius* thoracic vertebrae from Sevsk locality, Bryansk region: PIN 4353-2632, newborn calf, front view (a) and side view (b), and PIN 4353-527, 1-year-old calf, front view (c) and side view (d). 1 = vertebral body; 2 = spinous process; 3 = neural arch; 4 = transverse process; 5, 6 = cranial articular facet; 7 = same, caudal; 8 = caudal articular fossa for rib head; 9 = same, cranial; 10 = articular crest for rib head between cranial and caudal fossae; 11= neural arch leg; 12 = materia compacta on the lateral part of the vertebral body.

Bouw van *M. primigenius* borstwervels, vindplaats Sevsk, regio Bryansk: PIN 4353-2632, pasgeboren kalf, vooraanzicht (a) en zijaanzicht (b), en PIN 4353-527, jaarling, vooraanzicht (c) en zijaanzicht (d). 1 = wervellichaam; 2 = doornuitsteeksel; 3 = wervelboog; 4 = dwarsuitsteeksel; 5, 6 = voorste gewrichtsvlak; 7 = idem, achterste; 8 = achterste gewrichtskom voor ribhoofd; 9 = idem, voorste; 10 = gewrichtskam voor ribhoofd tussen voorste en achterste kommen; 11= wortel van wervelboog; 12 = compact beenweefsel aan zijkant van wervellichaam.

The formation process of the vertebral body may be illustrated with changes of the area occupied by the compact layer. In a newborn calf vertebra, almost the entire surface of the body is free of materia compacta. The only area where the layer is formed surrounds the ventral surface of the vertebra (PIN 4353-2633, fig. 29). At the age of three to four years, the area covered with materia compacta is much greater, the layer reaches 1-1.5 mm in thickness and covers practically the entire ventral surface of the vertebral body (figs. 27a, 27b: 7). The compact layer on the vertebras of adults usually is not thicker than 1.5 mm.

At the age of six to seven years the apophyses of the dorsal transverse and spinous processes remain unfused. To judge by the relief, the growth zone - of which the apophysis was initially the centre - is situated here (fig. 24a: 8). The fusion of the apophyses of the transverse and spinous processes was asynchronous. The apophyses of the transverse processes are the first to fuse, the suture between them and the transverse process persists until the age of fifteen to seventeen years (PIN 4353-3690, fig 27a, b: 2). The apophyses of the spinous processes fuse later, evidently after twenty years, and the suture between the processus spinosus and the apophysis persists for a long time (PIN 4353-3690, fig. 2b: 9).

The rib facets are formed on all thoracic vertebras by the age of one year (PIN 4353-934 to -951). In a one-year-old calf from Sevsk the first seventeen thoracic vertebras bear two facets: the fovea costalis cranialis and the fovea costalis caudalis. They are situated at the bases of the lateral parts of the neural arch and partially extend to the vertebral body (fig. 25b: 2). In adult individuals these facets are separated by a vertical crest (fig. 25b: 5). The anterior facet of one vertebra and the posterior facet of the previous one form a complete fossa for articulation of a rib head. The two posteriormost thoracic vertebras have only one facet, situated in the middle of the lateral surface at the foot of the neural arch (fig. 25b: 2; fig. 27c: 9).

The ventral and dorsal surfaces of a spinous process have two articular surfaces each: the facies articularis cranialis and the facies articularis caudalis. They are situated on the processus articularis cranialis and processus articularis caudalis respectively. The positions of these cranial and caudal articular facets are roughly the same in thoracic and lumbar vertebrae and are similar in calves and adult individuals (figs. 24-27 and 29). In *E. maximus* and *L. africana* the caudal articular process of trunk vertebrae is partly fused with the base of the spinous process that forms its dilatations. The caudal articular facets are situated on the dorsal surface of these prominences (fig. 24b, c: 3; fig. 26b: 7).

Neural arches fuse with the bodies of trunk vertebrae at later ontogenetic stages. At the age of fifteen to seventeen years the arches of all trunk vertebrae remain unfused. The relief on the feet of neural arches and the corresponding facets on the upper surfaces of the vertebral bodies suggests the presence of cartilage (fig. 24b: 11; fig. 25a: 11; fig. 29a, c: 11). The morphology of this zone changes at different stages of postnatal ontogenesis. In a newborn calf, facets are formed on the basis of the foot of the neural arch (pediculus arcus vertebrae) and the corresponding facet on the vertebral body (fig. 29a: 3, 11). By the age of one year they are already formed and remain without changes until the age of six to seven years (PIN 4353-641 to -644). At the expense of proliferation at the age of three to four years, the foot of the neural arch begins to form small areas in the dorsal part of the anterior and posterior surfaces of the vertebral body (fig. 24b: 10, 11) and by six to seven years a suture is formed on the border between the neural arch foot and the vertebral body. The bodies of sacral vertebras do not fuse with each other until the age of seven to ten years (fig. 28). Ossification of the epiphyses of the sacral vertebras takes place in a similar way as and simultaneously with that of the thoracic and lumbar vertebras. The growth zones are situated on the cranial and caudal surfaces of the vertebral body and between the surface of the body and the bases of the neural arch feet. Between seven to ten and fifteen to seventeen years the ossified epiphyses of the sacral vertebras fuse with each other but remain unfused with the bodies of the corresponding vertebras. Initially persisting sutures between two adjacent vertebral epiphyses later disappear (PIN 4353-3722, fig. 28c, d: 14). The process of fusion of the vertebral bodies with each other and with their

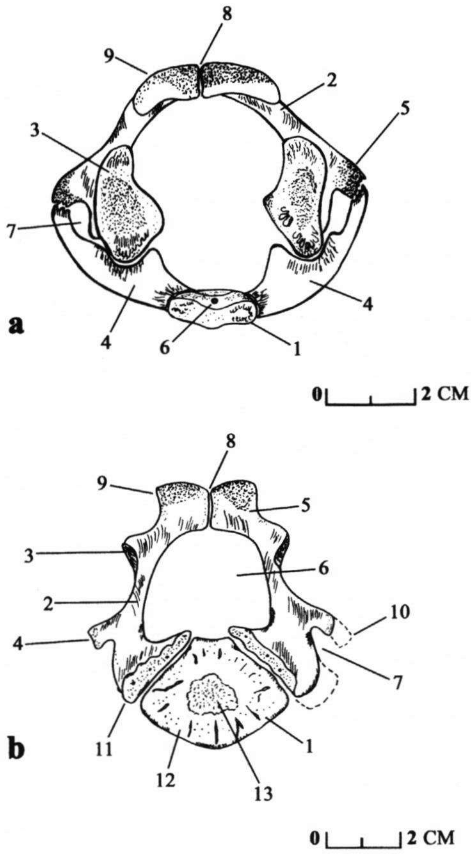

Fig. 30. Atlas (a), ZIN 34201(5), cranial surface, and axis (b), ZIN 3420(6), caudal surface, of a *M. primigenius* calf from Yamal Peninsula. a: 1 = ossification centre of ventral arch; 2 = dorsal arch; 3 = fovea articularis atlantis; 4 = ventral (cartilagineous) arch; 5 = process homologous to diaphysis; 6 = nutritive foramen; 7 = transverse foramen; 8 = suture between right and left halves of ossified dorsal arch; 9 = dorsal tuber. b: 1 = vertebral body; 2 = neural arch; 3 = caudal zygapophysis; 4 = dorsal transverse process; 5 = paired tuber of dorsal plate; 6 = vertebral foramen; 7 = transverse foramen; 8 = suture between right and left halves of neural arch; 9 = dorsal tuber; 10 = cartilagineous part of vertebra; 11 = rostro-caudal proliferation of neural arch legs that participate in shaping the caudal facies articularis; 12 = vertebral body surface covered by cartilago; 13 = same, not covered.

Atlas (a), ZIN 34201(5), vooraanzicht, en draaier (b), ZIN 3420(6), achteraanzicht, van een *M. primigenius* kalf van het schiereiland Yamal. a: 1 = beenvormingskern van onderste boog; 2 = bovenste boog; 3 = gewrichtskom; 4 = onderste (kraakbenige) boog; 5 = uitsteeksel homoloog aan een schacht; 6 = voedingskanaal; 7 = dwarskanaal; 8 = naad tussen linker en rechter helft van de verbeende bovenste boog; 9 = bovenste knobbel. b: 1 = wervellichaam; 2 = wervelboog; 3 = achterste zygapophyse; 4 = bovenste dwarsuitsteeksel; 5 = gepaarde knobbel van bovenste plaat; 6 = ruggemergskanaal; 7 = zijopening; 8 = naad tussen rechter en linker helft van wervelboog; 9 = bovenste knobbel; 10 = kraakbenig deel; 11 = uitbreiding van wervelboogwortels die deel uitmaken van het achterste gewrichtsvlak; 12 = oppervlak van wervellichaam, bedekt door kraakbeen; 13 = idem, niet bedekt.

epiphyses proceeds from the first sacral vertebrato the fourth. Fusion of vertebral bodies in other regions of the vertebral column, as observed in vertebras of one individual (PIN 4454), should be considered as age-related pathology.

The shape of the sacral vertebras differs from that of the vertebras of all other regions (fig. 28a, b): their postzygapophyses are oriented almost vertically (the surfaces are strongly inclined), the vertebral body is shallower (the ventral surface is flattened, the dorsal surface semicircular, with facets for the neural arch feet), the transverse process is situated at the base of the neural arch feet, and the feet are transversely widened. The neural arches become ossified most probably at the end of the prenatal ontogenesis (PIN 4353-2646 to -2649). By the age of six to seven years the lateral surfaces of the neural arches are widened and the arch foot bases fuse to form facets for the insertion of pelvic ligaments in adult animals (fig. 28c: 15). Evidently after the age of ten years, fusion of the neural arches takes place, beginning with the caudal articular facets of one vertebra and the cranial articular facets of the next one (PIN 4353-3722, figs. 28a, b, c: 5, 6, 7). In sexually mature individuals (over twenty?) transverse processes also fuse, so that the sacral bone consists of fused vertebral bodies and partially fused neural arches (figs. 28c, d). In old animals (over forty to forty-five years) the first sacral vertebra sometimes fuses with the last lumbar vertebra and, similarly, the last sacral vertebra may fuse with the first caudal one, so that the sacral bone may comprise five to six vertebrae (PIN 4454).

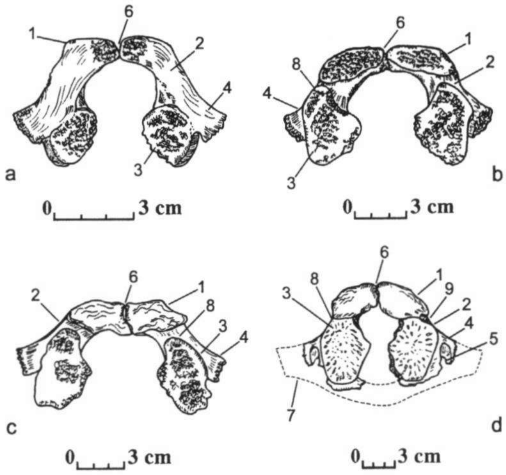

Fig. 31. Structure of the atlas of *M. primigenius* calves of different ages from Sevsk locality, Bryansk region, front view. a = PIN 4353-2614, newborn calf; b = PIN 4353-926, one-year-old calf; c =PIN 4353-503, 3 to 4-year-old calf; d = PIN 4353-664, 6 to 7-year-old individual. Scale bar: 3 cm. 1 = dorsal tuber; 2 = dorsal arch; 3 = fovea articularis atlantis; 4 = process homologous to diapophysis; 5 = transverse foramen; 6 = suture between right and left halves of ossified dorsal arch; 7 = reconstructed contour of ventral arch; 8 = dorsal outgrowth of articular fovea; 9 = canal between (8) and ventral outgrowth of (1).

Bouw van de atlas van *M. primigenius* kalveren van verschillende leeftijden, vindplaats Sevsk, regio Bryansk, vooraanzicht. a = PIN 4353-2614, pasgeboren kalf; b = PIN 4353-926, jaarling; c =PIN 4353-503, 3-4 jaar oud kalf; d = PIN 4353-664, 6-7 jaar oud kalf. Maatstreep 3 cm. 1 = bovenste knobbel; 2 = bovenste boog; 3 = gewrichtskom; 4 = uitsteeksel homoloog aan een schacht; 5 = dwarskanaal; 6 = naad tussen rechter en linker helft van verbeende bovenste boog; 7 = gereconstrueerde omtrek van onderste boog; 8 = uitgroei van gewrichtskom; 9 = kanaal tussen (8) en uitgroei van (1).

No data is available on the fusion of the sacral bone with the articular facets on the internal surface of the ilium. The ligaments attached to the facets on the lateral surfaces of the neural arches of the sacral vertebras do not become ossified. The facets are formed before the complete fusion of the sacral vertebras with each other (PIN 4353-3722).

The first cervical vertebra (atlas)

Morphology and formation process of the atlas differ from those of trunk vertebras in some important respects. At the beginning of postnatal ontogenesis the amount of cartilage in the atlas is relatively large. The ventral arch, which comprises a small ossification centre (homologous to the vertebral body), totally consists of cartilage. The growth zone between the left and right parts of the dorsal arch also comprises cartilage. To judge by the material available, the ventral arch to a large extent consists of cartilage until the age of six to seven years. The ossification process begins in the ossification centre and develops in lateral directions. The part of ventral arch that closes the transverse foramen ventrally and laterally is the last to become ossified. After the age of thirty the entire atlas is ossified. The epiphysis on the completely ossified process which is homologous to the diaphysis remains unfused. In females this epiphysis fuses earlier than in males, i.e., at the age of twenty-five(?) to thirty and thirty-five(?) to forty years respectively. Data on the dimensions of the ventral arch of the atlas in mammoth calves from Sevsk that represent the first six to seven years of postnatal ontogenesis is given in table 17.

Specimen ZIN 34201(4) is a complete atlas with a cartilaginous ventral arch. It belongs to the skeleton of a ca. one-month-old calf cadaver (fig. 30a) (Vereshchagin & Tikhonov, 1990; Hamada *et al.*, 1992; Kuzmina & Maschenko, 1999). The dorsal arch, the ossification centre of the ventral arch and the upper part of the process which is homologous to the diapophysis are ossified (fig. 30a: 1, 2, 5). The upper part of the process closes the transverse foramen dorsally. The medial part of the process (homologous to the parapophysis) remains cartilaginous. The surface of the ossification centre (20 x 1.5 mm) that protrudes from the cartilage of the ventral arch has one large (1.5 x 1 mm) and many small foramina (figs. 30a, b). The contact area between the cartilaginous and bony parts of the atlas is uneven, which is typical of a growth zone. The surface of the dorsal arch practically lacks materia compacta. A middle suture separates the left and right parts of the dorsal arch (fig. 30a: 8). The dorsal articular facet is slightly concave and separated from the rest of the surface of the dorsal arch. It constitutes the lower part of the dorsal arch and contacts immediately with the cartilage of the ventral arch (fig. 30a: 3).

In sp. PIN 4353-2614, the atlas of the skeleton of a newborn calf (fig. 31a), an ossified dorsal arch is preserved that exhibits the same morphological peculiarities as sp. ZIN 34201(4). At the stages of one year (PIN 4353-926), three to four years (PIN 4353-503), and six to seven years (PIN 4353-633), only the ossified dorsal arch is usually preserved. The degree of ossification is greater at each following stage (figs. 31b, c, d). It is possible that the ossification centre of the ventral arch begins to grow one month after birth or later. A gradual formation of a canal between the ventral outgrowth of the dorsal tubercle and the dorsal outgrowth of the fovea articularis atlantis (fig. 31: 8) takes place during ontogenesis. After six to seven years its walls are ossified almost completely (fig. 31d: 9) and only an insignificant part of the walls of the transverse foramen preserves cartilage (fig. 31d: 5).

The second cervical vertebra (axis)

At the begining of postnatal ontogenesis, the formation process of the body of the neural arch of the axis looks like those found in the trunk vertebras rather than like that in the atlas. At this ontogenetic stage it consists of an ossified dorsal arch (which comprises two parts that come into contact in the region of the dorsal tubercle) and a vertebral body (fig. 30b). The transverse process is formed by two processes: an ossified dorsal transverse process (by the beginning of the postnatal stage) and a cartilaginous ventral process (fig. 30b: 10). These processes close to shape the transverse foramen. The growth zones of the axis are situated between the two halves of the vertebral arch and between the vertebral arch feet and the vertebral body. At the beginning of postnatal ontogenesis, the latter itself is an ossification centre of the growth zone. The proximal part of the vertebral body with the facies articularis superior is formed at the expense of the outgrowth of the feet of the vertebral arch. The dimensions of axes of mammoth calves from Sevsk are represented in table 18.

In sp. ZIN 34201(6), the axis of an approximately one-month-old calf cadaver (fig. 30b), the cartilaginous parts are preserved. The neural arch and the vertebral body are ossified. Cartilage remains in the growth zone between the right and left parts of the neural arch (fig. 30b: 8) and between the feet of the vertebral arch and the body of the vertebra. The non-ossified epiphysis on the caudal surface of the vertebral body is ring-shaped. The ossified and non-ossified parts contribute equally to the formation of the transverse process (fig. 30b: 4, 7, 10). The outgrowth of the cartilaginous part of the foot base is possibly homologous to a rudimentary rib. The postero-anterior diameter of the neural arch foot is greater than the same diameter of the vertebral body. The foot of the vertebral arch forms the proximal part of the cranial articular facet on the cranial surface of the vertebral body, and the distal part of the caudal articular facet on the caudal surface (fig. 30b: 11). The vertebral body at this stage is represented by an ossification centre which is almost completely embedded in cartilage. Only the central region of its anterior and posterior surfaces is free of cartilage (fig. 30b: 12, 13). These regions exhibit the porous uneven structure of the centre with numerous tiny nutritive foramina.

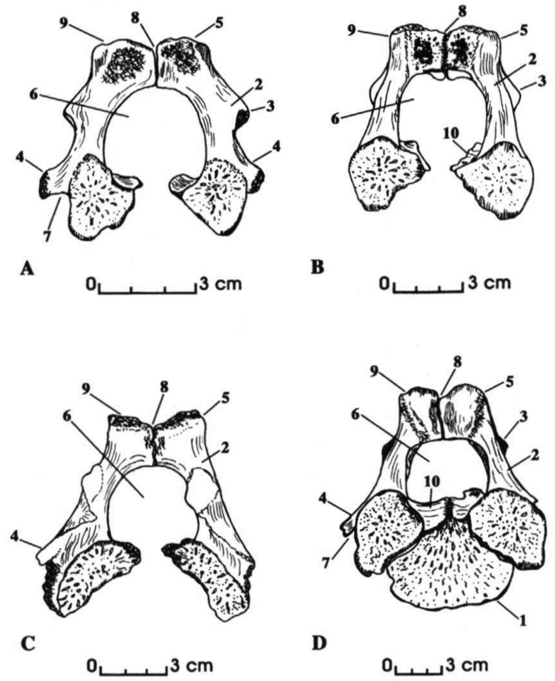

Fig. 32. Structure of the axis in *M. primigenius* calves of different ages, Sevsk locality, Bryansk region: a = PIN 4353-2493, newborn calf, posterior view; b = PIN 4353-922, one-year-old calf, front view; c = PIN 4353-503, 3- to 4-year-old calf, front view; d = PIN 4353-664, 6- to 7-year-old individual, front view. Sale bar: 3 cm. 1 = vertebral body; 2 = neural arch; 3 = caudal zygapophysis; 4 = dorsal transverse process; 5 = paired tuber of dorsal plate; 6 = vertebral foramen; 7 = transverse foramen; 8 = suture between right and left halves of neural arch; 9 = dorsal tuber; 10 = rostro-caudal proliferation of neural arch legs that participate in shaping caudal facies articularis

Bouw van de draaier van *M. primigenius* kalveren van verschillende leeftijden, vindplaats Sevsk, regio Bryansk: a = PIN 4353-2493, pasgeboren kalf, achteraanzicht; b = PIN 4353-922, jaarling, vooraanzicht; c = PIN 4353-503, 3-4 jaar oud kalf, vooraanzicht; d = PIN 4353-664, 6-7 jaar oud individu, vooraanzicht. Maatstreep 3 cm. 1 = wervellichaam; 2 = wervelboog; 3 = achterste zygapophyse; 4 = bovenste dwarsuitsteeksel; 5 = gepaarde knobbels van bovenste plaat; 6 = ruggemergskanaal; 7 = dwarskanaal; 8 = naad tussen rechter en linker helft van de wervelboog; 9 = bovenste knobbel; 10 = uitgroei van wortels van wervelboog die deel uitmaken van de achterste gewrichtsvlakte.

The neural arch of the axis of a newborn calf is subdivided into two parts separated by a suture between two paired tubercles of the dorsal plate (fig. 32a: 2, 5, 8; the vertebral body is a separate specimen, PIN 4353-2422, and is not depicted). The materia compacta is absent on the entire surface of the proximal part of the axis. It is present on the lateral surfaces of the neural arches, where its thickness reaches 1 mm. The caudal articular facets on postzygapophyses are incompletely formed. The antero-posterior diameter of the vertebral body (9 mm) is smaller than the same diameter of the bases of the neural arch feet (15 mm). There is practically no materia compacta on the vertebral body. The body of the axis at this stage is formed to lesser extent than the trunk vertebras of the same skeleton.

The bodies of the axes in sp. PIN 4353-925, a one-year-old calf, and sp. PIN 4353-504, a three to four-year-old calf, are not preserved (fig. 32b, c). Their neural arches are morphologically similar. The regions of the facet surfaces of the postzygapophyses and the ossified part of the transverse process are formed in a similar way as during early postnatal ontogenesis (PIN 4353-2495). The facets for the feet of the vertebral arch are clearly delimited. Both halves of the neural arch close tightly, the suture between them is distinct (fig. 32b: 5). In the axis of a six- to seven-year-old individual (PIN 4353-664, neural arch; PIN 4353-670, vertebral body) the parts of the neural arch are fused, and the width of the suture between them is 3-4 mm (fig. 32d: 8). The materia compacta is well developed on the surfaces of the paired tubercles of the dorsal plate, and similar to that on the lateral surface of the neural arch, but it is less thick on the tubercles (about 1 mm). During the previous ontogenetic stages no materia compacta was formed in these regions. The facets of the zygapophyses are completely formed. The transverse foramen is largely (for about three quarters) formed by the transverse process. The horizontal outgrowths of the feet of the neural arch proliferate medially to fuse with each other (fig. 32d: 10). The feet of the vertebral arch play a major role in the formation of the cranial and caudal articular facets. The relief of the entire region of the anterior and posterior surfaces suggests that the vertebral body is still functioning as an ossification centre and is embedded in the growth zone (fig. 32d: 1). The antero-posterior diameter of the vertebral body (30 mm) is smaller than the same diameter at the bases of the feet of the vertebral arch (38 mm). In comparison with the trunk vertebras, the formation process of the vertebral body in the axis develops with considerable retardation.

Ontogenetic changes in teeth and skeleton

Age-related changes and periods of ontogenesis

Isolated bones and teeth of mammoth calves were compared to those in calf skeletons from the Sevsk locality (newborn, one-year-old, three- to four-year-old, and six- to seven-year-old calves). This data was then compared to morphological data on adult individuals of *M. primigenius*, and the result suggests a subdivision of the ontogenesis of the species into three periods. These periods are not completely correlated to the periods traditionally accepted for the ontogenesis of other mammals, yet seem to be adequately grounded, for each one is specified by well-expressed morphological changes.

The first stage the mammoth passed was that of prenatal development and early childhood. It ended at the end of the first year, during which intense growth and substantial morphological and physiological changes occurred. The second was that of childhood, which was likewise characterized by a high growth speed. The third stage then comprised early puberty and puberty. This subdivision is certainly relative, but it reflects very important intervals, during which physiological changes occurred that can be traced in morphological changes in skeletal material.

Three very important periods of ontogenetic changes in skeletal morphology are thus observed. The first period covers the interval from the last prenatal stages up to one year of postnatal development. Notwithstanding the importance of the sharp difference between prenatal and postnatal ontogenesis, the major morphological changes in the structures of the dental system, the skull, the lower jaw and the postcranial skeleton, as they are known to have taken place in the mammoth, began within the prenatal and ended within the early postnatal stage. The concluding stages of prenatal ontogenesis can thus be grouped with the early postnatal ontogenesis. The second stage covered the period from one year to six or seven years, the third one lasted from the age of six or seven years until the end of the animal's life.

Basic morphological features of individual developmental stages

On the basis of data on morphological changes of separate bones of *M. primigenius* and the time intervals during which they took place, the following description of the three main developmental stages is proposed.

During the first period, morphological changes are mostly qualitative. They are connected with the rapid formation of both already existing as well as new bony structures of the skeleton and the first three tooth generations. Quantitative changes, expressed in growth of bones and changes of ratios between them also occur during this period. However, qualitative changes are dominant.

In the skull, the beginning of the first period is marked by the disappearance of cartilage in the sutures between the parietal, occipital and frontal bones and the first appearance of air cells on the inner surface of the frontal bones. The bones mentioned above are not completely fused and some cartilage tissue is still preserved. By the end of the first period, the ossification of the nasal bones ends, except for the nasal protrusion.

During the first stage of individual development, completely formed dp2 alveoli in the upper and lower jaws exist. The teeth of the next generations (dp3 - M3), do not have completely formed alveoli. From dp2 to M3, the alveolar wall between the teeth of subsequent generations becomes less expressed.

The alveolus of the deciduous tusk (di) is initially formed by the premaxillary only. In the process of formation of the permanent tusks (I), the alveolus gradually becomes a joint structure of the premaxillar and maxillar bones. During this stage the proportions of the alveolar and brain regions of the skull change only slightly, for the formation of the permanent tusk is not finished by the end of this stage and the tusk remains inside the alveolus.

During the first stage, the proportions of the lower jaw symphysis change, its relative length decreases and the mental process is formed. The angle between the interalveolar crest and the longitudinal axis of the horizontal part of the mandibular ramus increases following the increase in depth of the latter. Before the end of the first year, the symphyseal suture between the right and the left horizontal branches disappears and the completed dp_2 alveolus resorbs.

The compact layer is formed on the long bones and all vertebras. The bases of the neural arches and the dorsal surfaces of the vertebral centres are formed at their contact level. The dorsal arch is solidified only on the atlas. By the beginning of this stage, the compact layer of the long bones is already formed on the middle part of the shaft and on the formative processes at the ends. By the end of the first stage, the formation of the shaft ends shaft is completed and the growth zones are reduced to the area between the shaft ends and the forming epiphyses. This conclusion is based on the disappearance (within the period of the second to the fifth postnatal month) of the additional nutritional openings and grooves formed by the openings at the

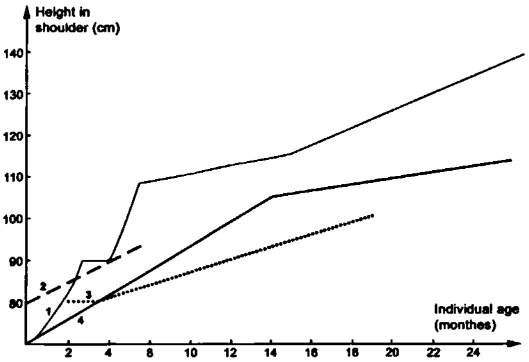

Fig. 33. Growth dynamics of calves of *M. primigenius* and *Elephas maximus* during the first two years of life. 1, 2, 3 = *E. maximus* calves from different zoos (data Reuther, 1969); 4 = mammoth calves from Sevsk locality, Bryansk region: PIN 4353-2619 to -2704, two weeks old; PIN 4353-871 to -986, 12 months old; PIN 4353-447 to -585, 3-4 years old

Groeicurves van kalveren van *M. primigenius* en de Indische olifant *E. maximus* gedurende de eerste twee levensjaren. 1, 2, 3 = *E. maximus* kalveren uit verschillende dierentuinen (gegevens uit Reuther, 1969); 4 = mammoetkalveren uit Sevsk: PIN 4353-2619 tot -2704, twee weken oud; PIN 4353-871 tot -986, jaarling; PIN 4353-447 tot -585, 3-4 jaar oud. Vertikaal: shouderhoogte in cm, horizontaal: leeftijd in maanden

shaft ends, accompanied by a relatively rapid increase in length. At this ontogenetic stage, the epiphyses are represented by paired (humerus, femur) or single (ulna, radius) small oval ossification centres. Simultaneously with the formation of the compact layer on the vertebras, the formation of the cranial and caudal articulatory facets as well as that of the articulatory notches for the ribs on the vertebral bodies takes place.

During the second period (between one year and six to seven years of age) the formation of many structures of the dental system, the skull, the lower jaw, and the postcranial skeleton that started during the previous stage continues and ends. The second stage includes the final stage of childhood and ends long before the end of early puberty. Qualitative and quantitative changes in skeletal morphology are represented equally, but quantitative changes are dominant by the end of the second stage.

The proportions of the ventral (facial) and dorsal part of the skull and the lower jaw change considerably, and so do the proportions of parts of long bones. By the end of this stage, the morphology of the skull, the lower jaw, and the postcranium in general acquires the features of adults. Differences related to sexual dimorphism are not very well expressed during this period. Near the end of this stage, these differences appear in an assemblage of features connected with the growth of tusks and a more rapid change of dimensions and proportions of the alveolar part of the skull in males as well as in females. Differences between males and females are either absent or insignificant.

Changes in the skull structure in *M. primigenius* during the second ontogenetic stage are expressed in the proportions between its facial and dorsal parts. The increased relative dimensions of the skull are caused by the increase in tooth size, particularly of the third generation teeth. Similarly, the change of proportions of the palate and the alveolar part of the skull is related to the growth of the permanent tusks (I).

During this stage, the part of the tusks that protrudes beyond the alveolar border becomes longer than the part contained within the alveolus. The formation of the permanent tusks finishes most probably by the age of two years. By the age of six to seven years, wear of the tusk tip causes loss of the initial trisegmented structure and the cross sections of the tusk approach a circle. The tusk of a young mammoth near the end of the second stage of ontogenesis does practically not differ from the tusks of the adult. Further changes in shape are connected with wear of the tusk tip, which is on its turn determined by individual peculiarities in the ways the tusks are used and by the change of the pulp cavity depth. The relative depth of the pulp cavity diminishes during postnatal ontogenesis. By the end of life the decrease of the pulp cavity depth becomes absolute.

The shape of the occipital, frontal and parietal bones changes according to the increase in skull height. Air cavities of the adult type are formed in the frontal and parietal bones. Simultaneously, skull bones fuse and sutures between them disappear. By the age of seven, the cerebral part of the skull is completely formed and resembles that in adult individuals. Traces of sutures may persist only between paired occipital bones. Similarly, the proportions of the cerebral and facial parts are approaching those of adults. The nasal bones are completely ossified, including the nasal protrusion.

Morphological changes in the lower jaw pass two stages. The first stage lasts until dp4 starts being worn (up to two or two and a half years), and the second one from two and a half to three years until six or seven years, when dp4 is fully functional. The end of this stage is marked initial wear of M1. The first stage is not accompanied by any significant change in the proportions of the lower jaw: the ratio of the symphyseal part to the horizontal branch changes very little. With the beginning of the second stage this relation changes. When big third generation teeth (dp4) are formed at the age of two and a half to three years, the proportions become similar to those observed in adults, at the expense of growth of the horizontal branch. The ascending branch becomes more vertical. The change in its orientation is best illustrated by the change of location of the angle of the lower jaw and the vertical orientation of the posterior edge of the ascending branch. The symphyseal part shows proportions similar to those found in adult individuals. There is but little further change in the shape of the mental process, and obviously its further growth is influenced most by the sex to which an individual belongs.

During the second ontogenetic period, the formation of the compact layer over the shaft surface of the long bones is completed. The growing ossification centres reciprocally fuse in femur and humerus. The single ossification centres in the ulna and tibia grow to form the shaft, so that the ossified non-fused epiphyses are formed independently of the shaft, with well-expressed epiphyseal sutures. By this time, the remaining portion of cartilage in the proximal and distal parts of the long bones becomes insignificant. The relations between portions in the different parts of the long bones apparently do not change after the age of three to four years has been reached.

On the vertebras, the formation of the compact layer continues on the neural arches and the centres, particularly in the middle of the dorsal surface of the latter. At the age of three to four years, the compact layer on the surface of the vertebral centres is similar to that in adult individuals. The bases of the neural arch pedicles extend in rostro-caudal and medial direction. From this time on, they form small areas on the dorsal part of the anterior and posterior surfaces of the centre. The neural arch remains unfused with the centre. The formation of the spinous process and the transverse processes continues at the expense of the non-ossified apophyses at their ends. The anterior and posterior epiphyses of the centre remain non-ossified. The dorsal arch of the atlas remains cartilagenous, and the part that forms a process which is homologous to the transverse process, is reduced during the entire second period of ontogenesis.

During the third ontogenetic period, which begins at six to seven years and continues until maturity, quantitative changes in all previously formed skeletal structures and in the dentition prevail. Only a few changes, which are completed during this period, are qualitative.

The formation of all bones of the skull, the lower jaw and the postcranial skeleton ends. The only exception are the teeth of the fifth and the sixth generations, the formation of which continues during a long time interval. The process, however, begins and continues chiefly during the second ontogenetic period.

During the third stage, the growth speed slows considerably. In *M. primigenius* females it finishes by the age of nineteen to twenty years, and by thirty to thirty-five years in males.

Changes in the morphology of the facial part of the skull predominantly consist of the change in the proportions of the facial and cerebral parts of the skull and the growth of the tusks. The overall dimensions of the alveolar part increase considerably. No structural changes in permanent tusks occur, but their size and weight increases both. The relative size reduction of the pulp cavity continues. The formation of the temporal lines on the occipital bones of the cerebral part of the skull also continues. These changes are connected first of all with the sex of the individual but may vary greatly both in males and females. The same is valid for the size and shape of the nasal bone process, which is larger in males.

The change in proportions of the lower jaw is relatively insignificant. The growth of the horizontal branch practically stops because of insignificant differences in size between the teeth of the M1 to M3 generations. The overall dimensions of the lower jaw evidently grow gradually until the age of fifteen to seventeen years. At the end of the ontogenesis, when the last generation tooth (M3) is more than one third worn, the absolute decrease in depth of the horizontal branch begins.

In females, some growth zones in the long bones disappear by the age of fifteen to seventeen years. After the epiphyses are completely formed, they fuse with the shaft, and the sutures are completely obliterated. The formation of non-ossified apophyses and epiphyses of the vertebral centres continues. Their ossification begins at the age of twelve to seventeen years and is initially incomplete. Their fusion, however, is completed much later, not before twenty years at least. After six to seven years, the ventral arch of the atlas has ossified completely, and the ossification of other cartilaginous parts continues. After fifteen to seventeen years, the neural arches and centres of the sacral vertebras fuse. After the age of thirty to forty, a complete fusion of two or three vertebras in the thoracic and lumbar regions may take place.

Growth peculiarities during the first years of life

Individual age, sex and size variability in *M. primigenius* are correlated. In spite of the fact that features of sexual dimorphism in the mammoth appear only at the beginning of puberty, size differences and individual variability are already present during the earliest stages. Population-bound differences indirectly affect variability. Serial skeletal material of mammoth calves allow one to observe peculiarities of mammoth growth in the form of changes in size of postcranial bones during different life periods. Differences in size between mammoth males and females, similar to those in modern elephants, as well as differences in the time of fusion of the epiphyses of long bones have been extensively studied (Baryshnikov *et al.*, 1977; Haynes, 1991; Averianov, 1996; Lister, 1999). On the other hand, no data on the growth of mammoth calves during their first years had been available before the excavation of the Sevsk material, and the only criteria for the determination of the individual age of mammoth calves were based on their dentition. Some arbitrary cases of individual age determination are considered below.

A body of a mammoth calf from the Yamal Peninsula (specimen ZIN 34201) poses a complicated problem for individual age determination (Tikhonov & Khrabry, 1989; Vereshchagin & Tikhonov, 1990; Hamada *et*

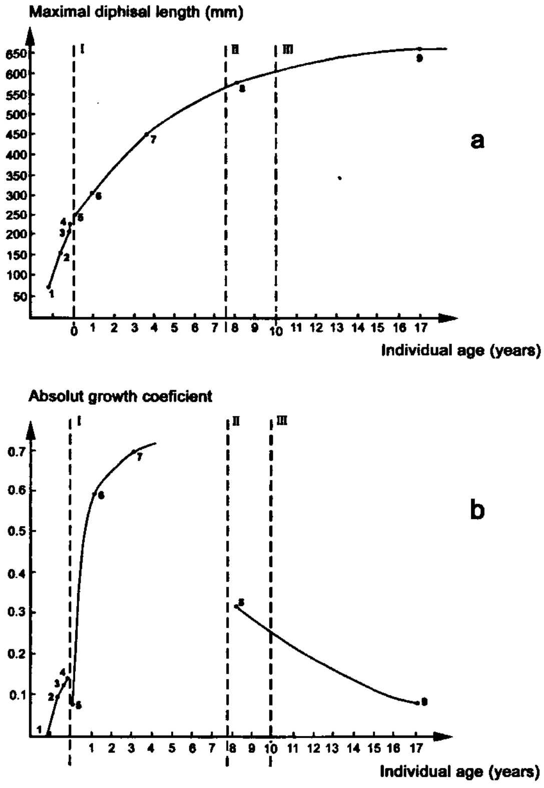

Fig. 34. Dimensional changes in the humerus and femur of *M. primigenius* during prenatal (from 9-10 to 20-21 months of gestation) and postnatal life (from birth to 16-17 years of age). a = absolute growth of the femur shaft during ontogenesis; b = absolute growth of femur depending on individual age, marked as in (a); c = absolute growth of humerus during ontogenesis; d = absolute growth of the humerus shaft during ontogenesis, marked as (c). I = at birth; II = beginning of maturation; III = at puberty. Estimated length of gestation in *M. primigenius* is approximately 22-23 months, the beginning of maturation is at 7-10 years of age, puberty at 10-11 years of ages (females). 1 = PIN 4353-3243; 2 = ZIN 31740(6) in a, b and ZIN 34386(3) in b, c; 3 = IAE, Sh-77, 5b; 4. ZIN 34419(10); 5. PIN 4353-2698; 6. PIN 4353-552; 7. PIN 4353-419; 8. PIN 4353-270; 9. PIN 4353-452

Lengte-toename in opperarm en dijbeen van *M. primigenius* gedurende prenataal (van 9-10 tot 20-21 maanden dracht) en postnataal leven (van geboorte tot 16-17 jaar). a = absolute groei van de dijbeenschacht gedurende de groeiperiode; b = absolute groei van het dijbeen afhankelijk van individuele leeftijd, als gegeven in (a); c = absolute groei van de opperarm gedurende de groeiperiode; d = absolute groei van de opperarmschacht gedurende de groeiperiode, als gegeven in (c). 1 = PIN 4353-3243; 2 = ZIN 31740(6) in a, b en ZIN 34386(3) in b, c; 3 = IAE, Sh-77, 5b; 4. ZIN 34419(10); 5. PIN 4353-2698; 6. PIN 4353-552; 7. PIN 4353-419; 8. PIN 4353-270; 9. PIN 4353-452; I = geboorte; II = begin rijping; III = puberteit. Geschatte lengte van de dracht in *M. primigenius* is ongeveer 22-23 maanden; het begin van de rijping is op een leeftijd van 7-10 jaar, en puberteit op een leeftijd van 10-11 jaar (vrouwtjes). Voor nummers, zie Engelstalig onderschrift

al., 1992; Kuzmina, 1999; Kuzmina & Maschenko, 1999). To judge by the stage of formation and wear of both dp2, the individual age may be determined as one month. The teeth are covered with cement and their four anterior plates are touched by wear. Data on the beginning of wear of dp2 in calves of modern *L. africana* testifies that the process begins simultaneously with the eruption of the tooth from the soft tissues of the gum as the calf tries to taste the food of the adults, which begins two weeks after birth (Sikes, 1966; Douglas-Hamilton & Douglas-Hamilton, 1975; Shoshani *et al.*, 1990). Comparable data exists on the beginning of wear in dp2 of *E. maximus* (Roth & Shoshani, 1988). It is highly probable that this data may be extrapolated to *M. primigenius* inasmuch as wear in dp2 begins before the completion of the crown formation, as was illustrated in the section dedicated to the formation of the first tooth generation. A small body size of the calf allows the assumption that the tooth began to function at the same time as, or, more probably, earlier than in modern elephants.

The body size of the Yamal calf is smaller than that of the two-weeks-old calf from the Sevsk locality (table 19). Some important differences exist between the body proportions of the Yamal calf and those of the Magadan calf (specimen ZIN C 70188) (Vereshchagin, 1989). It appears that the Magadan calf has a shorter body and longer legs than the Yamal calf (Kuzmina, 1999). However, comparison with the dimensions of the long bones of a newborn calf from Sevsk reveals less significant differences. Data on cadavers and complete skeletons of mammoth calves suggests that *M. primigenius* calves, similar to modern elephants, had a relatively short and high body. On the contrary, the body height of the Yamal calf is smaller than its length (Tikhonov & Khrabry, 1989; Vereshchagin & Tikhonov, 1990). The extremities of the Yamal calf cadaver appear to be relatively shorter than might be expected if one considers the proportions of other calf cadavers and skeletons. Such proportions are close to those of elephant foetusses. Even during the last prenatal months, modern elephant foetusses show a relatively long body in comparison with their height (Ananthanayana & Mariappa, 1950; Frade, 1955; Beyer *et al.*, 1990). This fact, combined with the small body size, gave rise to the suggestion that the Yamal specimen is a cadaver of an unborn calf. However, after tomographic study of the lungs this hypothesis was rejected: the lungs showed traces of normal respiration (Hamada *et al.*, 1992).

The small size of the Yamal calf and its foetal proportions probably result from an individual developmental deviation, i.e., from a premature birth. The effect of nutrition on the growth speed can be seen in a slow growth in the case of malnutrition, as well as in a retardation of bone formation and a late fusion of sutures, as is known for other mammals (Chervinsky, 1949; Lister, 1999). The small size of the Yamal calf may be an indication of a first birth given by a mammoth cow. This peculiarity is typical both of *M. primigenius* and modern of elephants. The first calf in *L. africana* is known to be 15% smaller than all subsequent ones, and deaths at birth or soon after birth are also more frequent for first births in this species (Douglas-Hamilton & Douglas-Hamilton, 1975).

Another example of arbitrary identification of individual age is provided by the skull and lower jaw of a mammoth embryo (ZIN 31661) from the Late Paleolithic site at Mal'ta (Irkutsk region, West Siberia) (fig 4; photo 1). Garrutt's (1999) identification of the specimen as a newborn calf is based on its unworn dp2. However, the dimensions of the specimen are about 30% smaller than those of a newborn from Sevsk (PIN 4353-2614) with dp2 at the same stage of formation (table 6). There are indications that specimen ZIN 31661 represents an earlier ontogenetic stage: Firstly, the dp3 formation is less advanced, and its anterior plates are preserved in the skull. Secondly, the dp2 and dp3 in this specimen sit deeper in their alveoli than is the case in the specimen from Sevsk. In ZIN 31661, the masticatory surfaces protrude only slightly above the edge of the alveolar bone. These peculiarities allow the identification of ZIN 31661 as a foetus in the final prenatal stage, and not as a newborn calf.

A certain degree of impreciseness arises when the individual age determination scale, which was developed on the basis of tooth generation stages in modern elephants, is applied to mammoths. The data on the skeletons of mammoth calves from Sevsk, in which minute postcranial details as well as peculiarities of the tooth development stages can be observed, permits one to calibrate the scale better, because postcranial data provides hitherto unknown information on the individual development of *M. primigenius.*

A series of skeletons of mammoth calves of different ages from Sevsk (radiocarbon-dated to 13,950 ± 70 years) provided data on the growth dynamics of calves that belong to a group of late representatives of the species *M. primigenius* from the Russian Plain. The morphological similarity with the Late Pleistocene mammoth calves from Siberia suggests that the growth regularities deduced from the Sevsk material were common in representatives of different populations of *M. primigenius.*

The skeletal dimensions of two mammoth calves from Sevsk, no more than one to two weeks old (PIN 4353-2614 to -2717, and PIN 4353-1222, -1233, -1558 to -1563) indicate that the body height of a newborn mammoth calf varied within the limits of 700 to 800 mm (this is a mammoth form from the end of the Late Pleistocene). Both individuals are characterized by the presence of unworn dp2 (the first tooth generation).

The greatest height in the thoracic region of the vertebral column of a mounted skeleton of a larger mammoth calf from Sevsk is 750 mm (PIN 4353-2619 to -2704). The combined length of humerus, ulna and scapula of this individual is 575 mm; humerus and ulna together measure 360-370 mm. The combined length of femur and tibia is 390-430 mm (table 19). In the reconstruction of the body height, the contribution of the non-preserved cartilaginous parts in the growth zones of the long bones, as well as of the bones of the feet and hands was taken into consideration, as was the thickness of the hide on the soles (Eales, 1926; Vereshchagin, 1981). Inclusion of these contributions in the calculation brings the total reconstructed height of this individual to 790-810 mm. The dimensions of the bones of another (incomplete) skeleton from Sevsk (PIN 4353-1222, -1233, -1558 to -1563; Maschenko, 1992) are smaller. The height of the mounted skeleton at the highest point is about 710 mm. The body height of this calf was determined according to the above-mentioned method, and is 730-750 mm. As the individual age of both calves was one to two weeks, a certain increase in body size after birth must be taken into consideration and, consequently, the height of the newborn must have been somewhat smaller, approximately 700 mm.

In *E. maximus* the body height of the newborn calves varies between 760 and 950 mm (Stanley, 1943). This data indicates that the body dimensions of newborn mammoths are smaller than those of newborn modern Asiatic elephants. In modern *L. africana* the body dimensions of newborns differ from *M. primigenius* even more. The largest newborn calves of this species are 1090 mm high (Laws *et al.*, 1975). The size of newborn calves in modern African elephants varies from 880 to 1090 mm (Lee & Moss, 1995).

On the basis of data on a series of calves' skeletons of different ages from Sevsk it is now possible to estimate the growth dynamics of the species during the first years of life. With regard to the first year, the estimation is based on two skeletons of newborn calves and a skeleton of a one-year-old calf (PIN 4353-21 to -217, -507, -570 to -573, -709 to -716, -810, -817, -873 to -880, -884 to -887, -894 to -965). The age determination of the latter was based on the stage of formation and wear of dp^2 (photo 6). The height of the mounted skeleton of this individual is about 1100 mm at the highest point of the back. The reconstructed body height of the individual, with non-preserved cartilaginous parts and hide thickness taken into account, is estimated between 1160 and 1180 mm. Such a height corresponds with, or is a little smaller than the mean values of body height in *L. africana* and *E. maximus* calves of the same individual age (Hyndley, 1934, Stanley, 1943, Laws, 1966; Sikes, 1967; Douglas-Hamilton, 1976).

If the height of the Sevsk newborn calf is fixed on 800 mm, the extra height gained during the first year is about 350 mm in this population. If the estimated height of a newborn calf is 700 mm, the growth within one year is still greater, i.e., 450 mm.

During the second and the third year of life, the growth speed slows down a little. Indicative of the body height surplus at this stage is a skeleton of a Sevsk mammoth calf of three to four years (PIN 4353-447 to -585). Its dp4 is in wear, and, based on the degree of wear with seven plates remaining, it's very likely that M1 is already in initial wear, though this cannot be proved, as only bases of M1 plates remain in the specimen. The height as determined by measurements of the mounted skeleton at the highest point of the back is 1350-1370 mm. Comparison with the height of a newborn shows that the surplus during the second and the third year of life is about 200 mm. In *E. maximus*, the surplus during the first year may reach 450 mm (for zoo animals), but the mean value is 250-300 mm (Reuther, 1969). In *L. africana,* the height surplus between the age of one and a half and three and a half years amounts to 410 mm (for zoo animals) (Johnson & Buss, 1965). After the first year of life the body growth of mammoth calves therefore slowed down in comparison with that of modern elephant calves (fig. 33).

This peculiarity of individual development in *M. primigenius* is accounted for by the ecology of the species, which differs radically from the ecology of modern elephants. The Late Pleistocene mammoths were adapted to a life in cold climatic conditions, which includes lengthy winters. The only explanation of rapid growth during the first year of life is the necessity for a calf to survive in winter. Towards the end of the first year the calf should reach the largest size possible and become strong enough to move together with the family group along their winter routes. On the one hand, the social structure of the group and the physical state of the members played a particularly important role for survival in wintertime. On the other hand, their size should help the animals in their intraspecific competition for food, which was scarce in this season. Another indirect cause of rapid growth during the first year of life was the unavoidable increase of the predator pressure on herbivores in wintertime, which is described very well for modern communities of large mammals that inhabit moderate and circumpolar regions.

Both the analysis of the relative growth speed of long bones (humerus, ulna) in *M. primigenius,* and the absolute growth diagram show different speeds at different periods of individual development. The surplus estimation for different time spans reveals several stages in postnatal growth that correspond with different periods of physical development similar to those in modern elephants and in the majority of mammals (Schmalhausen, 1935). Birth is a pivotal point of ontogenesis combined with major physiological restructuring of the organism, which is reflected in the picture of growth. The growth curve of mammals usually displays an abrupt break at this point. The growth curve of the femur of *M. primigenius* (fig. 34a) has practically no break at the point of birth, which may be accounted for by insufficient data and very large time intervals between two neighbouring values. This renders the 'resolution' of the diagram rather low. The absence of a break in the humerus growth curve may be accounted for in a similar way (fig. 34c).

In modern mammals, the empirical growth curves usually have a second break, which corresponds to the beginning of the maturation period. In similar curves constructed for humerus and femur growth in *M. primigenius,* the second break cannot be observed either (fig. 34c), because growth diagrams based on linear measurements only may not be sensitive to boundaries between the periods.

In *M. primigenius* the boundaries between the different periods of physiological development can be observed in the diagrams that reflect the absolute surplus during a certain time interval (via indices: fig. 31b, 31d). The absolute surplus formula is:

$A=[(L2-L1)/(T2-T1)]/100\%$ (Schmalhausen, 1935).

In this formula, the length surplus of the shafts of humerus and femur during a certain time interval (in months) is expressed as percentage of the shaft length. In this case, the femoral length (L1) is the shaft length of specimen PIN 4353-3243, and the humeral length (L2) is the shaft length of specimen PIN 4353-3242. For the calculation of values, the time of prenatal shaft development may be taken to be nine months, as in modern elephants (table 20).

In the diagrams, the boundary between the prenatal and postnatal periods is marked by a well-expressed break. As in other mammals, the prenatal ontogenesis is characterized by the greatest absolute growth speed. The diagrams illustrate the length increase of humerus and femur. During the postnatal ontogenesis, the speed remains relatively high in the beginning, especially during the first year of life. This was also observed with regard to the increase in body height during this period. Breaks in the diagrams correspond to qualitative changes in the process of individual development connected with important physiological changes. The first break in the curve corresponds to birth, the second one approximately corresponds to the beginning of maturation. According to this data, maturation in *M. primigenius* begins at the age of eight to ten years. Both diagrams reflect a considerable deceleration of growth during this time. A still greater deceleration occurs by the age of fifteen to seventeen years. In *E. maximus,* the deceleration of growth at this age is connected with the first pregnancy and the feeding of a calf (Stanley, 1943).

The diagram based on the material of females from Sevsk shows that after the age of seventeen to twenty years the growth of *M. primigenius* females practically stops. A particularly abrupt deceleration of growth is observed earlier, after twelve to thirteen years, which may correspond to first births given by the Sevsk females.

There is no data on growth peculiarities of males from Sevsk. However, males of *M. primigenius* from a number of Siberian sites show a continued growth after the age of thirty (Zalensky, 1903; Haynes, 1991; Averianov, 1996a; Tikhonov, 1997; Lister, 1999). Continuing growth of males, in contrast to females, was also indicated in American mammoths, *M. columbi* (Agenbroad, 1994; Saunders, 1999). This data suggests that in Sevsk males, too, the growth period was longer than in females. The only fragmentary skeleton that is attributed to a male allows the suggestion that at the age of forty-seven to fifty (14 posterior plates remaining in M^3 and M_3) the growth of Sevsk males stopped.

During the first two years of life, females of *E. maximus* show the same growth speed as males (Stanley, 1943; Hundley, 1934). Between the age of three and ten years, the mean yearly surplus of body height in males is 8 cm and in females 6 cm. From eleven to seventeen years, the yearly surplus of height in females becomes irregular (because of pregnancies) and by the age of twenty-four, females don't grow anymore in size, though body weight increases insignificantly. In some cases a growth stop at the age of twenty-four was registered also in males of this species that were kept in captivity. On average, according to observations of *E. maximus* males in captivity, they continue to grow until thirty to thirty-five years (Stanley, 1943).

A considerable difference between males and females in the duration of growth is known in modern African elephants. Continuing growth in males of *L. africana* was observed after the age of thirty-five (Roth, 1984; Laws *et al.*, 1975; Haynes, 1991). During the first five years of life, the body heigth in males of this species increases from 90-95 cm to 160-170 cm, and in females from 80-90 cm to 150-160 cm. Much greater differences are observed after the age of ten years. The average height of a male of this age is two metres (the average growth speed is 7-10 cm a year), and that of a female is 185-190 cm (with an average growth speed of 5-7 cm a year). Males of *L. africana* continue to grow 4-7 cm a year until the age of thirty, whereas growth in females practically stops before that time (Lee & Moss, 1995).

A more lengthy period of deceleration may be observed in diagrams that present the absolute length surplus of humerus and femur based on serial material similar to that from Sevsk, but pertaining to males of *M. primigenius*. Unlike diagrams based on females - that stop growing by the age of fifteen to seventeen - such diagrams have the potential to expose a growth deceleration that was prolonged beyond that age. To judge by data on material from other locations, the deceleration continued from fifteen to seventeen up to thirty-five to forty years. In the diagram that shows the absolute surplus based on the Sevsk data, the inclination of the curve suggests that all individuals (age three to four years) were most probably females, not males (figs. 34b, 31d), as it illustrates a growth stop at precisely fifteen to seventeen years.

Averianov (1996b, 1997) suggests that *M. primigenius* was capable of changing its reproductive strategy by shifting maturation to earlier ontogenetic stages, thus increasing the possible number of births by a female. However, the stages of maturation, puberty, and decelerating growth - reflected in morphological changes during ontogenesis - do not show any shift of the time of reproduction to earlier stages in the mammoth as compared to modern *E. maximus*, whereas the latter is an illustrative case of the q-strategy of reproduction.

The points at which the growth of females of *E. maximus* and *M. primigenius* slows down (after ten years in *M. primigenius* and after twelve to fifteen years in *E. maximus*; Eisenberg, 1980; Rensch & Harde, 1956) suggest that in both species the first births occurred at approximately the same age. It should also be taken into consideration that the time of maturation may have varied in different mammoth populations. In different populations of modern elephants, females give birth for the first time at different individual ages. Several researchers admit that maturity and first birth in modern *L. africana* may occur between the ages of eleven and seventeen, and depend on the living conditions of the population (Haynes, 1992; Lee & Moss, 1995; Douglas-Hamilton, 1975; Laws, 1970). In Asiatic elephants, the ages at which first birth is given also vary: between ten and seventeen years (Eisenberg, 1980).

The question of gestation length in *M. primigenius* remains open. Because many peculiarities of mammoth morphology and biochemistry are similar to those observed in *E. maximus*, it is permitted to extrapolate - from modern Asiatic elephants to the mammoth - a number of physiological parameters connected with reproduction. The data on the dimensions of newborn calves of *M. primigenius* shows that they were somewhat smaller than Asiatic elephant calves and much smaller than African elephant calves. Smaller size of a newborn in mammals may be indicative of a shorter pregnancy. The mammoth may support this indication. Under the climatic conditions of the last glaciation, mammoths may have given birth only in the warm season, i.e., in spring or early summer. The mating season for all large mammals of the Northern Hemisphere is late autumn. In this season, animals are in best shape after summertime with its abundant vegetation. If such seasonally fixed mating and giving birth is true of *M. primigenius* females, their gestation could not have lasted longer than 19 to 20 months, which is a little shorter than in modern elephants.

The normal gestation period in *E. maximus* ranges from twenty to twenty-three months (Hundley, 1934; Stanley, 1943; Ananthanarayana *et al.*, 1950; Beyer *et al.*, 1990; Shoshani & Eisenberg, 1992), and a comparable duration is observed in *L. africana* (Sikes, 1975; Shoshani *et al.*, 1991; Haynes, 1992). Data on births in captivity shows that the first pregnancy is slightly shorter than the normal length. That is why comparative data on the varability of embryos of *L. africana* and *E. maximus* can effectively be employed in the determination of the stage of uterine development of *M. primigenius* embryos only if it is corrected in consideration of the mammoth's two to three months shorter gestation period (table 20). Stages of the formation of shafts and of embryo bones in general provide the only practical criteria for the determination of the stage of gestation in *M. primigenius*.

Ontogenetic changes of *M. primigenius* compared to other Elephantids

Formation of first generation teeth in *Archidiskodon* and *Mammuthus*

The morphology of dp2 in *A. meridionalis* (*A. gromovi*) (GIN 300-13, 300-122) is similar to that of dp2 in *M. primigenius* (fig. 35, fig. 36: a; photo 26). All parts of the crown are formed simultaneously in the same sequence as in *M. primigenius*. Originally the plate consists of non-fused randomly grouped columns, later their size diminishes and the columns fuse to form the plate. The fusion proceeds from the base to the top. At the same stage of formation, the teeth are functional in *M. primigenius*, and still in the process of formation in *A. meridionalis*. A longer formation process of the crown is better observed in second and third generation teeth, whereas in *M. primigenius* it is well observed as early as in first generation teeth. This morphological peculiarity is important for attributing *M. primigenius* and *A. meridionalis* to different genera.

In *M. primigenius* dp^2 is smaller than in *A. meridionalis*, but its number of plates is the same in both species: five. The anterior root in *M. primigenius* is always situated under the first two plates; the posterior root is under the three posterior plates. In *A. meridionalis*, the anterior root is situated under the first three plates (GIN 300-122).

Dp^2 (GIN 300-13, fig. 35; photo 26) is an incompletely formed tooth. Its length is 26 mm, its width 20 mm, and its height 18 mm (all measured at the crown). The crown is composed of five plates, and is tapering from anterior to posterior. The maximal width of the crown is at the base. The plates are formed by enamel columns fused with each other along almost the complete vertical surfaces. To judge by their apexes, the widest plates (second and third) consist of ten and six columns respectively, the narrower anterior and posterior plates consist of four or five columns. The tallest plates are the third and the fourth. The first, second and third plate are transversal to the longitudinal axis of the crown, the rest are slightly inclined. Cement is absent. To judge by the root bases, there are two roots. The root walls are very thin, which in combination with the absence of cement on the crown is indicative of incomplete crown formation. The bases of three anterior plates are situated over the anterior root, the bases of two posterior plates are over the posterior root. The base of the first plate is higher than those of the other plates. As in dp^2 of *M. primigenius*, the posterior and anterior plates are almost equally high, but the base of the former is situated much below the level of the anterior plate base.

Specimen GIN 300-122 from a *A. meridionalis* (*A. gromovi*) skull (fig. 36a) is an example of a deviated dp^2 formation. The tooth sits in the upper jaw together with a functional M^1 (Garutt *et al.*, 1977; Garutt & Baiguseva, 1981). Two thirds of the crown are inside the alveolus. The crown length is 32 mm, and its width 22 mm. It is 18% larger than the specimen GIN 300-13, which is due to the fact that GIN 300-122 is completely covered with a 2 mm thick layer of tiny crystal substance reminding calcite in structure. This substance is neither cement, nor dentine or enamel.

The shape of specimen GIN 300-122 is similar to that of specimen GIN 300-13. The medial edge is wider than the distal. The buccal side is more convex than the lingual. The apexes of five plates are visible. There is an area of broken enamel on one of the central enamel columns of the third plate: the enamel layer here is about 1 mm thick (Fig. 36a: 6). The root canal of the root fragment preserved is partly filled with dentine and partly with the substance covering the crown. This might be a sign of the termination of tooth formation. However, the plates are less completely than in GIN 300-13. Their enamel columns are different in size, incompletely fused and large. The plates are most probably composed of few columns.

The position of dp^2 in front of M^1 in specimen GIN 300-122 allowed Garutt (1977) to assume a vertically directed substitution of teeth in the most ancient representatives of genus *Archidiskodon*. Originally, the specimen was determined as a P^3 or P^4, erupted to substitute dp^3. However, apart from its unusual position in the jaw and the superficial layer normally absent in a tooth in the process of formation, it does not differ from a regular dp^2 of *M. primigenius*. The number of enamel columns composing the plates and their position suggest that formation of specimen GIN 300-122 was interrupted at a rather early stage. The tooth remained in the alveole when dp^3 was functional and the regularly structured M^1 began to wear. There are traces of pressure on the anterior edge of M^1 as a result of contact with the preceeding tooth. In specimen GIN 300-122 the dp^2 bears no traces of pressure exerted by the next tooth; its crown is below the level of the masticatory surface of M^1. In the left jaw of the same skull dp^2 is completely inside the alveole. The crown of GIN 300-122 remains separated from the anterior root by a bony wall similar to the alveolar wall of dp^2 in *M. primigenius*. A complete and permanent bony wall exists only between the alveoli of dp^2 and dp^3 (Kuzmina & Maschenko, 1999). There are no such walls between the teeth of the next generations due to the horizontally directed process of substitution Should this tooth erupt to substitute dp^3 instead of dp^4, then a complete wall between this tooth and the following should have been absent, which is not the case here.

One can suggest that in the case of GIN 300-122 the development of dp^2 was retarded during its further

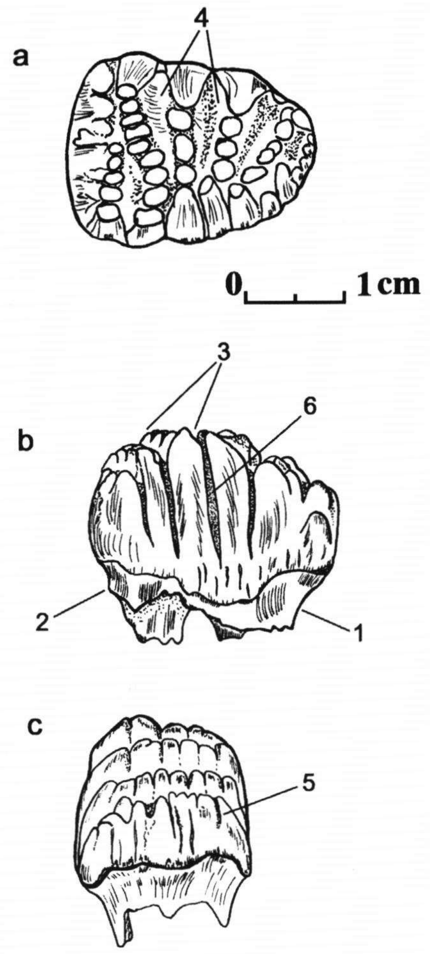

Fig. 35. Structure of a left dp^2 of a calf of *Archidiskodon gromovi* Garutt et Alexejeva, 1965, GIN 300/13, Charpy locality, Rostov region: a = masticatory surface; b = lingual surface; c = distal surface. Scale bar: 1 cm. 1 = posterior root base; 2 = anterior root base; 3 = apexes of enamel columns composing third plate of the crown; 4 = a greater gap between third and fourth plates; 5 = enamel columns composing the last plate of the crown; 6 = the deepest groove between third and fourth plates of the crown.

Bouw van een linker dp^2 van een kalf van *Archidiskodon gromovi*, GIN 300/13, vindplaats Charpy, regio Rostov: a = kauwvlakte; b = tongzijde; c = achterzijde. Maatstreep 1 cm. 1 = achterste wortelbasis; 2 = voorste wortelbasis; 3 = toppen van glazuurkolommen die de derde kroonplaat vormen; 4 = een grotere ruimte tussen de derde en vierde plaat; 5 = glazuurkolommen die de laatste kroonplaat vormen; 6 = de diepste groeve tussen de derde en vierde kroonplaat.

move in the alveolus, accompanied by the development of a calcified superficial layer. It is also possible that this is a case of a delayed eruption of an additional tooth, the precedessor of dp^2, which sometimes occurs in Elephantidae. Such a case has been described in *L. africana* (Morrison-Scott, 1938). Vertical substitution of premolars in Elephantidae was observed in *A. planifrons* and *A. imperator* (Falconer & Cantley, 1845; Pontier & Antony, 1933). In any case, the dp^2 from skull GIN 300-122 is an example of aberrant dentition. The presence of premolars in other representatives of the family Elephantidae, e.g. in *Elephas* from Southern Asia, may be questioned, for all the specimen described as premolars of *E. celebensis* (P^4: figs. 12, 13; P^3: figs. 14, 15) (Hooijer, 1953) are isolated teeth and do not show significant differences in the structure of crowns of dp^2 and dp_2. The described morphological peculiarities are most probably due to wear.

The morphology of dp^2 of *A. meridionalis* from Western Europe differs also only slightly from that of *M. primigenius* (Schreuder, 1945:186). The described specimen is a completely formed tooth with all five plates showing traces of wear. The position and the shape of the plates is similar to that of other known specimens of dp^2 of *A. meridionalis*. The wear pattern shows that the apexes of the enamel columns remain unfused.

The formation of dp3 and dp4 in *A. meridionalis* is very similar to that in *M. primigenius*: the process develops from the anterior end of the crown to the posterior (GIN 300-124, ZIN 29071, ZIN 30012, GIN 300-122) (fig. 36b, c; photos 17-19). Unlike in dp4 of *M. primigenius*, the plates above the anterior root (four in dp_4) are usually rather inclined medially (photo 19). The position of the bases of anterior and posterior plates in *M. primigenius* and in *A. meridionalis* are similar, and the same is true for the number and position of their roots. As in mammoths, during the crown formation the root canal closes and resorption occurs: first of the anterior root, then of the posterior one. To judge by specimen ZIN 29071 (dp_3 formation almost completed) the formation of cement starts on the apexes of the central part of the plates and goes on towards their basements, filling in also interplate gaps. The interplate gaps in this individual are less filled with cement than those in a completely formed dp3 of *M. primigenius*..

Morphological differences in second and third generation teeth of *M. primigenius* in comparison with *A. meridionalis* are determined by adaptive changes in crown structure, and are expressed in an increased number of plates, an increased height, a decreased enamel thickness and a decreased length of plates and interplate gaps in *M. primigenius* (Maglio, 1973). The studied dp3 teeth of *A. meridionalis* show that the plate forming enamel columns do not fuse completely as in *M. primigenius*. The number of enamel columns in *M. primigenius* is higher (up to twenty) than in *A. meridionalis* (maximal eight). In *A. meridionalis*, the wear pattern consists for a long time of several oval forms, corresponding to the separate enamel loops along the width of the plate. The differences in dp4 structure are weaker expressed than in dp3. These morphological plate peculiarities correspond to the generic level of differences between *M. primigenius* and *A. meridionalis*.

The morphology of dp_3 in *E. maximus* (SDM 421-12) is similar to that in *M. primigenius* and *A. gromovi*. The crown consists of seven plates completely covered with cement (fig. 37a, b). All plates show wear which suggests an individual age of eight to twelve months (Roths & Shoshani, 1988). When the posterior plate begins to wear, a specific pattern of a closed enamel loop appears. The crown dimensions are: length 67 mm, width 35 mm, plate length 8 mm, plate width 27.5 mm, interplate gap 5 mm. There are two roots, both with open root canals. The two anterior plates are situated over the base of the anterior root. The base of the third plate is between the roots. Plates four to seven are situated over the base of the posterior root.

In specimen ZIN 30012, a dp^4 of *A. gromovi,* all plates show wear (photo 29). It is possible that one or two anterior plates are worn down completely, and the total number of dp^4 plates is nine or ten. The length of the crown is 93 mm, width 47 mm. The length of the seventh plate is 8.5 mm, width 46 mm. The interplate gap is 8 mm, enamel thickness 2 mm. A small amount of cement remains on the bottom of the interplate gaps. The enamel on the crown base has a relief in the shape of vertical folds (photo 29, fig. 2). The specimen GIN 300-122, a dp^4 of *A. gromovi* from the skull of a young individual, comprises of eight plates, all in wear. It is possible that the anterior plate is worn down and the preserved base of an anterior plate belongs to the second anterior plate. From the fourth plate onwards, the wear pattern is represented by enamel loops corresponding to the apexes of the component enamel columns (Garutt *et al.,* 1977: 7, fig. 2). The cement covers the lateral surfaces of the crown and fills in the interplate gaps. The individual age must be ten to fifteen years. The length of the crown is 123 mm, its width 67 mm, the plate width 54 mm, the interplate gaps 5 and 6-8 mm. The plate frequency is seven per 10 cm.

The widened plates of dp4 - M3 in the genus *Archidiskodon* noted by Maglio (1987) are accounted for by the peculiarities of formation and structure of crowns that may be observed in dp^4 of *E. maximus* as well. In specimen SDM 3535, a dp^4 of *E. maximus* in the process of formation (the seven anterior plates are completely mineralized, the bases are unfused), the first plate is completely covered with cement. Plates two and three are in the process of being covered with cement, from their apexes to the bases, and from the middle parts to the lateral edges.

On the fifth plate the cement is being formed in the centres of the anterior and posterior surfaces (fig. 37c, d). A separate enamel column is fused to the posterior surface of the plate (fig. 37 c, d: 1). The plate consists of three parts, the central (the higher) part and two lateral (lower) parts (fig. 37e: 3, 4). The central part comprises six to eight enamel columns. The apexes of the enamel columns composing the lateral parts of the plate are on the same level with the apex of the additional (posterior) enamel column. The lateral parts comprise one to two enamel columns. The plate base is considerably wider than the apical part. The lateral segments are separated from the central part by gaps that do not reach the plate base (fig. 35c, e: 7). The horizontal line most probably marks the border between differently mineralized zones (fig. 37d: 6).

The specimens ZIN 29071 (a dp_3) and GIN 300-122 (a dp^4) of *A. gromovi* show a similar formation process. When the masticatory surface starts to wear, a loop-shaped enamel protrusion is formed in the centre of the middle plates as a result of wear of the additional column, just like the sine-shaped widening of M1 - M3 in *Archidiskodon* noted by Maglio (1978), depending on the dimensions of the additional column. This feature is important in the mammoth-like elephants' systematic biology. In *A. gromovi* the enamel loop is not closed in the beginning of wear as the apexes of the enamel columns are not fused and the plate is subdivided into the central and lateral segments. Later, when wear reaches the level of fusion of the enamel columns, a complete loop is formed. While wear goes on, the central widening disappears as the middle column is lower than the plate.

In *M. primigenius* , the degree of fusion of the plate apexes is much higher, and a completely formed plate is not subdivided into central and lateral segments, so the loop pattern in this species appears from the very beginning over the complete width of the plate. In *Archidiskodon,* the central widening of a plate persists for a long time and this feature is included into the diagnosis of *M. (Archidiskodon) meridionalis* (Maglio, 1978).

Deciduous (di) and permanent (I) tusks in *M. primigenius* and other Proboscids

Anthony (1933) was the first to subdivide the di alveolus of *E. maximus* into two compartments: an alveolus situated laterally and a depression separated from it by a bony wall. The di alveolus of *M. primigenius* is similarly subdivided during the last months of prenatal and the first months of postnatal development. The mesial compartment of the alveolus is most probably formed in connection with a budding rudimentary incisor. It is partly separated from the di alveolus by an incomplete wall which is reduced by the age of ten to twelve months.

A similar structure of the alveolus was studied in two well-preserved skulls: one of a foetus in the last prenatal stage ZIN 31661 (photo 1), and one of a one-month-old calf GIN 77 (fig. 7). The alveolar part of the skull is formed by two bones contributing differently to the formation. From above and outwards it is formed by the premaxillar bone only (fig. 7: 2; photo 8). From beneath and inwards it is formed by the maxillary. The inner wall of the tusk alveolus has a cellular structure. In specimen GIN 77 the outer wall of the alveolus is about 6 mm thick at the alveolar end; the diameter of the alveolus is 16 mm. The diameter of the alveolus decreases considerably towards the nasal opening and at the distance of 10 mm from the lower edge of the premaxillar bone it is 9 mm. The di root base and the neck of the tusk head sit precisely in this part of the alveolus.

In both specimens the alveolus is subdivided into two parts. The major part is situated laterally from the intermaxillary suture and represents the di alveolus proper (or the external canal) (fig. 7: 4). Medially from the suture there is a depression (the internal depression) separated from the external canal by an incomplete wall (fig. 7: 7). In specimen GIN 77 its depth is 26 mm, and the cross section is oval: 7.5 x 5 mm. The bed of the depression is porous, without large openings. The visible part of the external canal (the di alveolus proper) is curved, as well as the entire premaxillary. The size of the alveolar cavity corresponds only to the size of the first generation tusk, consequently, the formation of the second generation tusk (I) has not begun at this stage.

The subdivision of an alveolus into an external canal and an internal depression may be interpreted as a homology to the incisors of the most ancient Proboscids and their descendants, as suggested by Tassy (1987). In the sister Proboscid group *Moeritherium* (Tassy & Shoshani, 1988) and in some mastodonts, the incisors (*Moeritherium*) and the deciduous tusks (mastodonts) are homologous. The incisors of the milk generation and the permanent tusks are homologous to second incisors (dI^2), as denominated by Tassy (1987), the deciduous tusks (di) being homologous to third incisors (dI^3). These authors illustrate the idea by an analogy with rodents and Lagomorpha in which the incisors of the first (milk) generation grow continuously (hypsodonty) and do not change. These incisors, as well as permanent tusks of elephants, have a structure which is atypical for unspecialized incisors of mammals and lack roots.

In line with this hypothesis, the presence of an internal depression in mammoth alveoli is indicative of the budding of a rudimentary incisor homologous to the first generation incisors (deciduous tusk - dI^1). In *M.primigenius* calves, the rudimentary incisor occupies the most medial position inside the premaxillary and is homologous to incisor 1, the permanent tusk (I) is homologous to incisor 2 (dI^2) being situated laterally. The most lateral position is occupied by the first generation tusk (deciduous tusk) (di), homologous to incisor 3 (dI^3). Such a homology is possible if all the incisors pertain to one generation (being milk teeth).

Phylogenetic morphological features of mammoth-like elephants and the ontogenesis of *M. primigenius*

The ontogenetic studies of *M. primigenius* have revealed a similarity in early postnatal ontogenesis (till one to two months of age) of *M. primigenius* and *A. gromovi*. Illustrative in this respect is the similar morphology of the first generation teeth (dp2) and the deciduous tusks (di). Not only the structures of dp2 and di appear to be similar, but also their way of formation. Later ontogenetic stages show a certain recapitulation of morphological features acquired by the ancestors of mammoths in the process of divergence from the mammoth-like elephants.

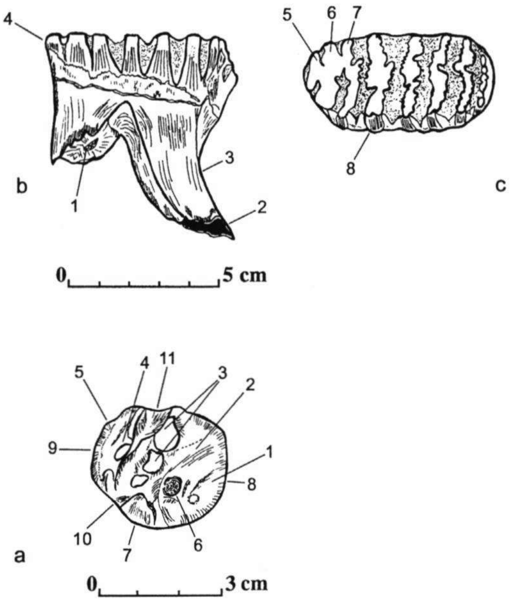

Fig. 36. Structure of a right dp^2 (a: GIN 300/122) and right dp_3 (b, c: GIN 300/124) of calves of *Archidiskodon gromovi* Garutt et Alexejeva, 1965, Charpy locality, Rostov region; masticatory surface (a, c) and buccal surface (b). Scale bar: 5 cm. a: 1 = anterior plate; 2 = second plate; 3 = third plate; 4 = fourth plate; 5 = fifth plate (talon); 6 = damaged apex of a central enamel column on the second plate; 7 = additional, separate tuber on lingual surface of the crown, probably part of third plate; 8 = medial edge of crown; 9 = distal edge of crown; 10 = lingual side; 11 = buccal side. b, c: 1 = root cavity of anterior root; 2 = root cavity of posterior root; 3 = posterior root; 4 = anterior end of the crown; 5 = anterior plate base; 6 = second plate base; 7 = third plate; 8 = vertical enamel folds on lateral surface of plate.

Bouw van een rechter dp^2 (a: GIN 300/122) en rechter dp_3 (b, c: GIN 300/124) van kalveren van *Archidiskodon gromovi* Garutt et Alexejeva, 1965, vindplaats Charpy, regio Rostov; kauwvlakte (a, c) en wangzijde (b). Maatstreep 5 cm. a: 1 = voorste plaat; 2 = tweede plaat; 3 = derde plaat; 4 = vierde plaat; 5 = vijfde plaat (talon); 6 = beschadigde top van een centrale glazuurkolom van de tweede plaat; 7 = extra, afzonderlijke knobbel aan de tongzijde van de kroon, waarschijnlijk deel van de derde plaat; 8 = binnenste kroonrand; 9 = achterste kroonrand; 10 = tongzijde; 11 = wangzijde. b, c: 1 = wortelkanaal van voorste wortel; 2 = wortelkanaal van achterste wortel; 3 = achterste wortel; 4 = voorste kroonrand; 5 = basis van voorste plaat; 6 = basis van tweede plaat; 7 = derde plaat; 8 = vertikale glazuurplooien op zijkant van de plaat.

Most morphological peculiarities, such as the dp4 to M3 formation, the structure and shortening of the occipital part of the skull, and the structure of the symphyseal part during ontogenesis, indicate adaptations for survival under conditions of long and cold winters and relatively short summers.

Most morphological features of *M. primigenius* analyzed in this study (e.g. cranial features and dentition) are important for the diagnosis of the genus and the species (Maglio, 1973; Garutt, 1986, 1987; Todd & Roth, 1996; Lister, 1996). In addition to transformations of the general proportions and the skull shape (ontogenetic changes) observed in different mammal groups, mammoths have their own specific peculiarities. Primarily it is the peculiarities of ontogenetic growth of relative dimensions of the alveolar part of the skull predetermined by the increasing size of the tusks and observed in the ontogenesis of other elephants of the family Elephantidae (Ambrosetti, 1968). In *M. primigenius* calves, the tusk alveoli are directed forward and downward, and during ontogenesis this direction changes to vertical (in the adults). This provides a diagnostic feature for the genus, because in *Archidiskodon* the tusk alveoli remain directed forward to a considerable extent (Lister, 1996). The length of the alveolar part of the tusk in grown-up representatives of the genus *Mammuthus* is greater (in relation to its total length) than in *Archidiskodon* (Maglio, 1975; Lister, 1996). In mammoths the greater relative length of the alveolar part of the tusk is predetermined by a qualitatively different load on the tusk (Chozatskii, 1990).

Another significant transformation that takes place in the skull morphology during ontogenesis is a change in the position of the nasal opening. In *M. primigenius* calves this opening is situated beyond the level of the eye sockets. The generic diagnosis of *Mammuthus* reflects the position of the nasal opening at the level of the orbits (Garutt, 1986, 1987). In the ancient mammoth-like elephants (*Archidiskodon*) the relatively low brain part of the skull and a nasal opening that is situated beyond the level of the orbits are diagnostic features (Maglio, 1973; Garutt, 1986; Osborn, 1942; Azarolli, 1977; Garutt *et al.*, 1981). In adult *M. primigenius* the width of the brain part of the skull (in the occipital area) is smaller than that of the facial part (in the area of supraorbital processes) but in calves (table 1) the brain part is wider than the facial part (Garutt, 1954; Garutt & Baigusheva, 1981), similar to adult *Archidiskodon.*

During ontogenesis the proportions and the orientation of the parietal bones change in *M. primigenius.* The parietal bones of adults are oriented almost vertically and have a convexity on their posterior edge. In newborns and calves under three to four of age the cranial apex is at contact with the frontal and the parietal bone (the masticatory surface of functional teeth being oriented horizontally). The contact area is situated more anteriorly than in adults and the parietal bones in calves are less inclined towards the horizontal plane than in adults. The apex of the skull in adults is situated in the area of the occipital bones, being the most posterior part of the skull. In *Archidiskodon* the highest point of the skull is at the contact area of the parietal and occipital bones, and does not coincide with the posteriormost part of the skull.

The supraoccipital and exoccipital bones remain separated in calves, but at six to seven years of age they start to fuse and the suture between them disappears. The upper part of the supraoccipital bone is inclined considerably backward (photo 2: 1; photo 3: 7). The difference in the shape of the occiput between calves and adults is well-expressed. In adults the occipital bones are orientated vertically and curved in the area of the suture between the supraoccipital and exoccipital bones (fig. 7). The ventral part of the occipital bone is vertical and is slightly inclined backward beyond the curvature (this is the posteriormost part of the skull). In adult *Archidiskodon* the ventral part of the occipital bone is inclined and the area of the occipital condyles appears to be the posteriormost part of the skull. Considering all varieties in shape of the occipital bones of *A. meridionalis* from different parts of Eurasia, this peculiarity, however, persists in general in all non-distorted skulls.

In adult individuals of *Archidiskodon* the occipital condyles are situated relatively lower than in adult *M. primigenius,* but similar to *M. primigenius* calves. In adult *M. primigenius* individuals, simultaneously with an increasing skull height, a relative displacement of the occipital condyles occurs towards the posterior edge of the teeth alveoli and below the basicranium. This position of the occipital bone and occipital condyles is accounted for by the posture of the mammoth head at feeding. *Mammuthus* is a form adapted to feeding on low vegetation (grass, bushes), especially during winter. When excavating food from snow the head is lowered down. A change of the point of attachment of the skull (occipital condyle), relative to the axis of the neck, provides a biomechanically better justified lever.

The length of the symphyseal part and the mental process are considered to be the most significant differences in the lower jaw between *Archidiskodon* and *Mammuthus* (Garutt, 1954; Baigysheva & Garutt, 1987; Dubrovo, 1960, 1966, 1990). In adult individuals of *M. primigenius* the symphyseal part is very short. The interalveolar crest makes an angle of 60° or more with the horizontal plane. The mental process is short. In adult individuals of *Archidiskodon* the symphyseal part is longer, the interalveolar crest makes an angle less than 60° with the horizontal plane and the mental process is long. In the most recent representatives of *Archidiskodon* deviations from the described pattern of the symphyseal part may be observed (Maglio, 1975).

As was shown at the description of the lower jaw of *M. primigenius,* newborn calves have a long symphyseal part. The angle between the interalveolar crest and the horizontal plane is much less than 40°. During postnatal development this angle becomes larger and the symphyseal part relatively shorter. Regardless of variability of shape and size of the mental process, which depends on individual peculiarities and probably also on sex, the direction of the process differs always between *M. primigenius* and *Archidiskodon.* A change in proportion of the lower jaw in *M. primigenius* is expressed in a smaller ratio of jaw length against jaw depth (from 2.28 to 1.76, approaching 1.0 in adults - table 2). In adult individuals of *Archidiskodon* , on the contrary, this ratio is about 3, close to the ratio in *M. primigenius* calves.

The proportions of the crown and the dimensions of di of *A. meridionalis* (ZIN 25094(1), table 4), particularly its triangular cross section that clearly differs from the

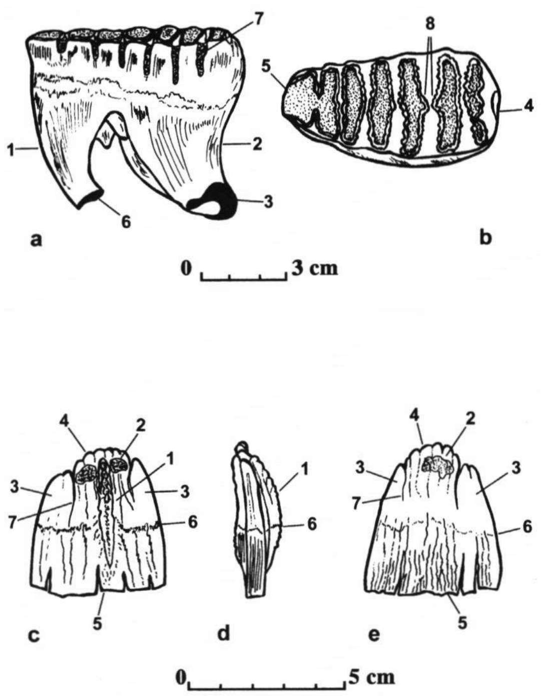

Fig. 37. Structure of a dp3 (a, b) and a dp4 (c, d, e: incomplete, only fifth plate) of a one-year-old calf of *Elephas maximus* in a left lower jaw (SDM 421-12); buccal view (a), masticatory surface (b), anterior view (c), lateral view (d), and posterior view (e). Scale bar: 3 cm. a, b: 1 = anterior root; 2 = posterior root; 3, 6 = root cavity of (2); 4 = deformation of distal edge of crown owing to contact with medial edge of next generation tooth; 5 = first and second plates worn to bases; 7 = interplate gap; 8 = middle thickening of plates; c, d, e: 1 = additional enamel column of posterior surface of plate; 2 = cement; 3 = lateral segments of plate; 4 = apexes of enamel columns of middle segment; 5 = plate base; 6 = horizontal line or border between zones with different degrees of mineralization; 7 = gap between central and lateral segments.

Bouw van tweede generatie kiezen (dp3: a, b; dp4: c, d, e: onvolledige kies, alleen de vijfde plaat aanwezig) van een jaarling kalf van de moderne Indische olifant *Elephas maximus* in een linker onderkaak (SDM 421-12); wangzijde (a), kauwvlak (b), voorzijde (c), zijkant (d), en achterzijde (e). Maatstreep 3 cm. a, b: 1 = voorste wortel; 2 = achterste wortel; 3, 6 = wortelkanaal van (2); 4 = deformatie van achterrand van de kroon door contact met de binnenrand van de kies van de volgende generatie; 5 = eerste en tweede platen tot op basis afgesleten; 7 = tussenplaatsruimte; 8 = centrale verdikking van de platen; c, d, e: 1 = extra glazuurkolom aan het achtervlak van de plaat; 2 = cement; 3 = zijsegmenten van de plaat; 4 = toppen van glazuurkolommen van middelste segment; 5 = plaatbasis; 6 = horizontale lijn of grens tussen zones met verschillende mineralisatiegraad; 7 = spleet tussen middelste en zijsegmenten.

oval cross section in *M. primigenius*, indicate realistic morphological differences irrespective of a similar structural type. These differences provide an additional reason for placing the meridional elephants and mammoths into different genera. However, the way di in *A. meridionalis* is formed probably does not differ much from that in mammoth and the stages of its formation may be similar. The larger size of di of *A. meridionalis* may be an indirect indication of the larger dimensions of calves compared to *M. primigenius* calves of the same age.

As we saw above, the tusk alveoli of *M. primigenius* during the last prenatal and the first postnatal months is separated into two sections. The medial one is probably formed in connection with the formation of a primordial incisor, or a homologous rudimentary structure. It is separated from the main alveolus (situated laterally) by an incomplete septum that disappears by the age of ten to twelve months.

In *E. maximus* a primordial I is formed either directly posterior of di, or slightly medial of it. The relative position of these teeth in *L. africana* is similar (Sikes, 1966). In *M. primigenius* skull PIN 4353-933 in which both di and I are preserved, the tusk (I) is situated medial of di. It might be that the rudimentary non-calcified incisor (or homologous structure), the deciduous tusk di and the permanent tusk are homologous to the first, second and third incisor, respectively. Based on his study of a *E. maximus* embryo, Antony (1933) considered that irrespective of its position in the premaxillar bone, the deciduous incisor di is homologous to the second incisor (dI^2), that the permanent tusk is homologous to the third incisor (I^3), and that they represent different generations. To the best of our knowledge, no researchers have ever noted that the alveolus may be separated into sections corresponding to the socket of a rudimentary incisor and the alveolus proper of the deciduous incisor di during the late prenatal or early postnatal ontogenesis (see, e.g., Eales, 1926; Sikes, 1966; Frad, 1955; Kingdon, 1979).

Comparing positions and structures of the upper jaw incisors in *Amebelodon floridanus* and *Platibelodon grengeri* with *Moeritherium*, Tassy & Shoshani (1988) concluded that both upper incisors (deciduous and permanent) in the two former species are the subsequent incisors of the milk generation. The authors introduce an analogy with the milk incisors of rodents and hares that grow continuously (hypsodonty), not in generations. These incisors, as well as the permanent tusks of elephants, have a structure atypical for mammals and lack roots. According to the positions in *Amebelodon floridanus*, it is suggested that di are homologous to dI^2 and the permanent tusks are homologous to dI^1 (Tassy, 1987). Similar homology is suggested for modern elephants *E. maximus* and *L. africana*. This opinion is inconsistent with Antony's (1933) idea that the permanent tusk is homologous to I^3. Luckett (1966) studied a primordeal tusk in a *L. africana* embryo of the first prenatal year and concluded that only a dI^2 primordium is formed at this stage, whereas the permanent tusk begins its formation at a later stage (probably during the second half of prenatal ontogenesis, or even later), and that the permanent tusk of *L. africana* is homologous to I^2.

The structure of the tusk alveolus in *M. primigenius* also suggests that the tusk is formed at a relatively late stage. Before the age of six to eight months there is no space in the alveolus at the place of I. The formation of I begins only after the alveolus enlarges by the inclusion of maxilla into its structure. The structure of I (PIN 4353-933) at an already mineralized stage of formation suggests that the mineralization of dentine, of which I consists predominantly, also takes place at a relatively late stage of postnatal ontogenesis (six to eight months and later).

The relative position of di and I in the alveolus of *M. primigenius* more likely testifies to the homology of di to the second incisor of the milk generation (dI^2) and of the permanent tusk to the second incisor of the permanent generation (I^2). That I pertains to the milk generation may be questioned sofar, as, on the one hand, the structure of continuously growing and rootless I is homologous to that of the transformed first generation incisors of rodents and lagomorphs, on the other hand, however, the structure of di is typical for mammals. The tusk head is completely formed representing a crown covered with enamel, with a pulp cavity, suggesting a transparent homology with the tooth crown of other mammals. The root with normal root cavity is most probably also homologous to teeth roots in other mammal groups. The formation of cement on the root base is also similar to that on the tooth neck in other mammals, in which cement together with ligaments fixes the tooth in the alveolus. While di is erupting from the alveolus, the head looses its cement, which remains only on the root.

One can hardly assume that teeth that erupt in sequence, one to substitute the other, each having a different structure (one being a typical anterior tooth, the other one a strongly specialized incisor), pertain to one and the same generation. It is thus more likely that they represent incisors of different generations. So the first generation in *M. primigenius* is represented by a rudimentary, non-calcified incisor being homologous to the first generation incisor, and a first generation tusk (di) homologous to a second or third incisor.

The next generation (permanent teeth) is represented only by one incisor, the permanent tusk. In *M. primigenius* and modern elephants (Ealis, 1926) this alveolus is formed both by the premaxillar and maxillar bone. At the time at which di is formed and functions, the alveolus is formed mainly by the premaxillar bone, and at the beginning of eight to ten months, when I is formed, the contribution of the premaxillar and maxillar bone into the structure of the alveolus becomes practically equal. In *Moeritherium*, the alveolus of the upper third incisor of the permanent generation is also formed by the premaxillar and maxillar bones (Andrews, 1906). This peculiarity possibly suggests a homology of this incisor and the permanent tusk of elephants. If this is true, the permanent tusk (I) is a highly specialized homology to the third incisor of the permanent generation.

If one assumes that the *M. primigenius* rudimentary incisor, first generation tusk di and second generation tusk I are the teeth of one and the same generation, then, considering their reciprocal positions in the premaxillar bone, the rudimentary primordium should be homologous to the first incisor, the permanent tusk to the second incisor and the first generation tusk to the third one. However, this is inconsistent with the data on differentiation of an embryo tooth plate in *E. maximus* (Luckett, 1996).

Not a single case of development of tusks in the lower jaw of *M. primigenius* is known. Development of lower jaw tusks is not typical of the Late Pleistocene representatives of the family Elephantidae. In the most ancient Asiatic representatives of the family, formation of small, rudimentary alveoli with thin walls have been noted, which might probably be the place of formation of primordial incisors, however, they never developed completely (Osborn, 1936; Falkoner & Cautley, 1845).

The formation of lower jaw incisors among representatives of the Elephantidae is known in *E. celebenis* (Hooijer, 1954, 1955), but this is interpreted as a retrograde morphological transformation in dwarf taxa of islands (Maglio, 1973). The dimensions of the lower incisor (horizontal/vertical transverse diameters - 56/36 mm) most probably suggest that this incisor should be the permanent tusk, which is confirmed by the relief of the upper surface in the shape of a longitudinal depression and concentric dentine layers typical of I in Elephantidae (Hooijer, 1954: 116, plate XXII, figs. 3-4). Elongation of the symphyseal part at early postnatal ontogenetic stages of *M. primigenius* is never accompanied by the formation of incisors or alveoli (Dobert, 1992). No lower incisors are known of *M. trogonterii* and *A. meridionalis*. Thus one must assume that only representatives of the genus *Elephas* pertain lower tusks among the Elephantidae, probably as a recessive feature.

The combination of these facts suggests that the formation and structure of the deciduous tusks in *A. meridionalis* and *M. primigenius* are very similar. Minor details indicate their generic difference. The data on di structure suggests that the structural differences are not connected with basic adaptations of *M. primigenius*, unlike other features of the postnatal ontogenesis (before one year) that have a major significance.

The new data on morphological transformations during ontogenetic development of *M. primigenius* may be taken into consideration in determining the volume of the genus *Mammuthus* in the biological system of elephants. The volume of the genus in this case becomes more restricted.

Traditionally up to seven species are described to compose the genus in case the complex of features of M3, skull and lower jaw is considered. Changes in crown morphology (plate height, enamel thickness and number of plates) are traditionally considered as generic or specific differences. Different authors attribute different taxonomic significance (weight) to these features depending on their particular conception of the evolution of mammoth-like elephants.

A very broad interpretation of the genus *Mammuthus* was given by Maglio (1973), whose system is widely spread now. Maglio attributed all mammoth-like elephants to one genus only: *Mammuthus*. The evolutionary stages within the group are considered as species. The origin of the genus lies in the Early Pliocene. According to Maglio, the early evolution of the genus took place in the tropical regions of Africa, the later evolution in the Eurasian regions with warm and moderate climates, and the latest stage in regions with a cold climate. The time range of the genus *Mammuthus* appears to be greater than those of many other mammal species and exceeds 5.5 million years.

The diagnosis by Maglio (1973) states that elephants of the genus *Mammuthus* are medium- to large-sized. The earlier forms have flat molars with shallow crowns; in later forms the teeth are relatively narrower. The early forms have eight plates in the M^3, in the latest forms this number approaches twenty-seven. The plate frequency of M_3 varies from three in earlier forms to eleven in the most late. Enamel thickness varies from 5.5 to 1.0 mm. Crown height is 75 to 300% of its width. The lower jaw in ancient forms has an elongated symphysis, a short trunk and a shallow coronoid process. The condyles are oval, positioned more backward in the ancient forms and remarkably forward in later forms. The skull is high, with no depression in the middle of the apical part. There are no parietal crests. The temporal pit becomes more rounded dorsally. The width of the skull at the level of the orbits equals or exceeds the occipital width. The occipital bones are inclined backward in early forms and become vertical or inclined forward in later representatives of the genus. The tusks are usually long, strongly curved and twisted spirally.

The diagnosis allows one to include into the genus *Mammuthus* many different elephants, the type species of the genus among them. Studies on the dentition suggest one-directedness of morphological changes of teeth in mammoth-like elephants. Consequently, Maglio considers a higher number of plates and increased crown height as changes at species level. However, similar changes took also place in other proboscids of the family Elephantidae, in the loxodont and elephantoid elephants, which was noted by Maglio (1973), too.

Although the changes in the dentition are considered unequivocally, the tooth morphology, however, does not necessarily reflect phylogenetic relations within genera or even between genera of a family. The change in climatic conditions of the habitats of the latest representatives of the mammoths reflects a transition to a dramatically different life, leading to significant morphological transformations not only in the dentition.

The different points of view on how the system of mammoth-like elephants should be built, including the question of the origin of the North American elephants, make clear that the use of a traditionally accepted diagnostical feature alone is insufficient to solve the problems (Sher *et al.*, 1995; Todd & Roth, 1996; Lister, 1996). The status of the genus *Archidiskodon* is also highly disputable (Azarolli, 1997; Lister, 1996).

The system of mammoth-like elephants proposed by Garutt (1997, 1986, 1987) comprises only two species and a number of subspecies into the genus *Mammuthus*. The throgontherial elephant is included into the genus *Archidiskodon*. This genus, together with the genus *Mammuthus*, is considered to constitute the subfamily Mammuthinae (Simpson, 1945; Garutt, 1987). In our opinion, such a concept of a restricted composition of the genus *Mammuthus* is highly desirable as it reflects more adequately the peculiarities of ontogenesis discussed in this work. Garutt's system looks as follows:

Family Elephantidae Gray, 1821
Subfamily Mammuthinae Simpson, 1945

Genus *Archidiskodon* Pohlig, 1885

A. subplanifrons Osborn, 1928; Late Pliocene of Africa
A. africanavus Aramburg, 1952; Late Pliocene of Africa
A. rumanus Stefanescu, 1928; Late Pliocene - Early Pleistocene of Eurasia
A. gromovi Garutt et Alexejeva, 1965; Late Pliocene of Eurasia
A. meridionalis (Nesti, 1825); Early - Middle Pleistocene of Eurasia and N. America
A. tamanesis (Dubrovo, 1964); Early Pleistocene of Eurasia
A. trogontherii (Pohlig, 1885); Middle Pleistocene of Eurasia and N. America
A. columbi (Falconer, 1857); Late Pleistocene of N. America

Genus *Mammuthus* Burnett, 1830

M. chosaricus (Dubrovo, 1966); Middle Pleistocene of Eurasia
M. primigenius (Blumenbach, 1799); Late Pleistocene of Eurasia

Dubrovo, in discussing the genus *Mammuthus*, includes the trogontherial elephant within that genus, and a number of species of the genus *Archidiskodon* are considered synonyms or subspecies of *A. meridionalis* (1964, 1966, 1990).

A broader conception of the genus *Mammuthus* includes all mammoth-like elephants of the beginning of the Pliocene, on the asumption of a phylogenetic succession between the ancient and the younger representatives of the group during Pliocene and Pleistocene. The status of the genus *Archidiskodon* then appears to be equivocal, as noted by Lister (1996).

According to the latest data, the most ancient representatives of the meridionalis group appear in Europe more than 2 million years ago. The total number of M3 plates in these forms is ten. Typical representatives of *A. meridionalis* are known mostly from Europe and Siberia; the Siberian finds might be somewhat younger than the European ones. The latest representatives of *A. meridionalis* are dated around 0.9 million years.

The representatives of the trogontherii group made their first appearance 0.7 million years ago and the earliest come from Western Europe (Soergel, 1912; Zakrevskaia, 1936; Dubrovo, 1966, 1975; Lister, 1996; Todd & Roth, 1996). The time range of the most typical *M. trogontherii* (*M. armeniacus*, nomen oblitum) is estimated from 0.6 to 0.3 million years ago. From 0.25-0.1 million years ago on, the species transforms into *M. primigenius*.

The structure of the lower jaw of the earliest representatives of the trogontherii group may vary, e.g., contemporaneous individuals with long and short symphyseal part and mental process are known from Sussenborn. In the forms known from younger localities the symphyseal parts of the lower jaw are short, e.g., a representative of a late throgontherii form from the Cherny Yar locality (PIN 4394-2; dated about 0.2-0.3 million years) has a short symphyseal part, and the angle between the intermaxillary crest and the horizontal plane approaches 90°.

Morphological differences between the early and the late representatives of the genus *M. trogontherii* formed the basis for the discrimination of two successive subspecies, corresponding to the time range of the typical representative of the species: *M. trogontherii trogontherii* (Pohlig, 1885) and *M. trogontherii chosaricus* Dubrovo, 1966 (Dubrovo, 1966, 1981). The latter form is a transitional stage between *M. trogontherii* and *M. primigenius* as its morphology is intermediate between the typical representatives of these species. *M. trogontherii chosaricus* is known from several localities of the Volga Basin, the Urals foothills and Germany (Stenheim).

The most ancient representatives of *M. primigenius* known from the European and Siberian localities are dated over 0.1 million years (Lister, 1966; Foronova, Zudin, 1999). Among the diagnostic features of the species *M. primigenius* are the following: M3 consists of twenty to twenty-seven plates, the angle of eruption and wear of teeth is between 39° and 66°, the enamel layer is thin (1-1.5 mm). The skull is strongly compressed in antero-posterior direction, the angle of inclination of the occipital bones is very large, the alveoli are relatively long and directed almost vertically, and the heigth to length ratio of the skull is 1.2 or more (in *M. trogontherii* ca. 1.09). The lower jaw is short and deep, and its symphyseal part is short. The carpal bones are positioned aserially (Lister, 1996).

According to Lister (1996), the taxonomy of the genus *Mammuthus* is as follows:

Family Elephantidae Gray, 1821
Genus *Mammuthus* Burnett, 1830
M. meridionalis (Nesti, 1825); Late Pliocene - Early Pleistocene of Eurasia
M. trogontherii (Pohlig, 1889); Middle Pleistocene of Eurasia
M. primigenius (Blumenbach, 1799); Late Pleistocene of Eurasia and N. America

The existence of transitional forms between the genera *Archidiskodon* and *Mammuthus* and the disputability of the taxonomical position of some representatives of the genus *Mammuthus* (species or subspecies) do not allow to delimit unequivocally the genus using only the features based on the structure of M3, skull and the lower jaw, for any feature may be equally expressed in forms with a different stratigraphical distribution and an obviously different taxonomical position . Consequently, other features should be added for delimiting the genus *Mammuthus* and determining the status of *M. primigenius* within that genus.

To solve these problems the following features are traditionally used: the direction of the alveoli, the relative length of the alveolar part of tusk, the position of the nasal opening, the width of occipital and cerebral parts of skull, the structure of the cranial apex, the shape of the occiput, the length of the symphysis and the horizontal branch of the lower jaw, the structure of M3 (enamel thickness, plate frequency, degree of hypsodonty, crown height to width ratio). In many cases, similar features are interpreted differently by different authors.

Considering the morphological transformations during *M. primigenius* ontogenesis, prior significance should be attached to the following features: the structure of occiput, the proportions of facial and cerebral parts of skull, the time of formation and the beginning of functioning of dp3-M3 teeth, the size of newborn calves, the growth speed of calves during the first postnatal year, the structure of dp2-d4, the structure of plates and the wear figures on the teeth.

The data discussed in this work signal a special morphological complex typical for the genus *Mammuthus* only, and are predetermined by the adaptation to a cold climate. In addition to the traditional generic features of *Mammuthus*, these are: eruption of teeth at an earlier stage of formation in comparison with ancestral forms (especially M1-M3 generations), a longer formation time of the crown, and wear of the anterior end of a tooth before the posterior plates are completely formed. Thus, despite still not very transparent phylogenetic relations within the mammoth-like elephants, the genus *Mammuthus* appears to be the only form in the family that is adapted to the conditions of a cold, seasonal climate.

In the more ancient genus *Archidiskodon*, M1-M3 begin to wear after their formation is completed, all plates mineralized and cement is formed. In *Mammuthus*, owing to feeding on coarse food, mainly grass (pastoral feeding *sensu* Lister, 1996), tooth wear is much faster than in ancient elephants of the mammoth-like lineage, which feed on combined herbal and branch vegetation. In mammoths, dp4 - M3 begin to function before the posterior plates are formed, and the cement is formed only on the anterior part of the crown. Together with other features of mammoth tooth morphology, this peculiarity provides a significant addition to the general picture of the dentition of late representatives of mammoth-like elephants, which allows us to discriminate between the early representatives the lineage and the representatives of genus *Mammuthus*.

Regardless of the intermediate skull and lower jaw morphology of *M. trogontherii*, i.e., a very high skull, vertically directed tusk alveoli with a relatively large alveolar part, intermediate body proportions, and especially some peculiarities of tooth formation, it is possible to include the species into the genus *Mammuthus*. During the formation of the teeth of the last generation and at time they begin to function, as well as in some peculiarities of cranial structure, *M. trogontherii* is closer to *M. primigenius*, and not to ancient forms. Together with structural morphology of the dentition, this makes it possible to include both species into one genus. Consequently, the genus *Mammuthus* comprises two species with different morphotypes but on the whole corresponding to the species *M. trogontherii* and *M. primigenius*. Accordingly, the volume of the genus and its origin should be connected with the adaptation to a life under Palearctic conditions, where the areal of the group varied greatly in the late Middle and Late Pleistocene, and during certain times elephant forms existed with a morphology intermediate between the trogontherial elephant and the wooly mammoth.

The genus *Mammuthus* appears to be a unique representative of the group. It originated and evolved in the Northern Hemisphere outside the distribution zone of most other mammoth-like elephants in particular and proboscids in general. Obviously, the volume of the genus should be restricted to forms with a complex of morphological features reflecting adaptational peculiarities of specifically northern mammoth-like elephants. This complex is based on the features connected with the sequence and speed of formation of last generations' teeth (dp4–M3) that appear only in this genus, as no other Elephantidae including other mammoth-like elephants, have ever adapted to similar conditions. Stratigraphical distribution of the genus falls within the time range between the second half of the Middle Pleistocene and the beginning of Holocene (Wrangel Island only).

The systematic start of the forms constituting the genus *Mammuthus* lies between the latest representatives of mammoth-like elephants, i.e., the forms described under the genus *Archidiskodon*, and the most ancient representatives of the genus *M. trogontherii*.

The genus *Mammuthus* moves to occupy a radically different ecological niche. This transition is well reflected in the change of distribution area of mammoth-like elephants in the latest Middle–Late Pleistocene. During winter these elephants were deprived of green forage because of a vegetation growth stop. In summer, they fed mostly on grasses, which are relatively coarser than bushes and tree branches, causing a faster wear of tooth crowns in mammoths in comparison with more ancient elephants of the mammoth-like lineage. The latter, including their latest representatives of the beginning of the Middle Pleistocene, lived under conditions of perennial vegetation. The greater number of plates constituting the crowns of *M. primigenius* teeth of third to sixth (dp4–M3) generation and consequently the longer time of crown functioning compensates for the faster abrasion.

As indicated earlier, the structure and scheme of formation of dp2 in *M. primigenius* and *A. gromovi* do not differ much: the tooth consists of the same number of plates, the plates are formed of roughly the same number of enamel columns that fuse to one scheme, from the crown base to its apex. In both forms the fusion of enamel columns is complete. When the crown of the first generation tooth starts to wear, a complete enamel loop across the complete plate's width is formed from the very beginning. To judge by the specimens that were available during our work, enamel thickness also differs only slightly. The cement formation on dp2 is similar, i.e., cement is formed simultaneously over the entire plate surface.

The structure of dp3 shows differences in the number of plates (eight to nine in *M. primigenius* and seven in *A. gromovi*). Beginning with the second generation, cement formation starts in the anterior end and spreads onto the posterior end of the crown as described for *M. primigenius*, which differs from that in *A. gromovi*. From the beginning on, the wear pattern on the masticatory surface of the mammoth tooth consists of an enamel loop across the entire plate width. In *A. gromovi* the apices of the enamel columns, even in completely formed plates, remain unfused, the top of the plate remains subdivided into three larger elements (one central and two lateral) and a number of smaller elements (according to the number of columns constituting each larger element). In modern *E. maximus*, a plate comes to the end of this stage before the plate formation is complete. However, in *Archidiskodon* this stage is the final one, so the wear pattern initially consists of three smaller loops and only the subsequent wear shapes one large, closed loop across the entire width of the plate. Several authors indicate this type of wear of M2 and M3 (Soergel, 1912; Gromova, 1965; Dubrovo, 1966; Maglio, 1973; Garutt, 1977; Foronova & Zudin, 1999).

The lack of significant differences in dp2 morphology and in the formation of dp3 plates suggests that the differences between *Archidiskodon* and *M. primigenius* are not much expressed during the early postnatal stage. This common and probably ancient (plesiomorhpic) feature is likely to persist in the ontogenesis of all mammoth-like elephants.

From dp4 on, the differences between *A. gromovi* and *M. primigenius* in eruption time and time of crown formation become significant, and they are even more significant in the teeth of subsequent generations. In specimen GIN 300-122 (*A. gromovi*, a skull of a young individual), M1 is partly exposed due to the broken-off alveolus. The crown comprises of ten plates. The tooth is not yet functional and sits inside the alveolus. All plates are formed completely and covered with cement. A similar degree of formation is shown by non-erupted teeth of subsequent generations in specimens ZIN 31216 (M_2) and GIN 270-10, ZIN 31217, both M^3 (photo 30, fig. 1: 3). In these specimens, the crown - formation is completed before the eruption of the tooth and, consequently, before it becomes functional. In *M. primigenius*, from dp4 on, the crown formation is completed after about one half of the constituting plates (six to nine) started to wear. In the subsequent teeth the time of crown formation increases from generation to generation.

Thus, this peculiarity of the formation of the dentition, together with the degree of fusion of enamel columns, is of major importance in the diagnosis of the genus *Mammuthus*. In combination with other features, it provides reliable criteria for delimiting this genus from more ancient representatives of the same lineage. As a consequence, mammoth-like elephants in which crown formation ends either before the crown becomes functional, or precisely when the tooth erupts, should be excluded from the genus.

The feature mentioned above is known for all representatives of *M. trogontherii*. The degree of expression of this peculiarity in *M. trogontherii* differs from that in *M. primigenius*: the time between eruption and the completion of formation is shorter. However, unlike in *Archidiskodon*, the crown is always functional before it is formed completely. So, the generic attribution of this elephant may be precise if the proposed scheme is used.

In the mammoth tooth M2 from Mauer, thirteen plates are preserved, of which the anterior ten show wear. The four posterior plates are incompletely covered with cement, and regardless of the considerable wear, are not yet fused (Soergel, 1912: tab. 1, fig. 10). In this specimen, a loop across the entire plate width is seen, and some slightly worn plates exhibit irregular wear patterns. This peculiarity allows one to attribute the specimen to the genus *Mammuthus* (photo 30: 4).

A similar degree of formation is exhibited by the M3 of *M. trogontherii* from Tiraspol. This one is a typical form of *M. trogontherii trogontherii* (Dubrovo, 1981) (photo 31). Eight anterior plates of M_3 are in wear, 4 posterior plates are incompletely formed and lack cement. Four anterior plates of M^3 are in wear and two posterior plates lack cement. The Tiraspol material was collected in the Kolkotova Balka ravine, a locality with the same age as Sussenborn and Mosbach (Kromer, ca. 0.5 million years). This suggests that the representatives of the genus *Mammuthus*, with features typical for the genus alone, were distributed over Eastern and Western Europe as early as the second half of the Middle Pleistocene.

The teeth of *M. trogontherii* from Bashkiria exhibit similar peculiarities of M3 crown formation. Specimen ZIN 31643(2), a M_3, is composed of twenty-two plates. The specimen is illustrative for the plate formation process. The anterior nine plates are in wear. The anterior sixteen plates are completely covered with cement, plate seventeen for one half from top to base, and plate eighteen for one-fifth. The two posterior plates are incomplete, their bases are still in the process of mineralization. In addition, the enamel columns constituting these two plates are incompletely fused. The number of columns constituting the last but one plate is ten; the third plate from the distal end of the molar consists of nine columns, and the fourth from distal of seven. These plates are indicative of the increasing number of constituting columns depending on the stage of plate formation. The already mineralized larger enamel columns become subdivided into smaller columns by partial individuation of the apexes of the columns of the second order. The fusion of the main enamel columns is directed from lateral to central, and the apexes of the central enamel columns are the last to fuse. The columns become consolidated so tightly that the plates of this specimen that are already in wear exhibit initially irregular wear figures, that quickly shape a large common enamel loop across the entire plate width.

This type of wear has already been described in mammoths and more ancient mammoth-like elephants, and the composition of a completely formed plate of one central and two lateral segments has been noted already (Soergel, 1913; Dubrovo, 1960). This formation stage is known of *M. primigenius*, *M. trogontherii* and *Elephas*, however, in the genus *Mammuthus* the constituting elements fuse at a later stage and a completely formed plate is not subdivided into a medial and two lateral segments. An irregular wear figure when a plate becomes functional is also typical for the genus *Mammuthus*. In the same way the M^3 of *M. trogontherii*, sp. ZIN 31642(3), 29896, 29963 are formed.

The specimen described as *M. armeniacus* (Falconer, 1856) from Erserum, Turkey (Adam, 1988:20) represents a heavily worn M_3 of *M. trogontherii*: one third of the crown is missing. So it is hard to determine how the process of formation developed and to what extent the features characterizing the genus *Mammuthus* are expressed. To judge by the enamel thickness, plate frequency and the wear pattern on the masticatory surface it may be attributed to the most ancient *M. trogontherii* (photo 30, fig. 5). It looks feasible in this case, in addition to generally accepted diagnostic features, to consider the above mentioned peculiarity of plate formation leading to the elimination of a subdivision of the plate into a central and two lateral elements and an almost complete fusion of enamel columns which is not typical for the more ancient mammoth-like elephants to attribute it to the genus *Archidiskodon*.

These features of tooth structure, together with the peculiarities of cranial morphology connected with an adaptation to feeding on low grasses and bushes and the quick growth of calves during the first postnatal year, suggest the inclusion of the majority of elephants attributed to the species *M. trogontherii* and to the species *M, primigenius* into the genus *Mammuthus*. The entire group of mammoth-like elephants from their most ancient representatives on should be included into one subfamily. However, the mammoth-like elephants that do not exhibit morphological peculiarities typical for the genus *Mammuthus* should be given the status of a genus. In this case, the subfamily includes two genera at least (including the genus *Mammuthus*). The generic system should be as follows,

Family Elephantidae Gray, 1821
Subfamily Mammutinae Simpson, 1945
Genus *Mammuthus* Burnett, 1830

M. trogontherii (Pohlig, 1885)
M. primigenius (Blumenbach, 1803)

The system proposed is by no means absolute or final, as no forms with transitional morphology have been considered in this work. However, the data represented and discussed in this book unequivocally suggest a drastic restriction of the genus *Mammuthus*, of which this system is a reflection.

Ecology and ethology of *M. primigenius*

Sevsk: a unique deposit of remains of a mammoth herd

The most important data on age and sex composition of a family group of *M. primigenius* individuals were obtained from a study of material from the Sevsk locality (Bryansk region, Russia). This locality is a unique natural deposit of remains of *M. primigenius* with an alluvial genesis.

With regard to the area occupied by the bone-bearing lens containing the mammoth remains and the number of bones found (about 4,000), the Sevsk locality appears to be the largest natural deposit of mammoth remains in Europe. All other large European accumulations of mammoth remains are connected with human activities, and thus artificial in origin (Lavrov & Maschenko, 1991; Maschenko, 2000), or, in the case of the North Sea, are not found in situ.

The Late Pleistocene mammoth sites and natural deposits of Eurasia and North America provide important comparative data on bone representation and age profiles of mammoths, but these data differ significantly from those gained from the Sevsk material (Vereschagin, 1972, 1977; Vereschagin & Nikolaev, 1982; Maschenko, 1992, 1994, 1995; Soffer, 1985; Frison & Todd, 1986; Haynes, 1985, 1989, 1990, 1992, 1999; Agenbroad, 1984, 1990, 1994; 1995; Agenbroad & Mead, 1994; Saunders, 1999).

The geological age of the Sevsk locality, determined by radiocarbon dating of mammoth bones from the main bone-bearing layer, is 13,950±70 years (GIN 5778); dating of a tusk from the highest level of the bone-bearing layer is 13,680±60 years (GIN 6209). The locality is situated in the southeastern part of the Bryansk region in the Sev river valley. The valley is about 3 km wide in the environment of the locality. The relief of the valley was formed during the Late Pleistocene and Holocene. Along the left side of the valley there are several ancient residual table-rocks. The locality is situated on the western flank of the largest one, 400 metres away from the modern bed of the river Sev. The bone-bearing lens is crescent-shaped with a southeast - northwest oriented axis. The area of the lens originally measured about 800-1200 square metres. Beyond the limits of the area no other Late Pleistocene mammal bones have been found so far (Maschenko, 1992). All deposits of Sevsk, including the bone-beds, are attributed to alluvial deposits of the Sev river valley and are illustrative for the formation history of the locality.

The burial of a single group of mammoths is a unique feature of the locality. The group was buried practically at the spot where the animals died. Their complete skeletons and isolated bones remained untouched in the bone-bearing lens and were not redeposited, which is unlike the situation that may be observed in places of mass deaths of modern *L. africana* (Haynes, 1992) and in *M. columbi* localities (Frison & Todd, 1986). The good preservation of five complete skeletons of mammoth calves of different individual age are indicative for this.

Geological data suggests that the formation of the main bone-bearing layer of the locality (the lower one) occurred very fast, probably within one season as indicated by the very homogeneous structure of the component middle-grained sands. Variations in thickness of the sand layer (from 15-30 to 50 cm) are accounted for by correlate depressions and uplifts of the bed of the ancient basin where the sedimentation and burial of mammoth remains occurred. The bone-bearing layer that covers the subjacent beds (flatly thin-layered, lightgrey, fine-grained sands) is partly washed. The structure of layers and the grain composition of the subjacent sands are suggestive for a slow-flow basin, probably a lake. The washing of the top segment of these sediments indicates a change in the hydrodynamic regime: a higher speed of the current before or during the formation of the bone-bearing sediments. In addition, cryogenic faults were observed at the border between the deepest level of the bone-bearing layer and the lacustrine depositions (Maschenko *et al.*, 1993).

The bone-bearing layer is covered by sandy to clayish deposits (up to 50 cm thick) that also contain mammoth remains. These are intermingled layers of sand, sandy loam and sandy clays each 1-4 cm thick, that form a complex of alluvial deposits, which is, in fact, another bone-bearing layer. About 20% of the total bone finds of the locality was collected from these deposits (Maschenko, 1992; Maschenko *et al.*, in press).

The main bone-bearing layer evidently was formed under conditions of a crescentic lake. As the covering sandy to clayish deposits of the upper bone-bearing layer suggest, this lake was later transformed into a part of a lowland floodplain with seasonal sedimentation of sands, sandy clays and loams.

Study of the diatom floras from the subjacent lacustrine sands, the main bone-bearing layer, the upper bone-bearing layer and the cover sediments (brown sandy loams up to 30-40 cm thick with lightgrey sand bands) reveals a gradual change in the generic composition of the diatom flora, which corresponds to changes of the basin type. Cold-resistent species that inhabit barred basins and basins with slow running water with a neutral pH (e.g., lakes) are typical of the main bone-bearing layer. The upper bone-bearing layer is characterized by species typical of waters with deviated pH, such as constricted ponds or marshy floodplains. In the upper part of the section species typical of marshes dominate. These data, combined with geological data, suggests a degradation of the basin from a crescentic lake with a slow current through marshy floodplain and finally to a marsh (Maschenko *et al.*, in press).

The main bone-bearing layer was evidently formed during the stage of the crescentic lake that accumulated dead animals' bodies during a flood. The formative mechanism of a similar bone accumulation in loop lakes was described for the Berelekh locality where about 8,000 bones were collected (Vereschagin, 1972, 1977; Baryshnikov *et al.*, 1977). As Vereschagin (1972) showed, the bodies of large mammals were washed into the looplakes during subsequent flood seasons in which the water rose quickly. Unlike the process in Berelekh, the formation of the Sevsk main bone-bearing layer occurred within a relatively short time, probably during one season only. The formation of the upper bone-bearing layer was accompanied by a partial redeposition of bones. In the case of Berelekh and similar localities, complete skeletons *in situ* were not discovered: bones from different individuals were shuffled during resedimentation by flood waters during subsequent seasons (Vereshchagin, 1979).

The outstanding preservation of the Sevsk mammoth remains differs from that in all other known Eurasian localities with *M. primigenius*. The main bone-bearing layer has preserved complete articulated skeletons of mammoth calves (from a newborn to individuals aged five to six years). Many partial skeletons with articulated bones have also been preserved. Most frequent among them are carpal and tarsal bones and vertebral columns with ribs. Less frequent are pelvic bones articulated with femurs, and scapulas with humeri, as well as humeri with ulnas and femurs with tibias (Maschenko, 1991, 1993, 2000; Maschenko *et al.*, 1993).

Well-preserved remains were concentrated in the central area of the bone-bearing lens, in the lowermost part of the ancient basin. Some bones of adult individuals were slightly moved away from the place of their original burial, but still in the place where the animal died. For modern African elephants, the mechanism of carcass decomposition under natural conditions was described by Haynes (1991). The description applies to the Sevsk locality as well, however, with some restrictions. Here the partial redistribution of bones over the site is better accounted for since the partial destruction of the bone-bearing layer during subsequent flood seasons amounts to a mere 15-40 cm. Parts of large bones that protruded from the layer were also destroyed by erosion, as well as by some other factors, including activities of carnivores and rodents. However, such bones consitute less than 1% of the total amount in Sevsk, and all bones damaged by rodents were collected from the upper bone-bearing layer only (Maschenko & Gablina, 1996; Maschenko, 2000; Maschenko *et al.*, in press).

The bones in the bone-bearing layers are not sorted either by size or weight, show no traces of water wear, and the long bones lack an unidirectional orientation such as is observed when bones are transported by the current (Efremov, 1950). During decomposition in the open air, the remains of a single body of a modern African elephant may cover an area of about 50-60 square metres (Haynes, 1991). In the Sevsk locality, bone material collected from areas adjacent to large partial skeletons appear to belong for the greater part to these

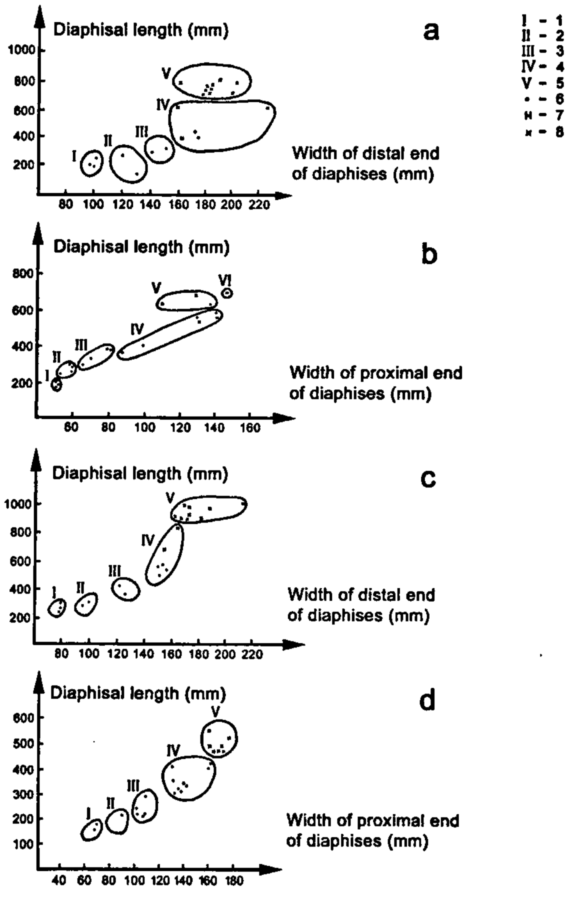

Fig. 38. Dimensional variability of the humerus (a), the ulna (b), the femur (c) and the tibia (d) in different age groups (I to V) of mammoths from Sevsk locality, Bryansk region: I = newborn upto 2 years of age; II = 2 upto 5-6 years of age; III = 7 upto 11-13 years of age; IV = 13 upto 35 years of age; V = over 40 years of age; VI = humerus of the largest individual (probably male) with non-fused epiphyses; x = specimens with completely fused proximal and distal epiphyses; •.= shafts with non-fused epiphyses; H = specimens with fused distal (a, c, d) or proximal (b) epiphyses.

Grootteverschillen in de schachtlengte van de opperarm (a), de ellepijp (b), het dijbeen (c) en het scheenbeen (d) in verschillende leeftijdsgroepen (I tot en met V) van mammoeten uit Sevsk: I = pasgeboren tot twee jaar; II = twee tot vijf-zes jaar; III = zeven tot elf-dertien jaar; IV = 13 tot 35 jaar; V = ouder dan 40 jaar; VI = opperarm van het grootste individue (waarschijnlijk mannelijk) met niet-vergroeide epiphysen; x = schachten met volledig vergroeide bovenste en onderste epiphysen; • = schachten met niet-vergroeide epiphysen; H = schachten met vergroeide onderste (bij a, c, en d) of bovenste (bij b) epiphysen. Vertikaal: schachtlengte; horizontaal: schachtbreedte, gemeten aan onderuiteinde.

same skeletons. In addition, in Sevsk, bones from a single individual are distributed over a smaller area than is typical for bone remains of African elephants. It is probable that some bones from the peripheral parts of the lens (about 20% of the total amount of bones) were redeposited from the lower (main) bone-bearing layer when the upper layer was formed. In the upper bone-bearing layer there are no partial skeletons with articulated bones, and these isolated bones are preserved worse than bones from the lower bone-bearing layer. A number of bones from the upper bone-bearing layer are broken, whereas there are only a few broken bones from the lower layer.

Observations on the decomposition of skeletons at places of animals' deaths show that complete decomposition of skeletons of adult individuals uncovered by sediments may take two to four years, while a calf skeleton under similar conditions is destroyed much faster (Haynes, 1991). The data of the Sevsk locality suggests that its formation took a very short time, as many complete skeletons of animals in different age categories are preserved there.

Several bones of other mammals were also collected in Sevsk, constituting less than 1% of all bone material collected at the locality (table 21). In the Berelekh locality, which was formed during several hundreds of years, remains of other large mammals constitute more than 8% of all finds. Though mammoth remains are dominant, bones of other mammals were also gradually accumulated here. Owing to the very fast formation of the Sevsk bone-bearing layer, bones of other mammals are only occasionally represented here.

With regard to the total number of individuals that died in Sevsk, a relatively large portion of the bones is preserved. The number of preserved specimens expressed as a percentage of the total possible number reaches 70% for some bones (table 22). The percentage quite probably might have been even higher, but part of the site (about 100-150 square metres) got lost when sand was taken for industrial purposes from the quarry in the spring of 1988 and the autumn of 1989.

Twelve large and six small siliceous chips, attributed to the Late Paleolithic on the base of typology, were collected in Sevsk (Maschenko, 1992). They were recovered from the basal level of the main bone-bearing layer. The absence of traces of patination suggests that they were a relatively very short time covered with sediments. However, they got into the main layer after its formation. The chips must have fallen and penetrated the loose sediments of the main bone-bearing layer (pers. comm. S.N. Alexeev, Anthropological Institute RAS, Moscow, and N.D. Praslov, Institute of Archaeology RAS, St Petersburg. Traces on the bones caused by humans (cuts, scrape scars, broken bones, etc.) are absent. The availability of undamaged and complete skeletons and large partial skeletons testifies to the absence of a relation between humans and the formation of the Sevsk deposit. Humans did not use bones from this burial.

The peculiarities discussed make Sevsk a unique natural (regarding its taphonomy) locality of *M. primigenius* remains. Owing to the fast formation of the bone-bearing layer without redeposition of any importance, the preservation of the material is very good. The availability of skeletons of calves of different ages is an outstanding event in the history of mammoth studies, which is enhanced by the simultaneous presence of remains of adults belonging to the same family group. The data on the Sevsk mammoths can tell us a number of peculiarities of the biological and social organization of *M. primigenius* that have hitherto been unknown.

The structure of *M. primigenius* family groups as revealed by the Sevsk mammoths

The assumed similarity of social organization and group structure between mammoths and modern elephants has been made more than once. Indirect evidence relating to similarity of age and sex composition between herds of *M. columbi* and of modern elephants was obtained from the studies of the Dent locality (Weld County, Colorado, USA) (Saunders, 1999). The Sevsk data supports that evidence as far as *M. primigenius* herds are concerned. The Sevsk mammoth herd consists of females and calves; remains of only one large individual might belong to a male. In other words, the composition of the Sevsk mammoths' family group does practically not differ from that of modern elephants. The analysis of age and sex composition of the Sevsk herd provides additional supporting evidence of a fast formation of the deposit, probably as a result of a catastrophic event.

The total number of bones recovered from Sevsk is 3,751 (collection PIN 4353) plus over hundred bones stored in the natural history museums of Sevsk and Bryansk. The number of individuals buried was calculated on the basis of preserved long bones (humerus, ulna, femur, tibia). Other bones, such as shoulder blades, pelvic bones, bones of the skull and lower jaw, were also taken into consideration. To determine the number of individuals more precisely, isolated epiphyses of long bones were counted separately and their number was compared with the number of long bones lacking epiphyses. In case the number of epiphyses was higher than the number of bones preserved, the surplus was considered long bones, as in the case of the tibias.

The total number of individuals was determined on the basis of the bones of the left side of the skeletons. In case the shafts of the left side were not preserved, the number of corresponding epiphyses was regarded as such. Sometimes bones from the right side of skeletons were taken into consideration, e.g., when corresponding bones with a given degree of epiphyseal fusion were lacking on the left side. Given the excellent preservation of the Sevsk mammoth remains, this type of calculation ensures utmost precision in the estimation of the number of individuals that died in Sevsk, which is 33 in this case; a less probable estimation is 34.

The method of determination of age and sex composition based on long bones of *M. primigenius* was worked out in studies of the Berelekh material (Baryshnikov *et al.*, 1977). The age groups were determined by the dimensions of the shaft of the long bones and the degree of fusion of the epiphyses. The ranges of age groups, established by means of the stage of development and the degree of fusion of long bones were defined more precisely for modern and some extinct elephants by Roth (1984), and, with relation to *M primigenius*, by Lister (1999). The determination of individual age based on the degree of epiphyseal fusion is more reliable if combined with data on the tooth generation in function. Among the adult Sevsk mammoths there were only two individuals of which the skeletal fragments were associated with the skull and the lower jaw. The age of the other adult individuals from Sevsk was determined based on comparison with reference data on the speed and sequence of epiphyseal fusion, and the dimensions of the long bones, combined with data on sexual dimorphism in modern elephants and mammoths. Special consideration was given to the possibility of a discrepancy between the individual age determined by tooth wear and by the stage of formation of the long bones owing to individual differences (Roth, 1984), which is the reason why the age grouping of the Sevsk mammoths differs from that proposed by other authors.

Complete skeletons of calves of different ages in the Sevsk mammoth collection provided the first opportunity to estimate the limits of size variability within age groups by means of isolated bones of immature individuals with unformed or unfused epiphyses (table 23). These skeletons also provided reference material for the purpose of determining bones of other calves with unfused epiphyses. The determination of their individual age was based on data on the growth speed of mammoth calves during the first years of life. Cross-comparison between individuals of the Sevsk herd and data on complete mammoth skeletons from other localities also helped in determining the sex of the adult individuals from Sevsk.

The following relatively complete immature skeletons from Sevsk were collected: an incomplete newborn skeleton (PIN 4353-2614 to -2717, photo 32: 1), a complete newborn skeleton (PIN 4353-1223, -1233, -1588 to -1563, -1594, -1596, -1838, -1844, -1885, -1888, -1980, -2162, -2163, -2225 to -2227, -2355, -2356, -2380, -2405, -2441, -2451 to -2460, -2464, -2495, -2499, -2507, -2543, -2544, -2549 to -2551, -2661, -2916 to -2920, -2923, -3100 to -3106, -3127, -3148), a complete skeleton of a one-year-old calf (PIN 4353-211 to -965, photo 32: 2), a complete skeleton of a calf aged three to four years (PIN 4353-447 to -585, photo 34: 1), and an incomplete skeleton of a youngster aged six to seven years (PIN 4353-14 to -1325, photo 34: 2).

From table 23 and fig. 39 it appears that out of the 33 individuals that died in Sevsk, five were in the age range from newborn up to two years (15.1% of the total number), four in the range from two up to five to six years (12.3%), five in the range from six to seven up to eleven to thirteen years (15.1%), nine in the range from thirteen up to thirthy to thirty-five years (27.2%), and ten individuals were over thirty-five to fourty years of age (30.3%).

The age composition of the Sevsk herd differs from that of mammoth groups from the Berelekh locality and most sites on the Russian Plain; the data on the group composition from the Mezen' site (Bryansk region, Russia) was used for comparison (Vereschagin, 1977, 1982; Soffer, 1985). It is an import observation that immature individuals (thirteen years and younger) constitute almost 45% of the group (fig. 39). The calves' sex can hardly be identified, but we assume that the sex ratio among newborns is on average one to one, as in modern elephants. In the Berelekh locality and the Mezen' site, immature individuals constitute only 11-12% of the total (Vereschagin, 1977, 1982). A similar percentage was calculated for other Late Paleolithic sites of the Russian Plain (Soffer, 1985). This is also a common death rate in populations of *L. africana* (Sikes, 1967; Haynes, 1992).

Among the nineteen adults, twelve or thirteen individuals have completely fused epiphyses on the long bones, and four or five individuals have an incomplete fusion of the distal epiphyses, with well-expressed epiphyseal sutures. These animals, especially females aged thirty to thirty-five years and older, appear as a distinct group in the size diagram of the long bones (fig. 38), but one individual, presumably a male, occupies a separate position in the diagram.

The profile of the Sevsk age diagram is very similar to the diagram of mass deaths of modern African elephants (Haynes, 1990, 1991). Haynes notes that during extreme droughts almost 90% of the animals of a population die, and that almost all deaths occur among females, immature individuals and calves. Assuming a simultaneous death of the Sevsk herd, one may conclude that the age and sex composition of the Sevsk family group is very similar to that in a *L. africana* family group; the age diagram is also indicative of a simultaneous death of the whole group.

Three out of five calf skeletons from Sevsk belong to the first age group (two newborns and one yearling). No isolated bones of calves at this stage of development were collected in Sevsk, so the proposed upper and lower limits of variability are based on the measurements of the bones from these three skeletons only (fig. 38: 1).

The second age group is represented by a skeleton of a calf aged three to four years (PIN 4353-447 to -585) (photo 23: 1). The preserved facial part of the skull contains functional dp^4 teeth. In spite of some damage,

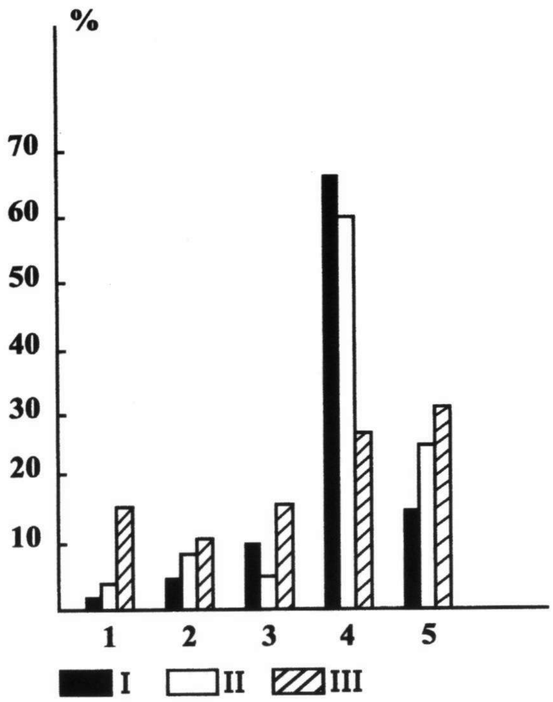

Fig. 39. Group composition of mammoths from Sevsk locality, the Mezen Site (both Bryansk region) and the Berelekh river (Vereschagin, 1977): I = Mezen; II = Berelekh; III = Sevsk; 1 = newborn upto 2 years of age; 2 = 2 upto 5-6 years of age; 3 = 7 upto 11-13 years of age; 4 = 13 upto 35 years of age; 5 = over 40 years of age.

Groepssamenstelling van mammoeten uit de vindplaatsen Sevsk, Mezen (allebei regio Bryansk) en de Berelekh rivier (Vereschagin, 1977), in procenten per leeftijdscategorie. I = Mezen; II = Berelekh; III = Sevsk; 1 = pasgeboren tot twee jaar oud; 2 = twee tot vijf-zes jaar oud; 3 = zeven tot elf-dertien jaar oud; 4 = 13 tot 35 jaar oud; 5 = ouder dan 40 jaar.

it is possible to ascertain that not all plates of the dp^{4}are touched by wear. The upper and the lower limits of this size group are based on an estimation of the growth speed of the long bones during the first post-natal years. As individual variability in young mammals may be very great, these dimensions cannot reflect completely all possible size variations in bones of mammoth calves of the second age group. They represent mean values, based on data on the reference specimen, the individual age of which had been reliably determined (fig. 38: 2). The size ranges of the ulna, measured by the diameters of the proximal ends, overlap in group I and II. However, the shafts in group II are longer. In group I and II the diameters of the proximal ends of the humeri also overlap, and in group II the shafts are also longer.

The third age group is represented by a skeleton of an individual aged six to seven years (PIN 4353-14 to -1325, photo 33: 2). The functional tooth generation preserved in the facial part of the skull is that of dp^4. The teeth are worn substantially; only ten plates remain. It is probable that at least four or five anterior plates were worn down completely. Other skulls of *M. primigenius* showing a dp^4 with a similar degree of wear have a M^1 in the first stage of wear.

This age group is represented by a relatively small number of remains from Sevsk. This is the reason why the upper limit of size variability is based on the measurements of the bones of this six-to-seven-year-old female: they are the largest in size of the entire age group III sample. The upper age limit in the third group is provisionally established at thirteen years. This is the age that roughly corresponds to the end of maturation, as far as can be judged from the diagram of absolute growth (fig. 34). The maximum size of long bones in the third group may be somewhat larger than those of the individual aged six to seven years. This deliberation takes into account that bone growth in mammoth cows slows down considerably (fig. 31).

The size diagram of the long bones (fig. 38a, b) shows that in groups II and III the maximum lengths of ulna and humerus slightly overlap, but the diameters of the proximal ends of the ulna and the distal ends of the humeral shafts are always greater in group III.

An outstanding example of the differences between mature male and female skeletons is provided by the Yuribei River (Gydan Peninsula, Tyumen' region, Russia) mammoth skeleton (PIN 3941-1 to -130). The individual age of this specimen (eleven to thirteen years) was determined on the basis of its tooth generation: all M1 plates are in wear (Dubrovo, 1982). This age corresponds to the third age group from Sevsk. Comparison of the measurements of the long bones of the Sevsk group III and the Yuribei mammoth reveals that the latter is much larger (table 23). The dimensions of the long bones of the Yuribei mammoth correspond to the dimensions of the long bones of an adult individual (over 35-40 years) from Sevsk, or to adults (13-35 years) from Berelekh (Baryshnikov *et al.*, 1977). The degree of epiphyseal fusion in the long bones of the Yuribei mammoth corresponds to that in the Sevsk group III (all epiphyses are unfused). This discrepancy between body size and individual age might be accounted for by slow tooth wear in the Yuribei specimen. However, it is not typical of *M. primigenius*. Even if a delayed tooth change is taken into consideration, the age of the Yuribei mammoth cannot be over thirteen to fifteen years; the size of the skeleton makes the mammoth stand out in the older age group. A more reasonable explanation of the large size of the Yuribei River mammoth (the mounted skeleton is 270 cm high) in comparison with other individuals of the same age is the assumption that this one is a male. From the end of maturation period (twelve to fifteen years), modern elephants show explicit sex dimorphism in the sizes of males and females (Stanley, 1943; Rench & Harde, 1956; Johnson & Buss, 1965; Lee & Moss, 1994; Sukumar *et al.*, 1988). If it is assumed that most specimens from the Sevsk groups III and IV are females, and the

Yuribei mammoth is a male, that could well account for the differences in size.

Age group IV is composed of remains of individuals whose growth was still continuing. The group is represented by an incomplete skeleton of a female (PIN 4353-4 to -3573, photo 34: 1). The functional teeth in the skull are M^1-M^2. The M^1 plates are all in wear; four anterior plates of M^2 are also in wear. To judge by the tooth generation, the individual age of this specimen should be fifteen to seventeen years. The height of the mounted skeleton at its highest point, the apex of the skull, is about 185 cm.

All humeri and femurs with fused distal epiphyses and incompletely fused epiphyseal sutures are referred to the fourth group. Humeral and femoral shafts that lack epiphyses but fall into the size range of the fourth group are also included here. This group also comprises all tibias and ulnas with incompletely fused distal epiphyses and tibial and ulnar shafts that lack distal epiphyses, but are larger in size than those in group III. Some lengths of ulna and tibia in the diagram of fig. 38 IV were conceived as the combined measurements of shaft and epiphyseal lengths. The dispersion of values in this group is the largest, because this period of ontogenesis is characterized by maximal physiological activity. In cows, this period is the apex of birth-giving capacity, in bulls the apex of reproductive activity (Haynes, 1991; Shoshani *et al.*, 1991). The diagram sketched in fig. 36 (group IV) does not reveal the significant differences that would be reflected if the sample included both males and females, as sex-bound size differences in modern elephants and in mammoths are very big during this period. Consequently, the sample consists of females only.

All long bones with completely fused proximal and distal epiphyses are referred to the fifth age group. Individual growth in this age group has stopped completely, so it comprises individuals over 35-40 years of age (fig. 38, V). Dimensions, proportions and variability of long bones of the individuals that compose this group show that all but one are females (table 23). The largest Sevsk individual referred to this age group is probably a male (PIN 4353-314 to -3837, photo 34: 2).

Comparison of the sizes of long bones of mammoths from Sevsk and Berelekh shows that the individuals from the former locality are smaller. It is probable that the Sevsk mammoth population consists of the smallest representatives of the genus *M. primigenius* in Eurasia. Considerable size differences between dispersed populations of *M. primigenius* at the end of the Pleistocene are well known (Vereshchagin, 1972, 1977; Vereshchagin & Nikolaev, 1982; Coope & Lister, 1987; Vartanyan *et al.*, 1993; Derevianko *et al.*, 1997; Kubiak, 1999). In particular the differences in body height range from 2 to 3,3 m. These facts testify to a significant polymorphism in late representatives of the genus *M. primigenius* that reflects real differences in the environments of populations that inhabited different areas of Eurasia.

In body size, the Sevsk mammoths are comparable with the small mammoth form described from the early Holocene of Wrangel Island, *M. primigenius vrangeliensis* Garutt, Averianov et Vartanian, 1993 (Averianov *et al.*, 1993). The description of this species was based on M^3 and M_3 only. The dimensions of the long bones are unknown, but indirect data indicates dimensional similarity between the Sevsk and the Wrangel populations. The relatively small M3 in all probability testifies to the small size of the Wrangel mammoths, perhaps the smallest representatives of the genus *M. primigenius*. However, there may be no direct correlation between tooth size and body size in elephants, so the dimensions of mammoths from the Wrangel population may even have been smaller than those of the Sevsk mammoths.

The M3's of Wrangel and Sevsk are similar in length and width, but differ in frequency of plates and enamel thickness (table 24). Data on the Berelekh and other Late Pleistocene localities of eastern Siberia shows that in all these regional populations the number of plates is higher and the enamel thickness smaller (Rusanov, 1968; Zerechova, 1977; Sher & Garutt, 1985a, 1985b; Lazarev & Tomskaia, 1987; Averianov *et al.*, 1993). In the Sevsk population, the enamel is thicker than in all other mammoth populations of eastern Siberia and central Russia (fig. 40). These differences are particularly significant in the enamel thickness of M3. A slightly increased enamel thickness and a decreased number of plates were noted in only one population of the latest *M. columbi* (Saunders, 1995).

The long bones of one individual are considerably more sizeable than those of all other adults, which suggests that this one might be a male. The femur of this individual (PIN 4353-2792, photo 24: 1) is 1010 mm, whereas the mean value among the adults is 880 mm (max. 920 mm). The tibia that most probably belongs to the same individual exhibits incompletely fused epiphyseal sutures (PIN 4353-555, photo 35: 1). All other tibias of adults with completely fused epiphyseal sutures are considerably smaller, e.g., that of the specimen PIN 4353-1240 (photo 35: 2). This tibia probably belongs to the smallest Sevsk adult: its length is 46 cm. The skeleton of this individual must have been 170-180 cm high (calculated with reference to the specimen PIN 4353-1240). The height of the mounted skeleton of the largest individual considered to be a male is 235 cm. The estimated live weight of the Sevsk mammoth bull based on its size is 3-3.5 tons, that of a mammoth cow is 1.8-2.2 tons.

There are a number of differences in dimensions and shape between mammoth tusks from the Late Pleistocene of Siberia and those from Sevsk (table 25). Studies by Vereshchagin & Tikhonov (1986, 1999) show that the tusks of the eastern Siberian mammoth cows are on the whole thinner and straighter, and those of the mammoth bulls thicker and spirally twisted. These authors used the curvature coefficient (K/k) to determine the sex to which an animal belongs. This coefficient provides reliable data on sexual dimorphism within the material they studied. The mean values of K/k are 46.7 for males and 31.7 for females (Vereshchagin & Tikhonov, 1986). The shape of the tusks in the only complete female skeleton from western Siberia (Oesh' River, Novosibirsk region, Russia) is illustrative of the existence of such differences between males and females all over Siberia (NNSM). The spirally curvature is insignificant and the tusks are almost straight. The length of the longer (right) tusk is 114 cm when measured by cord and 140 cm when measured along the curve. The greatest diameter of the tusk in cross section is 74 mm. The individual age of the female is 40-45 years (all plates in wear). The height of the mounted skeleton is ca. 215 cm.

In determining the sex of the Sevsk mammoths the use of the curvature coefficient alone is insufficient because this population shows some peculiarities. Some Sevsk mammoth cows had extremely twisted tusks, however small in diameter and length. On the other hand, the individual considered to be male had the largest tusks but they are only slightly twisted (table 25, nos 4353-3566, 3565). Besides, comparison of data published by Vereshchagin & Tikhonov (1986) with the Sevsk data shows that most tusks from Sevsk are considerably smaller than female tusks from Siberia (fig. 41). Only one individual from Sevsk has tusks that are comparable in size with female tusks from Siberia (fig. 41b: I), but this individual might be a male.

A striking peculiarity of the skeletal morphology of the Sevsk group is the presence of openings in spinal processes of thoracic vertebras (photo 35: 4, 5). Such holes were observed in at least three or four calves and one adult. In mammals such features are usually genetically fixed, they are inherited and preserved in family groups. Inheritance and distribution of similar features are described in humans from archeological sites and in domestic animals.

The data discussed above shows that most parameters of the Sevsk group are similar to those of a family group of modern elephants that consists of closely related females and calves only. Geological and taphonomic data on the Sevsk locality (e.g., the presence of remains of newborns) suggests that all animals constituting the group died simultaneously as a result of a certain catastrophic event, e.g., a quick rise of water in the ancient valley of the river Sev.

The structure and age profiles of *M. columbi* male and family groups

Comparative data on groups and group composition of mammoths are available only for *M. columbi* from two North American localities: Hot Springs (South Dakota, USA) and Dent (Colorado, USA). Apart from Sevsk, there is no data on age and sex composition of *M. primigenius* from other Eurasian localities, partly because all these did not result from the spontaneous death of a group, but were formed through many years of bone accumulation, and partly because of extensive bone-collecting in the places of mass accumulation.

Hot Springs is a major natural locality of remains of *M. columbi* in North America (Agenbroad, 1984, 1990; Agenbroad & Mead, 1995 (eds), 1996; Haynes, 1987, 1990, 1991). This site was a large natural trap that had existed for a very long time (ca. 1000 years). During that time about 100 mammoths met their death there. The radiocarbon age of the site is about 26,000 years (Agenbroad & Mead, 1996). Mammoths were attracted to the area most probably by the availability of water and, even more important, of mineral salts that covered the soil around the water source. A similar concentration of groups of *L. africana* around plots of soil that contain mineral substances was described by Shoshani *et al.* (1991). It was supposed that the locations of *M. columbi* and*Mammut americanum* in North America relate to sources of mineral substances (Abraczinskas, 1994). Some data has emerged that indicates sources of mineral substances as the areas where *M. primigenius* remains were accumulating because groups of animals visited these sources for many years (Leschinsky, 1999; Maschenko, 1999; Derevianko *et al.*, 2000).

In Hot Springs the mammoth remains consist of complete skeletons or large fragments, some bones of which have preserved their articulated position. Only a few groups of bones are relatively scarce (table 26). The majority of the remains represents individuals of twenty to thirty-nine years of age (55% of the total number of bones), whereas individuals of ten to nineteen years of age constitute the minor part (40% of the total number of bones). There are not more than three individuals aged over thirty-nine (Agenbroad & Mead, 1996). The dimensions of the tusks, the structure of the skulls, and some other peculiarities of the skeleton as well as the large size of the individuals (the skeletons are from 295 to 377 cm tall) suggest that the assemblage consists of the remains of young males (Agenbroad, 1990; Haynes, 1990). The researchers reached that conclusion after studying sexual dimorphism in *M. columbi*: the estimated greatest shoulder height of males is 395 cm and that of females 290 cm (Haynes, 1990, 1991). This estimation forms the basis of their assertion that the site contained remains of males from male groups. Remains of females and calves are not represented in the locality.

Deaths of mammoths in Hot Springs might be explained by casual trapping of young mammoths that either dwelled in the environs or occasionally visited the area. This explains why the age profile of the Hot Springs mammoths does not coincide with any of the four age profile types observed in different death assemblages in modern *L. africana*. According to Haynes (1990, 1991), the remains at Hot Springs form a peculiar type of mammoth site, which was formed as a result of nonselective deaths (C-type deaths in populations) under the special condition of the functioning of a natural trap. The assemblage reflects the sex composition of the groups of Columbian mammoths that visited the locality (Haynes, 1991).

The Dent site (Colorado) is one of the latest locations of *M. columbi* in North America. Dated by radiocarbon, its geological age is 10,800 years. Data on material from this site supports the idea that family groups in late representatives of *M. columbi* existed, as far as, at least for the Dent site, a simultaneous death of a hunted group of females and calves of both sexes was established. The group consists of fourteen individuals and their death was partly caused by a mass kill (Haynes, 1985; Saunders, 1995, 1999).

The Sevsk, Dent and Hot Springs sites suggest that family groups consisting of females and calves only (Sevsk, Dent) and groups consisting of males only (Hot Springs) existed in populations of both *M. primigenius* and *M. columbi*. The data on these localities lay the ground for reliable judgements of the structure of groups, the social organization of mammoths and earlier unknown biological facts related to the species, which appear to have almost identical counterparts in the biology of the two modern elephant species in Africa and Asia.

The composition of family groups in recent elephants

Comparison of data on the social organization of modern elephants reveals no significant differences in group structure between *L. africana* and *E. maximus*. Both African and Indian elephants form family groups consisting of cows and calves and male groups consisting exclusively of bulls of different individual ages. Solitary males are also frequent among both species (Sikes, 1966, 1971; Laws & Parker, 1968; Laws, 1970; Eisenberg & Lockhart, 1972; Eisenberg, 1980; Douglas-Hamilton, I., & Douglas-Hamilton, O., 1972; Hanks, 1972; Mc Kay, 1973; Laws *et al.*, 1975; Shoshani & Eisenberg, 1982; Kingdon, 1979; Shoshani *et al.*, 1991; Haynes, 1991).

A family group in *L. africana* consists of an adult female and her offspring of different individual ages. Other adults in such a group are the grown-up daughters of the oldest (dominant) cow. The oldest cow leads the group, determining intra-group relations and relations with other family groups. The group has a rather rigid hierarchical structure. Social ties within the group are based on relations of the mother-child, sister-sister type and on a not very strict domination of the oldest female. Mature females remain in the group. In favorable conditions, the number of individuals that composes the group increases. Adult cows that start reproducing either remain in the group with their offspring of different ages, or leave it for some time, or permanently. In the last case they form a family group of their own.

The normal length of gestation in *L. africana* is 21-22 (23?) months, lactation lasts about two to five years. The interval between two subsequent births lasts about four and a half to five years, sometimes six to seven years if the population lives under extremely unfavourable conditions. An African elephant cow can reproduce at least till the age of fifty (age determination is based on M3 wear in lactant females). The oldest cow remains the group leader until she dies, or till the end of her reproductive period. After that, if the group remains together, leadership is taken over by one of her elder daughters. When the matriarch dies, the group sometimes splits into a few new ones. The first birth occurs at different ages in different populations. Under natural conditions it usually takes place at the age of thirteen years, but may also occur at ten or seventeen. Calves are born in different seasons.

Males stay in their family groups till the beginning of maturation, i.e., until they reach the age of thirteen to fifteen years. At this age they leave the family group and either join a male group or start leading a solitary life. Sometimes a family group may comprise two to three adult sisters. Usually one of the sister cows is dominant and leads the group. Such a group may number twenty-one to twenty-two individuals. Groups composed of only one adult cow and her offspring are usually smaller and count from two to three to six to eighteen individuals. A family group dwells in a permanent territory and sticks to it even in most extreme situations. Male groups and solitary males roam around in the territories of different family groups. Under unfavourable conditions, males are the first to form large groups for migration to other territories. Groups comprising many individuals are observed during most favourable seasons, when sufficient food and water are available. When the quantity of food within the territory inhabited by a family group is reduced, the group breaks down into smaller units that usually consist of one cow with one or occasionally two calves of different ages.

The number of individuals and the composition of a male group are not constant. Changes depend on the season, and also on the age and physiological state of the males constituting the group. Solitary males that never join male groups are rather frequent. The death rate among males that have left their family group rises. The change of their way of life and the breaking of reliable social ties, in addition to other unfavourable factors, most probably cause psychological stress among the animals. Besides, at this age a young male is not experienced enough to do well without support from his family group. This enhances the probability of death substantially.

The age of individuals composing a male group may differ. However, a group usually comprises males of the same age and, especially, more or less equal size and strength because during maturation and, particularly, during the period of sexual activities, males are mutually rather aggressive. During copulative periods males leave their male groups, but do not stay in family groups for long. Separation of a male and female from a family group for two to five days is occasionally observed. After that time the female returns to her family group.

Sometimes mammoth cows and calves build formations larger than a family group. It was observed that during migrations several family groups unite. Groups comprising females, calves and males may number 60-80 individuals. Usually such a group covers no more than 40-60 km in several days because the calves are unable to walk more than six to eight km a day. At the beginning of the 20th century large seasonal migration groups numbering upto several thousands of individuals could be observed in Africa. Under the conditions of modern national parks with their limited territories no such migrations of large groups are observed.

Territoriality is typical of family groups of African elephants. As a rule, a family group dwells permanently in a limited territory. The dominant female, the matriarch, is believed to pass her whole life in such a territory. During the year, the female leads her family group through the territory, the route depending on the season and the availability of food. The matriarch knows her territory very well, and chooses optimal paths in the search for food and water in accordance with the season. No defensive behaviour against trespassing has been observed. However, a family group will not stay on alien territory for long and leaves it very soon. Similarly, it is extremely difficult to make a family group leave their own territory.

Under the conditions of a modern national park, the territory of one family group is usually 40-50 km across. During favourable years the territory may expand and sometimes overlap territories of other family groups. During unfavourable years the territory shrinks and many family and male groups concentrate around the scarce sources of water and food. If the conditions deteriorate further, most male groups migrate to remote areas, sometimes covering very great distances. Family groups are considerably less mobile. During severe droughts, cows with calves that leave their family groups die almost all. However, they leave their family territory only in exceptional cases.

In comparison with data on African elephants, data on family and male group composition in *E. maximus* is much more scarce, because even in restricted territories they stick to less-accessible areas, where systematic observation is hindered. No longitudinal studies of Indian elephants have been undertaken comparable with those that were made of *L. africana* family groups. The normal composition of family groups of Indian elephants on Sri Lanka is eight to twenty one individuals, but most frequent are family groups of six to eight members. Groups numbering over forty individuals were observed only three times in the national parks in the southern part of Sri Lanka. A group is led by the oldest female while she is in her reproductive age. All other females in the group are her daughters and granddaughters. Indian elephant cows mature by the age of ten years and give birth every two and a half to four years.

Under natural conditions males begin to reproduce at the age of fifteen to seventeen years, though they reach puberty already at the age of ten to twelve years. From the age of seven to eight years, males break away from their family group or form a subgroup of three to four young males that stays peripheral to the family group. Such subgroups stay separated from the adult males that may remain within the family group for a long time. Cases were observed in which a family group with females was accompanied by two adult males during the mating season. In large family groups, up to eight adult males together were observed. Male groups seldom occur among Indian elephants. All occurrences of male groups were observed in territories that during a certain season are abundant in food, and are also visited by family groups and solitary males. Male groups usually number three to five individuals. Observations show that about 90% of the mature males that do not join a family group remain solitary.

The family groups on Sri Lanka are not known to stick to a certain territory. Their distribution is determined by the availability of water. Usually a family group visits a watering place twice a day, so several family groups stay in the vicinity of the place within six to eight km distance, as the calves under one year cannot walk more than twelve to fifteen km a day. It is the attachment to one watering place that determines the concentration of family groups in the vicinity. Towards the end of the wet and dry seasons, several family groups may unite for migration. Usually they migrate no more than sixty to eighty km. However, because of the limited area of modern national parks, such migrations simply cannot be longer. Family groups formed during humid seasons are more numerous than those formed during dry seasons. This behaviour may be accounted for by competition between the group members for scarce food, which leads (as it does among African elephants) to the splitting of large family groups into smaller ones that usually comprise one female and two or three calves of different ages.

The social organization of these two modern elephant species, their biological peculiarities and behavioural plasticity provide an exemplary model of successful interaction between giant herbivores and their environment, even under continuous anthropogenic pressure. These and other data on biology and behaviour of modern elephants, as well as a combination with data on anatomy and reconstructed physiological peculiarities of mammoths lay the ground for a reconstruction of some biological features of *M. primigenius*. One may accept Haynes's (1990, 1991) opinion, based on the study of mass deaths of African elephants, that

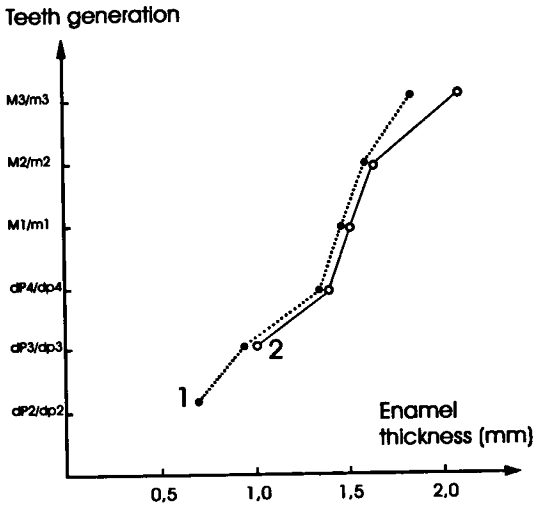

Fig. 40. Change of enamel thickness of dp2-M3 of mammoth populations from the Russian Plain and Eastern Siberia: 1 = Berelekh mammoths (Zherechova, 1977); 2 = Sevsk mammoths.

Verandering in glazuurdikte van dp2-M3 in mammoetpopulaties van de Russische Vlakte en oostelijk Siberië: 1 = Berelekh mammoeten (naar Zherechova, 1977); 2 = Sevsk mammoeten. Verticaal: kiesgeneratie; horizontaal: glazuurdikte (in mm).

the social structure of groups of mammoths should be directly connected with their biological peculiarities. The general morphological and anatomical features in large herbivores closely correlate with the behavioural patterns that are most important for the survival of a given species. In *M. primigenius* studies, age profiles do not only generate very precise information on group composition, but also on a number of other peculiarities of mammoth biology. Morphological features, such as the degree and expression of sexual dimorphism, the age at the onset of puberty, the group composition and growth peculiarities reflect both the main biological peculiarities and the most important adaptations of the mammoth. The suggestions concerning the character of these peculiarities we made earlier are supported by the available data on mammoths, comparative data on modern elephants and the new data from the Sevsk locality.

Ecology, ethology and adaptations of *M. primigenius*

Among all adaptations of the mammoth, the successive changes in the dentition of mammoth-like elephants are best studied (Maglio, 1973; Lister, 1996). Many other peculiarities of *M. primigenius* as opposed to other Proboscidea have become known only recently. Certain changes in tooth morphology of *M. primigenius* of the late Middle and Late Pleistocene do not fit into the general direction of changes in the lineage of mammoth-like elephants. These changes in M3 morphology of *M. primigenius* may be accounted for by secular environmental fluctuations within different phases of falls and rises in mean temperatures during the Late Pleistocene. Part of these morphological deviations of M3 may be of micro-evolutionary origin and they were observed in the latest representatives of *M. columbi* and *M. primigenius* (Maschenko, 1998; Saunders, 1999; Foronova & Zudin, 1999).

Morphological changes in the last-generation molars, however, form only a minor part of the peculiarities that make up the unique specialization of the woolly mammoth. The adaptations of *M. primigenius* to seasonal colds over most of the inhabited area were the most significant for this mammoth. These adaptations determined the peculiarities of ecology, ethology and morphology of mammoths in comparison with modern elephants. The adaptations affected a large complex of morpho-physiological peculiarities of the mammoth, and made the species hyper-specialized. All existing data on the habitat of *M. primigenius* suggests that the species inhabited areas with a cold and dry climate and a long winter season in Eurasia and North America.

The adaptational complex affected the mammoth's individual development. In a cold climate, births are possible in spring or early summer, like in most modern large mammals that inhabit arctic and moderate zones. The first data in support of this suggestion was obtained from studies of a carcass of a mammoth calf from the Kirgiliach river. The reliably determined individual age (about seven months) and the time of death (late autumn) indicate that the calf could only have been born in spring (Vereshchagin, 1981; Shilo *et al.*, 1983; Vereshchagin & Tikhonov, 1999). One may further suggest that during the Late Pleistocene the time of birth in the Kolyma river area was April.

Similar data was obtained from the Sevsk mammoths that died in a sudden catastrophic event. Among them there are two newborn and two yearling calves. Seasonal births suggest a seasonal coupling time; a feature which is not found in modern elephants, because they couple at various times throughout the year. Considering a shorter gestation period in *M. primigenius* than in modern elephants, one may suggest that mammoths mated in autumn, most probably in September-October. This suggestion is supported by the existence of similar copulation periods in large modern arctic herbivores, of which they are typical representatives.

The determination of the length of the lactation period in the mammoth may be based on the data on eruption and speed of wear of the first-generation teeth. This data is indirectly indicative of the time when vegetal food becomes dominant in the animal's diet and, consequently, suggests decrease of lactation in the mammoth cow. As was shown earlier, in *M. primigenius* dp2 and particularly dp3 and dp4 erupted and began to wear earlier than in modern elephants. The wear of dp2 in *M. primigenius* and *L. africana* takes a comparable amount of time. In the African elephant, dp4 is worn after three years, but the distal part of dp3 remains functional until the age of four and a half years (Sikes, 1966, 1971). Similar data was obtained from wear of the first three tooth generations in *E. maximus* (Roth & Shoshani, 1988).

The very early eruption and intensive wear of dp3 in *M. primigenius* during the first year of life (roughly half a year earlier than in modern elephants) suggest that from the age of six to seven months a calf lived on combined food. By the end of the first year, milk was secondary food. The erupted and functional dp4 marks the end of the lactation period very precisely. In mammoth calves dp4 fully replaces dp3 at the age of two years. The occurrence of dp4 replacing dp3 at two and a half to three years is evidently an exception (Kuzmina & Maschenko, 1999). Thus, in *M. primigenius*, dp4 becomes functional one to one and a half years earlier than in *L. africana*. This data suggests that a mammoth calf began to feed systematically on vegetation approximately one to one and a half years earlier than modern elephant calves. To judge by the speed of wear and the time of eruption, a calf of one and a half year fed almost exclusively on vegetation and, consequently, the lactation period had ended by that time.

These differences between mammoths and modern elephants can be accounted for by a dramatically reduced lactation in mammoth cows in winter time when the animals fed on dry vegetable food and branches. A calf was obliged to shift to adult food to survive. It is possible that the lactation finished completely by the end of the cold season, thus twelve months after parturition, so that the total length of the period of lactation was two times shorter than in modern elephants.

Mammoths gave birth to smaller calves than Indian and African elephants: *L. africana* newborns are 25-30 cm taller (*E. maximus* 15-20 cm) than mammoth newborns. Data on growth dynamics of the first year of the mammoth's life shows that, regardless of the small size of newborns, by the end of the first year a mammoth calf reached the size of yearling calves of modern elephants. In other words, the growth rate of mammoth calves during the first six to twenty-three months was higher. This important peculiarity of mammoth biology may be accounted for by the necessity to reach a body size that was indispensable for survival in winter time and to endure migration to the winter area. In search for food mammoths must have roamed over a much vaster territory than modern elephants, which live in areas with tropical climate and continuous plant vegetation.

The sudden death of the Sevsk mammoths in a river valley is indicative of ecological ties of mammoths with water meadows. During the Pleistocene, adequate quantities of food for numerous giant herbivores were available primarily in the floodplains (Vereshchagin, 1972, 1977). The Sevsk mammoth group evidently was unable to leave the dangerous area and died as a whole. However, catastrophic events of this sort may have been a rare occurrence. By analogy with modern elephants, one may suggest that family groups were the first to die in such catastrophes. In *L. africana* up to 100% of the cows and calves die in severe droughts because family groups are bound to their territories and their migrations are short. The death rate among African elephant bulls is much lower (Haynes, 1991). Mammoth bulls, being much stronger and more mobile than cows and calves, supposedly were able to avoid death in such events. Age profiles from Berelekh and Sevsk support these considerations (Baryshnikov *et al.*, 1977; Vereschagin, 1977).

The ecological restriction of mammoths to river valleys is the reason why their remains are predominantly found in such areas. Mass accumulation of their remains in river valleys, however, is indicative of regular deaths in areas of mass dwelling (as in African elephants) rather than of frequent catastrophic events causing mass group deaths. It is possible that the animals concentrated in dangerous places of river valleys on their migration routes. In such places the most feeble animals, e.g., calves, may have died every year when, for example, they were crossing the river over the ice.

Now the question of whether and to what extent *M. primigenius* was a vagabond or a settler with well-expressed territorial behaviour may be considered from the point of view of the data on family and male group composition. For a more complete reconstruction of some behavioural peculiarities and the ecology of the mammoth, one may directly extrapolate the data on modern elephants connected with the survival of these giant herbivore mammals. Also of great importance is the data on the climatic conditions of the Late Pleistocene and composition of the flora in the areas inhabited by mammoths.

The peculiarities of the social organization and some biological data on *M. primigenius* allow one to conclude that there were two distinct periods within the animal's cycle. During these periods feeding strategies were dramatically different. Data on the bioproductivity of Pleistocene vegetation communities shows that in summer a family group of mammoths might live on the resources of a relatively small part of their territory, a situation similar to that of a family group of modern elephants (Sukachev, 1914; Tikhomirov, 1958; Solovenich *et al.*, 1977; Ukraintseva, 1981, 1991; Gorlova, 1982; Kozhevnikov & Ukraintseva, 1999). The area of such a field occupied by a family group of mammoths was probably two to three times larger than one of *L. africana*, given the lower productivity of North Asiatic vegetal communities in the Late Pleistocene. Family groups including calves born in spring stayed in their areas during the entire spring and summer season, and in autumn and winter were compelled to continuously migrate because the vegetation disappeared.

Such territorial behaviour of a family group was their best survival strategy. The strategy of a relative residence only permits survival and growth of newborns that cannot walk for long, until they have reached a certain age. By analogy with modern elephants, a group including calves born in spring could not cover distances of more than ten to twelve km within the limits of the family group territory.

The dramatic difference between modern elephants and mammoths lies in the change of behaviour and feeding strategy in winter. When the vegetation ceased growing, the bioproductivity of the family group's territory dropped severely and a much more extensive area was needed for the group to feed on. There is no direct analogy between the winter conditions met with by mammoths and modern elephants, though there exists a certain similarity in the usage of different foods by modern *L. africana* and *E. maximus* (Oliver, 1983). Because of the poverty of the north Eurasian flora in comparison with the tropical flora, mammoths were considerably more specialized in the use of resources than modern elephants. In all parts of the inhabited area mammoths were able to survive owing to a great heterogeneity of vegetal communities. In comparison with modern arctic and moderate zones, this Pleistocene heterogeneity caused the greater vegetal productivity (Sher, 1976; Ukraintseva, 1991).

In regard to the vegetation mammoths fed on, conclusions may be drawn from the analysis of the stomach contents of several mammoths recovered from the permafrost. All these specimens died at the end of summer or the beginning of autumn, so it is possible to reliably determine the composition of their summer food. The plant remains from the stomachs show that, during the period of summer vegetation, mammoths predominantly fed on grasses and the portion of bushes and trees was substantially smaller (Zalensky, 1903; Gorlova, 1982; Ukraintseva, 1991; Kozhevnikov & Ukraintseva, 1999). Adult individuals of *L. africana* heavier than five tons consume more than 300 kg of green pulp a day (Sikes, 1966, 1971; Laws & Parker, 1968; Hamilton, 1973; Laws *et al.*, 1975; Moss & Poole, 1983). The daily mass of green vegetation needed by an adult mammoth weighing two and a half to three and a half tons may have equalled 150-200 kg. Since the assimilability percentage and nutritive value of vegetal species in the food of mammoths and modern elephants differ only slightly, the estimation of the mammoth's daily need for food may be based on analogy (Oliver, 1983).

However, the differences in food composition caused by the alternation of humid and dry seasons, as they are observed in relation to modern elephants, cannot simply be equated with temporal differences in the composition of mammoth food just because the alternation of summer and winter seems to have created an analogous situation, although, of course, the change of food certainly occurred in connection with the growth stop of the vegetation in winter.

The data on the food composition of mammoths during winter is scarce. Indirect evidence, however, allows the suggestion that during winter they fed on dry grass and branches of bushes and trees. The relative quantity of grasses was lower than during summer. Feeding on the past year's grass was possible for adults and hindered in immature individuals and calves because it required removal of the snow cover with the tusks. It is possible that individuals with larger tusks had a certain advantage in intragroup competition for food.

Compared with other Late Pleistocene mammals, mammoths were more restricted to river valleys because foraging on pastures of relatively low productivity required an optimized use of energy. River valleys seem to be the most important parts of family group territories. During their winter migrations, which most probably took place along river valleys, groups may also have used other territories. The climatic conditions of the Late Pleistocene suggest that these could have been the southern slopes of river forelands.

The total standstill of vegetation growth during winter is not comparable with the retarded growth of vegetation in the tropical zones during dry periods. A decrease of productivity per unit of area is unavoidably followed by an expansion of the territory where the animals forage. In addition to this, the necessity to optimize the energy expenditure was much more strict for mammoths than for modern elephants in view of the higher energy expenditure of mammals that inhabit subarctic areas. This required a higher motility of mammoth family groups in winter when vast territories were roamed in search for food. Even those parts of a territory that were the richest in food could not be used for the second time during the six to seven cold months before spring, when the growth of vegetation started again. During winter a group had to move continuously in search for food without coming back to the spots already used for this purpose.

Migrations most probably were directed to the south and, from the second half of winter, back to the north. By analogy with *L. africana* it was supposed that mammoths covered a distance of about two thousand km within two months, i.e., approximately thirty-five to forty km a day (Oliver, 1982). However, this could not be so if a group included calves younger than one year. During their winter migrations family groups most probably moved some 900-1200 km away from their summer territory within three to three and a half months. In addition, the speed of seasonal migration was limited because of the lower productivity of the arctic Siberian pastures in comparison with the tropical zone. A daily march during winter migration may have been no longer than twenty km, inasmuch the giant mammals had to spend about 75% of their time foraging food (McKay, 1973). This consideration makes it clear that a fast growth of mammoth calves during their first year formed an important part of their survival strategy. The fatigues connected with

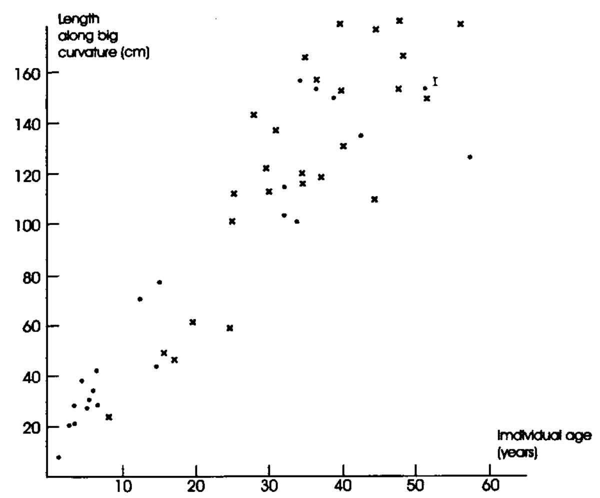

Fig. 41. Dimensions of tusks of female mammoths from Eastern Siberian populations (after Vereschgin & Tikhonov, 1986) and from the Sevsk locality: × = tusks from Eastern Siberia; x = tusks from Sevsk; I = largest tusk (male?) from the Sevsk locality

Maten van slagtanden van vrouwelijke mammoeten van oost-Siberische populaties (naar Vereschagin & Tikhonov, 1986) en van de vindplaats Sevsk: × = slagtanden uit Oost Siberië; x = slagtanden uit Sevsk; I = grootste slagtand (mannelijk?) uit Sevsk. Verticaal: tandlengte gemeten aan grootste kromming (in cm); horizontaal: individuele leeftijd (in jaren)

the extended winter migrations of family groups were a harsh factor of natural selection. In modern medium-sized mammals with a different biology (*Rangifer tarandus*) the length of a daily march amounts to several dozens of kilometres.

Thus, the annual cycle of M. *primigenius* consisted of summer and winter periods characterized by different survival strategies. In summer a family group dwelled permanently in one area. During this time the young were born or nourished. In winter, groups continuously moved from one place to another because food resources were not renewed. It is possible that during this unfavourable period groups split up into smaller subgroups consisting of a mother and her calves, a development also seen among modern elephants. A similar annual cycle is observed in modern large mammals of the Arctic.

The transition to life under cold climatic conditions, which was accompanied with forage from under the snow cover in winter, is reflected in the morphology of *M. primigenius*. First, there are the exterior peculiarities observed in northern forms by contrast with their southern close relatives, such as relatively small ears, a shorter tail, and relatively shorter limbs. These changes in the mammoth by contrast with modern elephants were described by Zalensky (1903), and Vereshchagin & Tikhonov (1999). Furthermore, a relatively lower and longer body and a larger head are observed in the lineage of mammoth-like elephants (photo 37). The development of subcutaneous fat, which is important when animals experience food scarcity in winter, was also reliably established in mammoths.

The development of fur in *M. primigenius* has a number of peculiarities that makes it different from all other arctic mammals. The barbed hairs of mammoths are about four times thicker than similar hairs in all other mammals. The barbs are rather dispersed and there are no subcutaneous muscles capable of making the fur to stand upright in order to raise thermal protection. In this connection it is suggested that the system of blood supply to the peripheral parts of the limbs and the body surface may have played a more important role than the fur (Shilo *et al.*, 1983). No development of sebaceous glands that could have added to thermal protection when the fur was wet has been noted (Sokolov & Sumina, 1982). This data on hair morphology and thermal regulation in mammoths is in good agreement with the concept of adaptation of the species to the conditions of a cold and dry climate.

The alveolar parts of mammoth tusks are elongated in comparison with those of modern elephants and go almost plumb as they leave the alveoli. Evidently this is an adaptation that enabled mammoths to remove snow. The alveolar part of the tusks of the woolly mammoth is elongated in comparison with other ancient elephants of the mammoth lineage. This is a compensatory extension of the tooth surface within the alveolus and indicative of the load on the tusks caused by removing snow. It is exactly during snow removal that a wear face is formed on the outer and lower surface of tusk ends (Vereschagin & Tikhonov, 1986, 1990). On large tusks of males the length of such a facet may reach fifty cm. Direction and shape of the micro-furrows usually observed on the surfaces of such facets are indicative of wear against the surface of frozen soil. The spiral twist of the tusks in this connection is considered to be a biomechanical adaptation that enhances the durability of tusks used for snow removal. In *M. primigenius* this adaptation is expressed to the maximum (Chozatskii, 1990).

Another peculiar feature of mammoth morphology connected with feeding on low vegetation is the shortened neck. Baigusheva & Garutt (1987) put this peculiarity into the diagnosis of the genus *Mammuthus*. When the head is lowered to remove snow, the load on the cervical part of the vertebral column has to be resisted, and in this respect a shortened neck gives a certain biomechanical advantage. The relative size increase of the head occurred simultaneously and is quite marked, even in comparison with closely related forms of the mammoth lineage from the Early Pleistocene (photo 36).

The structure of the occipital bones and condyles in *M. primigenius* as compared with more ancient mammoth-like elephants also reflects a transition to feeding on the low cover. The condyles are relatively displaced forward and downward in the direction of the posterior edge of the tooth alveoli. The ratios of the distances between the upper edge of the condyles and the masticatory surfaces in *L. africana, E. maximus* and *M. primigenius* are 1.7, 1.5, and 1.2 respectively, which is indicative of a change of proportions determined in its turn by different types of load. The occipital bones in *M. primigenius* are placed vertically, so that raising the head is hindered. As for the shortened neck, the relatively long spinal processes of the cervical vertebrae testify to a well-developed muscular complex for supporting and lowering the head. In *L. africana,* that feeds on various types of vegetation, the occipital condyles are relatively displaced backward and the occipital bones are inclined forward, and so cause the rounded shape of the occiput in side view. With the distal part of the skull structured like this, it is easier for the African elephants to reach food at different levels (from grass to branches of trees that hang above the head). The range of feeding specializations of this species is therefore much broader than in *M. primigenius.*

Ecological restriction of mammoths to specific parts of their area as well as some peculiarities of their biology evidently caused concentration of the animals on territories that offered the best living conditions, whereas their numbers in other parts of the area were significantly lower, especially during unfavourable seasons. At the end of the Pleistocene this played a negative role and was probably among the factors that contributed to the extinction of the species.

Mammoths quickly changed ecosystems favourable to them, as do modern elephants in places where they are concentrated. At the end of the Pleistocene, when the climate changed dramatically, the number of areas favourable to mammoths was significantly reduced. The range of the species split up into several smaller regions, and evidently many groups of mammoths were concentrated on relatively small territories. As was learnt from African elephant populations, a quickly growing number of individuals on a small territory causes a crisis in the plant community and its rapid transformation into a community of a different type, less favourable not only to the giant mammals, but also to many other species of large mammals. The overpopulation usually led to a dramatic reduction (up to 8%) of the elephant population (Sikes, 1971; Douglas-Hamilton, 1973). A quick and efficient elimination of other large herbivorous mammals radically impoverishes biodiversity and is a side effect of mass pressure of proboscideans on ecosystems (Kingdon, 1979). During the Late Pleistocene this may have created additional opportunities for Late Paleolithic human tribes to specialize in hunting mammoths, thus aggravating the conditions under which the species still lived in disunited areas of its previous range.

However, there is no reliable data on systematic and specialized mammoth hunting of Late Paleolithic groups of humans. Nor have specific methods of such dangerous hunting been studied, though one can not totally deny the possibility that it was practised during the Late Pleistocene. Not a single picture of a wounded mammoth reliably dated to the Late Pleistocene is known, whereas all other contemporaneous mammals are systematically depicted as an object of hunting (Bozinski, 1995; Vereshchagin & Tikhonov, 1999). The data on Europe and Siberia shows that killings of adult individuals by hunters were rather singular cases (Onoratini *et al.,* 1995; Derevianko *et al.,* 2000). It is more probable that, being aware of the biological and behavioural peculiarities of mammoths, the ancient people were able to kill weak and solitary animals, or, still more probable, utilize carcasses of animals that had died recently.

Bone accumulations at Late Paleolithic sites of central and eastern Europe are associated with bone collecting in places where the bones had accumulated in a natural way (Soffer, 1985, 1993, 1997; Abramova, 1995; Chonbur, 1995). Even those accumulations that were not used by humans (e.g., the Sevsk locality) were visited. The use of mammoth bones in the Late Paleolithic human economy prompted people to search for such depositions (Maschenko, 1992).

There is no reliable data on the effect of weapons used in hunting, which is usually expressed in terms of pierced bones or parts of flint arrow and spearheads stuck in the bones. Two cases in which pieces of projectile heads were found in bones from the Kostionki Paleolithic site (Voronezh region) were reported by N. Praslov (pers. comm.). In one case the projectile head was in the frontal bone of the skull of an adult mammoth, in the other it was broken as it hit a rib of a young individual. The position of the projectile head in the skull cannot be taken as evidence of hunting, because the use of flint-headed weapons is inefficient when they are thrown into the head (skull bones cannot be pierced with such weapons). The position of a flint head fragment in the middle part of a fourth to seventh right rib shows that the animal was hit from the right upward, into the area of the heart. However, it is impossible to imagine such a stroke if the animal stood upright. As the animal was about 160-170 cm tall, the stroke could have been inflicted only if it, or the carcass, lay on the ground. Both cases are better accounted for not by hunting, but by the use of already dead animals' bodies.

Conclusion

The emergence and evolution of the genus *Mammuthus* is due to the adaptation of one group of mammoth-like elephants to feeding on mostly grass and bush vegetation under the conditions of a seasonal climate with cold winters when the growth of vegetation is interrupted. The morphology of the Middle and Late Pleistocene representatives of the group testifies to such an adaptation. The morphology and the specific taxonomic position among other Elephantida determine the distribution of the group, which, unlike earlier mammoth-like elephants, are found mostly in holarctic areas with a moderate or cold climate. The radiation of *Mammuthus* into the inner regions of Asia as far as Inner Mongolia, is well accounted for by the availability of satisfactory conditions for survival at the time of the lowest temperature drops during the Pleistocene.

The appearance of these adaptive morphological features at very early ontogenetic stages provides a solid ground for restricting the volume of the genus *Mammuthus*. The longer time of formation of not only the teeth of the last generation, but also of dp2, is very important in determining the position of *M. primigenius* in the biological system of the mammoth-like elephants. The mammoth teeth with their longer formation process become functional before the process has finished. In *A. meridionalis* , dp3 and dp4 start to wear at later formation stages. The longer formation time is connected with the greater number of plates (from dp4 onward), which is, in its turn, a compensatory adaptation to a faster wear of the tooth crowns in *Mammuthus*. Changes in tooth morphology, e.g., thinning of the enamel and an increase of the number of plates and of plate height, may be observed in all groups of the family Elephantidae. These are the features that compensate for the wear of dp4 to M3. The expression of these features reaches its maximum at the end of the Middle and during the Late Pleistocene. The Middle and Late Pleistocene mammoth-like elephants that were distributed over northern Eurasia and North America and displayed a feature complex adapted to a cold climate, should be attributed to the genus *Mammuthus*.

The data on stratigraphic distribution and morphology of mammoth-like elephants from the Pleistocene of Eurasia shows that in *Mammuthus* the definitive formation of a feature complex adapted to cold winters took place at the end of the Middle Pleistocene. The genus *Mammuthus* emerges in northeastern Eurasia during the end of the Middle and the beginning of the Late Pleistocene and persists until the beginning of the Holocene in the arctic regions of eastern Siberia. The forms that combine morphological features of *M. trogontherii* and *M. primigenius* were widely spread, but, to judge by the data available, they existed for a relatively short time. The unique complex of adaptations to cold conditions, the only known among Elephantidae, allows the separation of the mammoth-like elephants of the Middle and Late Pleistocene of Eurasia from more ancient mammoth-like elephants. The morphology of M1 to M3 in the latter group is similar to that in all other ancient Elephantidae, whereas strictly speaking it is different in the genus *Mammuthus* owing to the above-mentioned adaptations. Such being the case, the genus *Mammuthus* should be restricted to two species only: *M. primigenius* (the type species) and *M. trogontherii.*

In comparison with those of all other Elephantidae, the peculiarities expressed in the dental and skeletal morphology of *M. primigenius* are indicative of its specialization. The specialization of dentition and skeleton forms part of the set of morphological and biological adaptations of the species, that also comprise its specific body proportions, larger head, flattened occipital bones, short cervical part of the vertebral column, specific shape and structure of the tusks, development of wool and subcutaneous fat, and peculiarities of physiology at early stages of postnatal ontogenesis. Peculiar features of tooth morphology appear as early as during the first postnatal year, but they develop during the entire postnatal ontogenesis. The morphology of dp2 is similar in all Eurasian mammoth-like elephants, including *M. primigenius.* Some features of dp4 to M3, characteristic of *M. primigenius* and the genus *Mammuthus*, are expressed at later ontogenetic stages and are not known from more ancient mammoth-like elephants (*Archidiskodon*). Features of skull and lower jaw morphology that are characteristic of the species appear in *M. primigenius* at later stages of postnatal development and are evidently combined with the expression of secondary sexual characters. The former features may be considered not only as ontogenetic modifications, but most obviously also as recapitulations of phylogenetic modifications. At least changes in the proportions of the lower jaw directly correspond to modifications in the phylogenesis of mammoth-like elephants.

The sequences of morphological changes in dp4 to M3, in the skull and lower jaw during the late stages of postnatal ontogenesis of *M. primigenius* reflect the sequence of these modifications in the phylogenesis of mammoth-like elephants. The way by which these modifications are expressed allows the proposition that the divergence of the group took place in the Middle Pleistocene, not later, because early ontogenetic stages (before the age of one year) in *M. primigenius* and *A. gromovi* are notably similar.

The features on which the diagnosis of the genus *Mammuthus* is based are expressed at different ontogenetic stages. This peculiarity should be considered when their diagnostic value is estimated. In some respects, mammoth calves are similar to adult representatives of the genus *Archidiskodon*. In the course of ontogenetic development the differences in features increase, each feature being specifically expressed at a different stage of individual development. Such specific features as the position of the nasal opening, the shape of occipital bones, the direction of the tusk alveoli, the proportions of the facial and brain parts of the skull, the proportions and shape of the mental process become typical of adult *M. primigenius* only during the second ontogenetic period, the period of maturation. Together with structural features of the last tooth generation that are traditionally used in the diagnosis of the genus *Mammuthus* (hypsodonty, crown proportions, enamel thickness, and number of plates), the beginning of functioning of dp3 through M3 before the end of the crown formation should be considered as typical of this genus.

It has been reliably established that in the genus *Mammuthus* the eruption of the teeth of the generations dp4 through M3 took place during early stages of formation, i.e., before the formation of their posterior plates had been finished and the posterior part of the crown had been covered with cement. In more ancient mammoth-like elephants the formation of the crown by the time of eruption was more complete and included the cement coating. In comparison with modern elephants, e.g., the Indian species, wear of the first three tooth generations took place considerably faster. In *M. primigenius* the completely formed plates of dp4 consist of tightly fused enamel columns. In the process of tooth formation, the constituent plates show a stage at which they are subdivided into three lobes (one central and two lateral) which fuse later, beginning at the bottom and proceding toward their apexes, with the extreme apical parts remaining separated. In comparison with more ancient mammoth-like elephants, the fusion of the plate lobes in the mammoth has the greatest extent. That is why the wear figures at the masticatory surface of mammoth teeth quickly acquires the shape of a loop along the width of the whole plate.

The described sequence of expressions of phylogenetic features during ontogenesis is applicable to the morphology and position of di and I in the alveolus. The material that bears upon deciduous and permanent tusks of the Sevsk mammoth calves allow the reliable attribution of the di and I to different tooth generations, based on peculiarities of their substitution process. The positions of di and I in alveoli of *M. primigenius* provide solid grounds for a conclusion on the homology of tusks in Elephantidae. The morphology of the permanent incisor and the structure of its alveolus - which is formed by the premaxillary and maxillary bones - suggest homology of the rudimentary incisor with dI, of the deciduous tusk with dI^2, and of the permanent tusk with I^3. The preservation of incisors of both generations in all representatives of the family Elephantidae is suggested as well. Likewise indicative of this is the structural similarity of the tusk alveolus in the sister group *Moeritherium*.

The morphological adaptations to the holarctic cold climate had a great effect on the reproductive physiology and survival strategy of the mammoth. These formed an adaptational complex in response to the cold climate with its long winters. This complex included the quick growth of mammoth calves during the first six to eight months, within which period they reached the dimensions of one-year-old calves of modern elephants in spite of having been relatively smaller at birth. On the whole, the growth of *M. primigenius* during the first ten to seventeen years demonstrates stages corresponding with basic periods of physiological development in other mammals that inhabit regions with cold seasons. The growth speed varies between different periods and between sexes. From the beginning of the maturation period (from ten up to fifteen or seventeen years) on, males grow faster than females, and the growth process in males lasts longer. Some data on Late Pleistocene mammoths from south western Siberia suggest that size differences based on sexual dimorphism could reach 50% in some populations of *M. primigenius*, although this is not supported statistically. If this figure is correct, it far exceeds that for *L. africana*. Mammoths formed family groups composed of females and calves only, and male groups comprising males of different ages. The age profile of the *M. primigenius* specimens from the Sevsk locality is similar to that found in family groups of modern African and Indian elephants.

The survival strategy under cold climatic conditions is a most peculiar feature of the biology of *M. primigenius*. The annual cycle is subdivided into two periods of unequal length, summer and winter, during which the animals used considerably different strategies of feeding and behaviour. This life strategy optimized the energy expenses connected with the search for food and for locations adequate for survival under unfavourable conditions.

During the shorter summer period a family group dwelt on one terrain (family group territory) where it lived permanently after returning from its winter migrations. Calves were born on this terrain, and passed the first stages of their lives there together with their family group. The longer winter time was spent by continuous and relatively slow roaming of the group (evidently from north to south and back) over a vast territory that was not delimited so strictly as the family group territory and may have been rather different from year to year.

The extinction of the genus *Mammuthus* was connected with a complex of factors accompanying the global climatic change in the Holarctic at the end of the

Pleistocene. This was a rather long process that developed unevenly among the late representatives of *M. primigenius*, which suggests that at the end of the Pleistocene the Eurasian range of *M. primigenius* was torn into several isolated pieces. Polymorphism may also be indicative of unfavorable conditions across the major part of the mammoth's former range. The data available allows the suggestion that the total number of mammoths was reduced by the end of the Pleistocene, but at the same time that some parts of the area they formerly inhabited were overpopulated because favourable living conditions persisted there. It is also possible that mammoths, being the largest Late Pleistocene mammals, disrupted the balance in such ecosystems and thus aggravated the already unfavourable conditions at that time.

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Tables and photos to the text

Table 1. Skull measurements (in mm) of *M. primigenius* foetusses and calves; specimens are ordered in growing individual age. 1. length from the distal edge of the premaxillary bones to the vertex of the skull; 2. length from the occipital condyle to the distal edge of the tusk alveolus; 3. length of the forehead from the vertex to the upper edge of the nasal opening; 4. length from the vertex to the bottom of the nasal bones; 5. greatest length and width of the nasal opening; 6. greatest distance between the left and right zygomatic bone; 7. greatest distance between the left and right occipital bone; 8. width of premaxillary on the level of the infraorbital foramen; 9. smallest width of the frontal bones; 10. diameter of the tusk alveolus; 11. height of the skull from the vertex to the level of masticatory surface; 12. height from the vertex to the lower edge of the condyle; 13. length of the zygomatic bones; 14. greatest distance between anterior and posterior edge of the alveolus; 15. height / width ratio of the condyle.

Tabel 1. Schedelmaten (in mm) van *M. primigenius* ongeboren vruchten en kalveren, geordend in oplopende individuele leeftijd. 1. lengte van de onderrand van het premaxillare tot de vertex van de schedel; 2. lengte van de achterhoofdsknobbel tot de onderrand van de tandkas van de slagtand; 3. lengte van het voorhoofd van vertex tot bovenrand van de neusopening; 4. lengte van de vertex tot de onderrand van de neusbeenderen; 5. grootste lengte en breedte van de neusopening; 6. grootste afstand tussen rechter en linker jukbeen; 7. grootste afstand tussen linker en rechter achterhoofdsbeen; 8. breedte van het premaxillare op het niveau van het infraorbitale foramen; 9. kleinste breedte van de voorhoofdsbeenderen; 10. diameter van de tandkas van de slagtand; 11. schedelhoogte van de vertex tot het niveau van het kauwvlak; 12. hoogte van de vertex tot de onderrand van de achterhoofdsknobbel; 13. lengte van de jukbeenderen; 14. grootste afstand tussen voor- en achterrand van de tandkas; 15. hoogte en breedte verhouding van de achterhoofdsknobbel.

Collection number and individual age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
ZIN 34416, foetus 19-20 (?) months	252(?)	-	143	97	81/28	-	172(?)	75/72(?)	130	-	-	-	81(?)	20/20	-
ZIN 31661, foetus 20-21 (?) months	268	255(?)	-	92	-	185(?)	178	79/76	134	16	160(?)	130(?)	87(?)	24/31	22/18
PIN 4353-2614, New-born calf	306	345	150(?)	123	-	236(?)	216	-/196(?)	148	-	223	136	124	32/34	30/24
GIN 77, calf, 1 month	-	-	-	107	-	190	-	81/81	-	16	-	-	-	25/37	-
ZIN 31771(1), calf, 10-11 months	-	-	-	-	-	287	272	-/103	-	-	-	-	153	29/35	43/28
PIN 4353-933, calf, 1 year	390	405	176(?)	160	-	280	260	103/112	173	22	295	173	180	33/45	50/32

Table 2. Mandible measurements (in mm) of *M. primigenius* foetuses and calves. 1. greatest width; 2. greatest length and depth of the body; 3. depth of the body at the posterior edge of the alveolus; 4. thickness of the body at the posterior edge of the alveolus; 5. symphysis length; 6. length of interalveolar crest; 7. smallest width of the ascending branch; 8. size of the glenoid head (length/width); 9. distance between the teeth (anteriorly/posteriorly).

Tabel 2. Onderkaaksmaten (in mm) van *M. primigenius* ongeboren vruchten en kalveren. 1. grootste breedte; 2. grootste lengte en diepte van het lichaam van de onderkaak; 3. diepte van het lichaam van de onderkaak ter hoogte van de achterrand van de tandkas; 4. dikte van het lichaam van de onderaak op hetzelfde punt; 5. lengte van de symphyse; 6. afstand tussen de tandkassen; 7. kleinste breedte van de opgaande tak; 8. lengte en breedte van de gewrichtsknobbel; 9. afstand tussen de kiezen (voorrand, achterrand).

Collection number and individual age	1	2	3	4	5	6	7	8	9
ZIN 31661, foetus 20-21 (?) months	123	153/(?)	42	24	34	51	-	-	43/39
ZIN 29843, foetus 21-22 (?) months	-	-	43(?)	29(?)	39	54(?)	-	-	-
ZIN 28392(4), foetus or newborn calf	-	-	38(?)	22(?)	30	57(?)	-	-	-
ZIN 34419(24), foetus or newborn calf	-	-	-	-	38	56(?)	-	-	-
PIN 4353-2615, newborn calf	142	205/110	55	42	35	74	89	36/25	53/53
ZIN 34201(1), calf, 1 month	-	-/128	50.5	46	-	-	75	25/31	-
GIN 77, calf, 1 month	168(?)	222/97	47	44	42	68(?)	88	23/28(?)	-
ZIN34426, calf, 8-11 months	-	-	53	49	32	91	-	-	-
PIN 2323-12, calf, 8-11 months	-	-	55	53	28	76	-	-	-
Field number: Kostionki 1, 1994, calf, 11-12 months	215	310/-	64	57	60	108	128(?)	-	38/45
PIN 778-1, calf, 14-18 months	250	290(?)/-	68	47	62	115	-	-	47/52
PIN 4531-12, calf, 14-18 months	280	275/152	64	58	48	92	125	34/40	32/39
PIN 4353-591, calf, 3 years	327	335/190	81.5	90	57	127	165	40/47	65/97
ZIN 31278(1), calf, 3.5-4 years	372	-	96	98	73	145(?)	-	-	47/67

Table 3. Mandible measurements (in mm) and proportions of *M. primigenius* foetuses and calves.

Tabel 3. Onderkaaksmaten (in mm) en verhoudingen van *M. primigenius* ongeboren vruchten en kalveren.

Collection number	Length of ascending branch	Length of symphysis	Ratio length brach/length symphysis	Individual age	Greatest length
From D. Dobert, (1992)	135	60	2.07	2 weeks - 1 month (?)	195(?)
PIN 2323-12	-	63	-	8-11 months	-
GIN 77	152	67	2.26	1 month	222
PIN 4353-2615	140	75	1.86	newborn calf	205
ZIN 31661	90	50	1.8	foetus	153(?)
Field number: Kostionki 1, 1994,	229	76.5	2.9	1 year	310
PIN 4531-12	205	75	2.73	14-18 months	175
PIN 4353-678	260	93	2.79	14-18 months	353
PIN 4353-591	257	70	3.67	3-3.5 years	327
ZIN 31278(1)	-	-	-	3.5-4 years	372

Table 4. Measurements (in mm) of the deciduous tusk (di) of *M. primigenius* calves from the Russian Plain. 1. length; 2. greatest crown length; 3. same, greatest transverse diameters; 4. greatest transverse diameters of the root; 5. root canal; 6. wear of crown enamel and the presence of cement.

Tabel 4. Maten (in mm) van de melkslagtand (di) van *M. primigenius* kalveren van de Russische Vlakte. 1. lengte; 2. grootste kroonlengte; 3. grooste kroondiameters; 4. grooste worteldiameters; 5. wortelkanaal; 6. slijtage van glazuur op de slagtandkroon en de aanwezigheid van cement.

Collection number and individual age	1	2	3	4	5	6
ZIN 31661, foetus	48(?)	11(?)	9/5.5	8.5/6	Root canal of the tusk is open. Root walls are thin	Enamel is not worn and proposedly covered with cement
ZIN 31372(1), calf, 1-2 weeks (?)	52	12	10/7	8/6	Root canal of the tusk is open	Enamel is not worn. The cement is partly preserved on the tusk head
PIN 4353-3240), calf, 1-2 weeks	53	9.5(?)	11/-	9.3/-	Root canal of the tusk is open	Enamel is not worn. The tusk head lacks cement
ZIN 32572(3), calf, 1-4 months	-	13	11/6	-	Root canal of the tusk is open	Enamel on the tusk head begins to wear. Cement preserved only on the head basis
ZIN 28392(2), calf, 1-4 months	48	12	10/7	9/7	Root canal of the tusk is open	Enamel on the tusk head begins to wear and has a relief of longitudinal grooves. Cement preserved on the head basis
ZIN 32572(5), calf, 6-9 months	45(?)	12	10/7.5	9/7.5	Root canal of the tusk is open	Entire surface of the head is touched by enamel bearing
ZIN 34422, calf, 6-9 months.	45	13	10.5/7	10/7	Root canal of the tusk pactically closed. Root end resorbed	Entire surface of the head is touched by enamel bearing
ZIN 32572(2), calf, 6-9 months.	-	18	10.3/6.5	-	Root canal of the tusk is closed (?). Root walls are thick	Entire surface of the head is touched by enamel bearing
PIN 4353-3241, calf, 6-9 months.	52	15	10/-	12/-	Root canal of the tusk is closed. Root is not touched by resorption	Enamel of the tusk head is heavily worn. Tusk head lacks cement
PIN 4353-933, calf, 1 year	-	-	-	-	Root canal of the tusk is closed. Approx. 50 % of root length is resorbed	Enamel of the tusk head is heavily worn. Tusk head lacks cement
ZIN 32572(4), calf, 1 year	-	11	10/7	8/7	Root canal of the tusk is closed	Enamel of the tusk head is heavily worn. Tusk head enamel lacks relief. Tusk head lacks cement

Table 5. Measurements (in mm) of the permanent tusk (I) of calves of woolly mammoth (*M. primigenius*) and Indian elephant (*E. maximus*).

Tabel 5. Maten (in mm) van de blijvende slagtand (I) van kalveren van de wolharige mammoet (*M. primigenius*) en een kalf van de Indische olifant (*E. maximus*).

Collection number and individual age	Tusk length	Maximal transverse diameters (vertical/horizontal)	Pulp cavity depth	Transverse diameters of the dentine tusk tip (vertical/horizontal)	Width/lenght of depression on the inner surface of the tusk
PIN 4353-1008, calf, 1.5-2 years	-	18/24	20 (?)	12/6	5/15
PIN 4353-1000, calf, 1.5-2 years	-	17/23	-	14/6	4/23
PIN 4531-25, calf, 1.5-2 years	215	25/28	70	13/6	5/46
SDM 421-1 (*E. maximus*), calf, 1 year (?)	73	21/25	50	-	-
PIN 4353-933, calf, 1 year	64	11/17	-	-	7/(?)
PIN 4531-24, calf, 1.2 years (?)	160	24/31	-	14/7	no depression

Table 6. Measurements (in mm) of dp^2 and dp_2 of *M. primigenius* calves from the Russian Plain.

Tabel 6. Maten (in mm) van eerste generatie melkkiezen (dp^2 en dp_2) van *M. primigenius* kalveren van de Russische Vlakte.

Collection number	Tooth	Length/ width of the tooth	Total number of plates	Length/ width of the plate	Enamel thickness	Number of worn plates	Grinding surface length
ZIN 32572(9)	dp^2	17.5/15	5	3.5/14	-	0	0
ZIN 32572(7)	dp^2	17/14	5	3.5/14.5	0.5(?)	5	12
ZIN 32572(8)	dp^2	20/15	6	3/14	0.8	0	0
ZIN 29843(255)	dp^2	15.5/13	5	2.9/13	0.8	0	0
ZIN 29842	dp^2	16/17	-	-	0.5	all plates	16
ZIN 28392(1)	dp^2	17/14.5	5	3/12	0.4	0	0
ZIN 29841(255)	dp^2	15/13	5	3.5/11	0.4	2	5
ZIN 31541(13)	dp^2	15/13	3 plates remain	3/11.5	0.5	4	15
ZIN 30932	dp^2	20.5/17	5	-/15	0.8	5	18
ZIN 29070	dp^2	16/13	4 plates remain	-/10	0.5	all plates	15.5
ZIN 31771	dp^2	18/16	completely worn	-/14	-	all plates	18
ZIN 34416	dp^2	18/16	5	3.2/14.5	-	0	0
PIN 4353-2614	dp^2	15/11.5	5	-	-	0	0
ZIN 34419(31)	dp_2	12/9.5	5	2.5/9	0.4	0	0
ZIN 28392(3)	dp_2	12	-	-	0.5	all plates	11
ZIN 28392(4)	dp_2	11.5/7	4	3/12	0.4	0	0
ZIN 34421	dp_2	11/7	4	3.5/-	0.5	0	0
ZIN 29843	dp_2	13/9	5	3.5/8.5	0.5	0	0
ZIN 29842	dp_2	14.5/9	5	2.5/8.0	-	0	0
ZIN 34201	dp_2	15/11.5	5	3.5/11	0.8	3	9
ZIN 31517(1)	dp_2	13/11	completely worn	-	0.5	all plates	13
ZIN 31541(12)	dp_2	-/11	completely worn	-	0.5	all plates	12
ZIN 31836(1)	dp_2	-	completely worn	-	-	-	12
PIN 4353-2615	dp_2	13.5/11	4	-	-	0	0

Table 7. Comparison of sizes (in mm) of dp^2 and dp$_2$ of *M. primigenius* calves from the Russian Plain and East Siberian sites (Zerechova, 1977; Urbanas, 1980; Sher & Garutt, 1985a, b). For East Siberia (Berelekh locality), the mean value for plate length is given (Zerechova, 1977).

Tabel 7. Vergelijking van maten (in mm) van eerste generatie melkkiezen (dp^2 en dp$_2$) van *M. primigenius* kalveren van de Russische Vlakte en Oost-Siberië (Zerechova, 1977; Urbanas, 1980; Sher & Garutt, 1985a, b). Voor Berelekh (Oost-Siberië) wordt de gemiddelde waarde van de plaatlengte opgegeven (Zerechova, 1977).

Region	Length of the tooth	Width of the tooth	Total number of plates	Length of the plate	Enamel thickness
Russian Plain	15-20.5 11-15	13-17 7-11	5 4 One dp^2 specimen with six plates	2.9-3.5 2.5-3.5	0.5-0.9 0.4-0.8
East Siberia	14.3-18 14	12 - 20 8 - 16	5 5	3-3.6 2.8	0.7-0.8 0.7

Table 8. Measurements (in mm) of dp^3 of *M. primigenius* calves from the Russian Plain.

Tabel 8. Maten (in mm) van tweede generatie bovenkaaksmelkkiezen (dp^3) van *M. primigenius* kalveren van de Russische Vlakte.

Collection number	Length/ width of the tooth	Total number of plates	Length/ width of the plate	Interplate width	Enamel thickness	Number of worn plates / grinding surface length (mm)
ZIN 2907	56/35	8	4/35	2.5	0.5	2/11
ZIN 29880	59/40	7 plates remain	5(?)/33.5	4	0.6	7/59
ZIN 31540(21)	57(?)/35	8	4.5/33	4	0.5	8/59
ZIN 30934	55/36	7 plates remain	5(?)/30	3	0.8	7/55
ZIN 31771	65/32	8	4.5(?)/-	5.5	0.8	6/49
ZIN 31773	57/43	7 plates remain	5(?)/42	4	0.8	7/57
ZIN 31277(1)	59/38.5	6 plates remain	5/34	3.5	0.8	5/59
ZIN 31722	55/39	8	7/35	2.5	0.5	8/55
ZIN 31689	67/39	7	5/38	5	0.5	7/62
ZIN 30932	57/34	8	5/34	3.5	0.6	2/13
ZIN 30928	54/39(?)	7 plates remain	6/32	4.5	-	7/54
ZIN 30925	59/39	(?)	4.5/37	3.5	0.6	7/59
ZIN 30926(1)	57/39	7 plates remain	4.8/32	2.5	0.8	7/57
ZIN 25550(1)	-	7 plates remain	5/22	4	0.5	6/-
PIN 4353-933	57/33	7 plates remain	5/24	4.5	0.9 (?)	7/51
PIN 4353-2824	-/42	3 plates remain	-	-	1 (?)	3/52

Table 9. Comparison of sizes (in mm) of dp^3 and dp_3 between *M. primigenius* calves from the Russian Plain and from East Siberian sites (Urbanas, 1980; Sher & Garutt, 1985a, b).

Tabel 9. Vergelijking van maten (in mm) van tweede generatie melkkiezen (dp^3 en dp_3) tussen *M. primigenius* kalveren van de Russiche Vlakte en van Oost-Siberië (Urbanas, 1980; Sher & Garutt, 1985a, b).

Region	Tooth length	Tooth width	Total number of plates	Plate length	Enamel thickness
Russian Plain	54 - 67 43.5-66	32 - 43 28.5-37	7 - 8 7 - 9	4 - 6 4-5.5	0.5-0.8 0.5-1
East Siberia	53 - 56.5 28.5 - 37	28 - 40 26 - 36	7 - 9 7 -10	6.6-7.9 7.2-7.6	0.7-1.3 0.7-1

Table 10. Measurements (in mm) of dp_3 of *M. primigenius* calves from the Russian Plain.

Tabel 10. Maten (in mm) van tweede generatie onderkaaksmelkkiezen (dp_3) van *M. primigenius* kalveren van de Russische Vlakte.

Collection number	Length/ width of the tooth	Total number of plates	Length / width of the plate	Interplate width	Enamel thickness	Number of worn plates / grinding surface length
Field number: Kostionki 1, 1994	45/30	6 (?)	4.5/24	3.5	0.5	6/39
ZIN 29872	53.5/34	7(?)	5.5/30.5	3.5	0.8(?)	7/53.5
ZIN 32572(1)	43.5/28.5	6 plates remain	5/27	3.2	0.5	6/43.5
ZIN 28284	54/34.5	9	4(?)/33(?)	4.5	0.7	2/16
ZIN ^{1}30924	53/35	6 plates remain	4.5(?)/30	2.7	0.8	6/53
ZIN 25860(1)	54.5/30	7	5.5/23(?)	4	0.5	6/47
ZIN 34419(27)	62/37	7	5/32	3	0.8(?)	7/62
Field number: Bliznetsov Cave, 1968, å/1,2	64/36	9	4.5/35	4.5	1	7/54
Field number: Bliznetsov Cave, 1968, D/1	66/35	9	4.5/34(?)	5(?)	0.5	7/52
ZIN 34427	59.5/30.5	9	4.5/20(?)	5	0.8(?)	7/49
ZIN 34426	47/28	8	3.5/26(?)	3.5	0.5	(?)
ZIN 31836(1)	31/29	(?)	-	-	0.8(?)	-/29

Table 11. Measurements (in mm) of dp^4 and dp_4 of *M. primigenius* calves from the Kostionki site, Voronezh region.

Tabel 11. Maten (in mm) van derde generatie melkkiezen (dp^4 en dp_4) van *M. primigenius* kalveren uit Kostionki, regio Voronezh.

Collection number, position in mandible	Length/ width of the tooth	Total number of plates	Length / width of the plate	Interplate width	*Lamella* frequency (in distance 10 cm)	Enamel thickness	Number of worn plates / grinding surface length
ZIN 31252; dp^4	-/53(?)	11(?)	4.5/53	3.5	-	0.9	1/15
ZIN 30937; dp^4	-	9 plates remain	5.5/52	4	-	1	-/-
ZIN 31773; dp^4	110(?)/53	12	6.5/39	5.5	11	0.9	6/60
ZIN 31772; dp^4	104/48(?)	13	5/48	3	13	1	3/28
ZIN 31837; dp^4	105/56	12	5.5/41(?)	5.5	12	1	7/63
ZIN 31836(1); dp_4	94/43(?)	12(?)	5.5/34	3(?)	-	0.9	7/59
ZIN 31278(1); dp_4	112/52	12(?)	6/42	5	11	1	12/109
ZIN 28284; dp_4	100(?)/54	11 plates remain	6.5/50	4.5	-	1	11/114
ZIN 31250; dp_4	108/52	12	5/48	5	11	0.9	10/80
ZIN 30936; dp_4	111/56(?)	11 plates remain	5/54	4	11	0.9	11/110

Table 12. Comparison of sizes (in mm) of dp^4 and dp_4 between *M. primigenius* calves from the Russian Plain and from East Siberian sites (Urbanas, 1980; Sher & Garutt, 1985 a, b).

Tabel 12. Vergelijking van maten (in mm) van derde generatie melkkiezen (dp^4 en dp_4) tussen *M. primigenius* kalveren van de Russische Vlakte en van Oost-Siberië (Urbanas, 1980; Sher & Garutt, 1985a, b).

Region	Tooth length	Tooth width	Total number of plates	Plate length	Enamel thickness
Russian Plain	104-110 94-128	48-56 45-58	11-13 11-12	4.5-6.5 5-6	0.95 0.95
East Siberia		42 - 62 41(?)-56	10 - 14 11 - 14	-	-

Table 13. Measurements (in mm) of humeri of foetusses and calves of *M. primigenius* from the Russian Plain.

Tabel 13. Maten (in mm) van opperarmbeenderen van ongeboren vruchten en kalveren van *M. primigenius* van de Russische Vlakte.

Measurements	ZIN 32572(1)	ZIN 31740 (2)	IAE Sh-77, 4â	ZIN 31744(1)	ZIN 34419(17)	ZIN 20564(54)	PIN 4353-2658	PIN 4353-713	PIN 4353-630	ZIN 34386 (3)	PIN 4353-493
Diaphyseal length	-	-	168(?)	-	-	-	204	244	426 (560 including ephyfises)	-	320
Medio-lateral diameter of the distal end of diaphyis	62	-	80	78	80	70(?)	98	107	180	-	141
Antero-posterior diameter of the distal end of diaphysis	19(?)	-	35	29	21	28	46	60	95	-	80
Sortest medio-lateral diameter of diaphysis	20	18	26.5	30	25	24	34	37	65/60	26/21	49
Antero-posterior diameter of the proximal end of diaphysis	-	-	63	-	-	54(?)	81	107	170	46	113
Medio-lateral diameter of the proximal end of diaphysis	-	-	48	-	-	-	61	78	140	29	107
Height from the end of *crista epicondylus lateralis* to the distal end of diaphysis	46	-	52	59(?)	56	60(?)	50	80	-	-	-
Individual age	Foetus (beginnig (?) of the second year of preg-nancy)	Foetus (beginnig (?) of the second year of preg-nancy)	Foetus (last period of pregnancy)	Newborn 1 week (?)	Newborn 1 week (?)	Newborn 1 week (?)	Newborn 1 week (?)	Calf 1 year	Subadalt 6-7 years	Foetus (last period of pregnancy15-18? monthes)	Calf 3 years (?)

Table 14. Measurements (in mm) of ulnae of foetusses and calves of *M. primigenius* from the Russian Plain.

Tabel 14. Maten (in mm) van ellepijpen van ongeboren vruchten en kalveren van *M. primigenius* van de Russische Vlakte.

Measurements	ZIN 31740(3)	PIN 4353-2659	ZIN 34201	ZIN 31740(5)	ZIN 31740(4)	ZIN 34419 (13)	PIN 4353-878	ZIN 31744 (3)	PIN 4353-499	ZIN 31744 (4)	GIN 77
Maximal diaphyseal length	126	184	195	193	190(?)	213	226	258	285	307	188
Length from the anterior edge of crescent notch to the distal end of diaphysis	108(?)	162	153(?)	154	162	175	184	212	238	254	157
Width of articulated surface of the crescent notch	40(?)	78	56	75	72	80(?)	85	103	117	118	65
Antero-posterior diameter at the level of articulated surface of the crescent notch	46	69	25	57	57	80	51	95	100	108	65
Medio-lateral diameter of the distal end of diaphysis	24(?)	48	43	48	37(?)	45(?)	59	57	79	76	42
Antero-posterior diameter of the distal end of diaphysis	28(?)	40	-	-	45	42(?)	51	66	-	82	51
Minimal transversal diameter of diaphysis	16	26	22	27	28	32	36	37	44	42	20
Shortest medio-lateral diameter of diaphysis	20	28	26.5	24	32	33	-	37	-	45	25
Individual age	Foetus (last prenatal stage)	Newborn	Calf, 1month (?)	Calf, 1 month (?)	Calf, 1 month (?)	Calf, 1 month (?)	Calf, 1 year	Calf, 1 year (?)	Calf, 3-4 years	Subadult, 6-7 years	Calf, 1 month (?)

Table 15. Measurements (in mm) of femora of *M. primigenius* calves from the Russian Plain.

Tabel 15. Maten (in mm) van dijbeenderen van *M. primigenius* kalveren van de Russische Vlakte.

Measurements	ZIN 31740 (6)	ZIN 32572 (10)	ZIN 34419(10)	PIN 4353-2698	ZIN 34201 (4)	ZIN 34419 (12)	ZIN 31744(5)	ZIN 34419 (11)	ZIN 31744 (5)	PIN 4353-552	PIN 4353-419	IAE Sh-77, 5b
Transverse/ longitudinal diameters of head	27/24	-	48/40	51/-	50/48	50/45	61/58	71/64	74/68	74/69	92/86	-
Mediolateral diameter of the distal shaft end	36	-	63	80	72	81	-	106	116	96	124	60.5
Anteroposterior diameter of the distal shaft end	32	-	53	62	54	69	-	84	92	81	100	49
Shortest mediolateral diameter of shaft	24	26	33	40	32	38	52	50	50	47	66	29.5
Shortest anteroposterior diameter of shaft	19	24	27	34	24	30	38	43	49	41	49	28
Greatest shaft length	156	-	226	250	245	280	-	365	392	310	450	208(?)
Longitudinal / transverse diameter of the neck	26/35	24/35(?)	33/51	45/59	36/52	48/62	50/71	53/82	64/85	53/70	109/-	-
Shaft length (to trochanter major)	143	-	198	210.5	211	243	-	306	333	270	400	183
Individual age	Foetus (last prenatal stag)	Foetus (last prenatal stage)	Newborn	Newborn	Calf, 1 month (?)	Calf, 1-1.5 years (?)	Calf, 1-1.5 years (?)	Calf, 1-1.5 years (?)	Calf, 1-1.5 years (?)	Calf, 1 year	Subadult, 6-7 years	Foetus (last stage of pregnancy)

Table 16. Measurements (in mm) of tibiae of *M. primigenius* calves from the Russian Plain.

Tabel 16. Maten (in mm) van scheenbeenderen van *M. primigenius* kalveren van de Russische Vlakte.

Measurements	ZIN 31740 (7)	ZIN 34419 (16)	ZIN 31740	ZIN 31740 (9)	PIN 4353-2703	ZIN 34201 (2)	34419 (14)	ZIN 31740 (8)	ZIN 34419 (15)	ZIN 31744 (6)	PIN 4353-873	PIN 4353-1709	IAE Sh-77, 3g	PIN 4353-625
Maximal diaphyseal length	95	117	135	146	160	156	186	200	207	262	240	184	127.5	340
Transversal/anteroposterior diameters of proximal end of diaphysis	30.5/24	38/29(?)	52/36(?)	57/48	69/51	66/65	86/65	93/76	94/75	105/-	98/73	88/63	51/39	135/95
Minimal antero-posterior/transversal diameters of diaphysis.	22/19	25/21	29/25	33/27	34/27	33/26	43/35	44/36	42/37	51/48	50/45	40/35	25/25	65/58
Transversal / anteroposterior diameters of diaphysis distal end	23.5/23	32/27	38(?)/37	47/37(?)	60/42	66/45	65(?)/46	79/58	76/59	81(?)/66	83/68	63(?)\53	43.5/34	110/90
Individual age	Foetus, beginning of the second year of pregnancy	Foetus, last stage of pregnancy	Foetus, last stage of pregnancy	Newborn (?)	Newborn	Newborn	Calf, 1 year (?)	Calf, 1 year (?)	Calf, 1 year (?)	Calf, 4 years (?)	Calf, 3-4 years	Calf, 1 year	Foetus, last stage of pregnancy	Subadult, 6-7 years

Table 17. Measurements (in mm) of the atlas of *M. primigenius* calves; for numbers, see fig. 3.

Tabel 17. Maten (in mm) van de atlas van *M. primigenius* kalveren; voor nummers, zie fig. 3.

Measurement	PUN 4353-2614	ZIN 34201 (5)	PIN 4353-926	PIN 4353-503	PIN 4353-633
1.	5(?)	82	103	142	175
2.	36(?)	48	72	77	104
3.	34	31	45	58	74
4.	24	19	33	35	58
5/6	-	35/46	-	-	-
7/8	5/-	5.5/9.5	5/-	9/17	52/89(?)
9.	-	53	-	-	133(?)
10.	66(?)	-	96	122	130
11.	13	10	10(?)	13	25
12.	53	-	83	115	125
13.	18	-	24	31	47
Individual age	Newborn	Calf, 1 month (?)	Calf, 1 year	Calf, 3-4 years	Subadult, 6-7 years

Table 18. Measurements (in mm) of the axis of *M. primigenius* calves; for numbers, see fig. 3.

Tabel 18. Maten (in mm) van de draaier van *M. primigenius* kalveren; voor nummers, zie fig. 3.

Numbers	ÏÈÍ ¹4353-2495	ÇÈÍ ¹34201(6)	ÏÈÍ ¹4353-925	ÏÈÍ ¹4353-504	ÏÈÍ ¹4353-664
1.	22	25	46	-	57
2.	67	73	-	-	150
3.	24	30	-	-	67
4.	59	58	77	90	131
5/6.	31/29	36/33	37/28(?)	-	41/50
7.	67(?)	64	80(?)	-	-
8.	29	37	50(?)	-	89
9/10.	-/9	-	-/7(?)	-/10	-/18
11.	38(?)	44	65	-	88
12.	14	11	22	21	106
13.	22	-	29	29	46
14.	22	-	27	33	63
15/16.	24/20	-	33/28	41/35	67/49
17. Maximal thickness of vertebral *centra*	9	15	-	-	30
Individual age	Newborn	Calf, 1 month (?)	Calf, 1 year	Calf, 3-4 years	Subadult, 6-7 years

Table 19. Measurements (in cm) of cadavers and skeletons of *M. primigenius* calves (Vereshchagin, 1981; Vereshchagin & Tikhonov, 1999; Kuzmina, 1999).

Tabel 19. Maten (in cm) van kadavers en skeletten van *M. primigenius* kalveren (Vereshchagin, 1981; Vereshchagin & Tikhonov, 1999; Kuzmina, 1999).

Measurements	ZIN 34416 (Kostionki 1, skull)	PIN 4353-2619-2704 (Sevsk, skeleton)	ZIN 34201 (Yamal peninsula, cadaver)	ZIN Ñ 70188 (Magadan Region, cadaver)	PIN 4353-871-986 (Sevsk, skeleton)
Length of body (skeleton), from back of the head to base of the tail	-	72	97	97.5-104	-
Body height (skeleton) in head (skull)	-	75	71	104	115
Length of head (from tusk alveolus edge to occiput). Length skull (from the occipital condyle to the distal edge of the tusk alveolus)	25.2	30.6	43	48	39
Shaft length:					
humerus	-	20.4	19.8	25	24.4
ulna		18.4	19.5	26	22.6
femur		25	24.6	30	30
tibia		15.5	15.7	20.5	18.6
Individual age	Foetus, last prenatal stage	Calf, 1-2 weeks	Calf, 1 month (?)	Calf, 7-8 months (?)	Calf, 1 year

Table 20. Measurements (in mm) of foetuses of *L. africana* and *E. maximus* on different stages of gestation (Ananthanarayana & Marippa, 1950; Frade, 1955; Deraniyagala, 1955; Beyer *et al.*, 1990).

Tabel 20. Maten (in mm) van foetussen van de Afrikaanse olifant *L. africana* en de Indische olifant *E. maximus* gedurende verschillende stadia van de dracht (Ananthanarayana & Marippa, 1950; Frade, 1955; Deraniyagala, 1955; Beyer *et al.*, 1990).

	E. maximus				*L. africana*		
Specimen	1	2	3	4	1	2	3
Shoulder height	57	92	225	-	-	250	780
Length of front leg	34	53	140	-	-	-	-
Length of hind leg	33	53	140	-	-	-	-
Length of body, from back of the head to base of the tail	193	315	685	330	230	330	1100
Stage of pregnancy	4-5 months	10 months	15 months (?)	10 months (?)	5 months	10 months	20 months

Table 21. Mammalian species from the Sevsk locality (Maschenko *et al.*, in press).

Tabel 21. Zoogdiersoorten uit Sevsk (Maschenko *et al.*, in press).

Species	Number of remains
Mammuthus primigenius	3800
Equus caballus	3
Cervus sp.	1
Coelodonta antiquitatis	1
Bos sp.	1
Lagurus lagurus	16
Microtus gregalis	8

Table 22. Comparison of number and composition of some bone groups from the Sevsk and Berelekh sites (Vereshchagin, 1977).

Tabel 22. Vergelijking van aantal en samenstelling van enkele botgroepen uit Sevsk en Berelekh (Vereshchagin, 1977).

	Number of bones		Percentage (from total number of mammoth bones)	
	Sevsk	Berelekh	Sevsk	Berelekh
Tibia	52	169	1.4	2.01
Femur	52	179	1.4	2.12
Fibula	49	86	1.3	1.02
Humerus	53	86	1.4	1.85
Ulna	50	155	1.39	1.84
Radius	39	143	1	1.7
Pelvis	25	215	0.7	2.55
Scapula	30	156	0.8	1.85
Vertebra	740	1328	20	15.7
Cranium	24	-	0.6	-
Mandibula	23	128	0.59	1.44
Tusks	40	44	1	0.5
Individuals	33	156	-	-
Percentage of bones preserved (relatively to expected number)	57%	24%	-	-

Table 23. Comparison of sizes (in mm) of long bones of *M. primigenius* from the Sevsk, Berelekh, and Yuribei sites (Baryshnikov *et al.*, 1977; Dubrovo, 1982).

Tabel 23. Vergelijking van maten (in mm) van pijpbeenderen van *M. primigenius* uit Sevsk, Berelekh en Yuribei (Baryshnikov *et al.*, 1977; Dubrovo, 1982).

	Greatest length			Width of distal shaft end of (humerus, femur) - Width of distal epiphysis (tibia, ulna)			Age group		
				Sevsk	Berelekh	Yuribei	Sevsk	Berelekh	Yuribei
Humerus	200-260	155-180		96-103	65-80		I.1-24 months	I. Foetuses	
Ulna	186-235	220-240	-	35-53	75-90	-			-
Femur	240-350	190-230		75-79	30-35				
Tibia	153-204	134-150		65-75	45-55				
Humerus	260-360	250-490		123-130	115-170		II. 2-6 years	II. 1-10 years	
Ulna	243-290	290-400	-	45-63	110-145	-			-
Femur	320-359	350-610		94-100	50-90				
Tibia	200-235	200-340		75-97	75-135				
Humerus	375-420	480-620	760	135-150	160-180	214	III. 7-13 years	III.10-20 years	10-12 years
Ulna	282-370	380-550	547 (no distal epiphysis)	63-73	150-170	117			
Femur	374-540	600-720	-	100-125	80-100	197			
Tibia	250-340	320-450	475	103-120	130-169	169			
Humerus	450-640	640-750		158-185	170-215		IV. 30-35 years	IV. Adults older than 40 years	
Ulna	380-500	500-650	-	87-98	170-210	-			-
Femur	554–710	700-850		150-165	100-120				
Tibia	356-435	400-480		132-168	150-185				
Humerus	718-825	750-940		165-193	200-275		V. Adults older than 35-40 years	V. Adults older than 40 years	
Ulna	532-672	600-780	-	128-165	180-225	-			-
Femur	790-1010	850-1130		158-210	100-150				
Tibia	460-555	470-570		168-187	160-225				

Table 24. Comparison of sizes (in mm) of M^3 and M_3 of *M. primigenius* from Wrangel Island (Garutt *et al.*, 1993; Averianov *et al.*, 1995) and the Sevsk locality.

Tabel 24. Vergelijking van maten (in mm) van M^3 en M_3 van *M. primigenius* van het eiland Wrangel (Garutt *et al.*, 1993; Averianov *et al.*, 1995) en uit Sevsk.

M^3	Wrangel Island	Sevsk Locality
Tooth length	204-240	173(?)-220
Tooth width	63-72	87-92
Number of plates	21-25	18(?)
Enamel thickness	1-1.4	1.8-2.5
M_3	Wrangel Island	Sevsk Locality
Tooth length	148-225	173(?)-250
Tooth width Number of plates	46-74	80-93
Enamel thickness	17-26	18(?)-22
	1-1.6	1.8-2.5

Table 25. Measurements (in mm) of tusks of *M. primigenius* from the Sevsk locality.

Tabel 25. Maten (in mm) van slagtanden van *M. primigenius* uit Sevsk.

Measurements	PIN 4353-687	PIN 4353-3567	PIN 4353-1502	PIN 4353-320	PIN 4353-1098	PIN 4353-3564	PIN 4353-3569	PIN 4353-3562	PIN 4353-3566	PIN 4353-3565	PIN 4353-445	PIN 4353-3561	PIN 4353-3561	PIN 4353-1213
Maximal diameter	57	89	41	63	83	75	75	73	101	96	27	64	68	43
Length by the outside curvature	770	1260	445	713	1360	1528	1590	1524	1430	244	1042	1480	1156	387
Straight line (alveolus to tip)	656	856	410	560	920	1220	1080	770	940	970	227	745	1063	356
Index of curvature	0.85	0.68	0.9	0.79	0.68	0.79	0.68	0.65	0.66	0.66	0.93	0.71	0.91	0.91
Length of alveolar part of tusk	280	480	-	247	364	-	500	490	590	-	155(?)	-	-	-
Age (years)	17	60(?)	7	12(?)	50(?)	30(?)	35(?)	40	50	50	5	35(?)	30(?)	6

Table 26. Comparison of the number of different bones from Sevsk (Bryansk region, Russia) and Hot Springs (Dakota, USA; data from Haynes, 1992), as percentage of the total expected number.

Tabel 26. Vergelijking van de aantallen van verschillende botten uit Sevsk (Bryansk, Rusland) en Hot Springs (Dakota, USA; gegevens uit Haynes, 1992), als percentage van het totaal aantal verwachte exemplaren.

	Sevsk	Hot Springs
Lower jaw	69	56
Humerus	80	16
Femur	78	20
Scapula	46	22
Ulna	76	18
Tibia	79	28
Radius	59	30
Tusks	60	100
Skulls	79	58

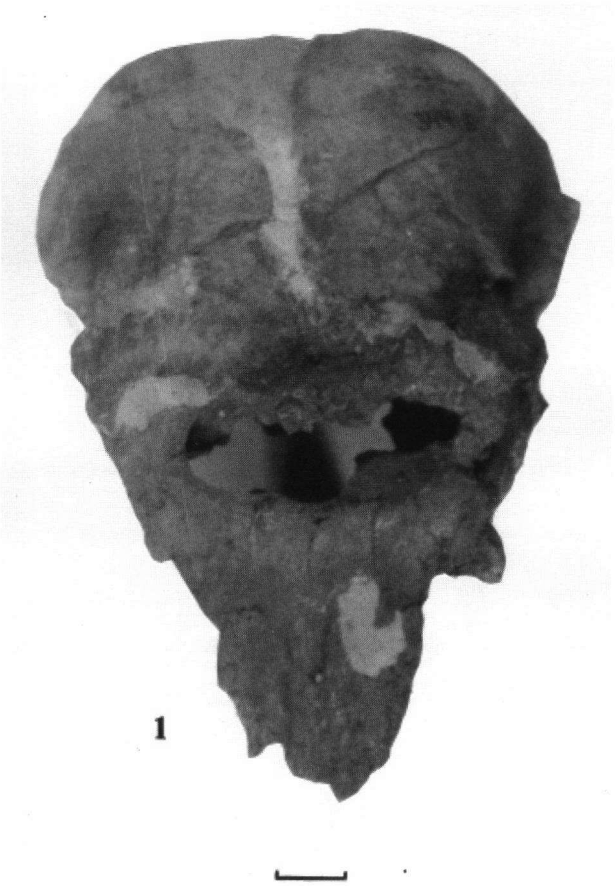


Photo 1. Skull of a *M. primigenius* foetus, approximately 19-20 months of gestation, ZIN 34416, Kostionki 12, Voronezh region. Non-preserved parts are reconstructed with gypsum (white). Dorsal view.

Foto 1. Schedel van een ongeboren *M. primigenius*, ongeveer 19-20 maanden dracht, ZIN 34416, Kostionki 12, Voronezh. Niet-bewaard gebleven delen zijn met gips gereconstrueerd (wit). Bovenaanzicht.

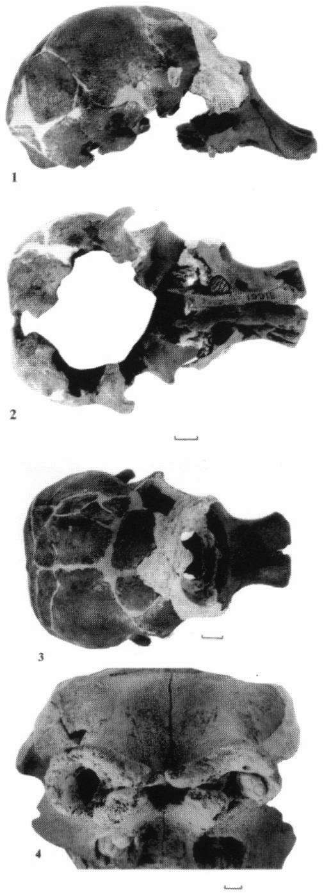


Photo 2. Skull of a *M. primigenius* foetus, approximately 20-21 months of gestation, ZIN 31661, Malta' locality, Irkutsk region. Non-preserved parts are reconstructed with gypsum (white). 1 = side view; 2 = dorsal view; 3 = ventral view; 4 = alveolar structure.

Foto 2. Schedel van een ongeboren *M. primigenius*, ongeveer 20-21 maanden dracht, ZIN 31661, vindplaats Malta', Irkutsk. Niet-bewaard gebleven delen zijn met gips gereconstureerd (wit). 1 = zijaanzicht; 2 = bovenaanzicht; 3 = onderaanzicht; 4 = tandkas.

Photo 3. Skull of a newborn calf of *M. primigenius*, approximately two weeks old, PIN 4353-2614, Sevsk, Bryansk region. Non-preserved parts are reconstructed with gypsum (white). 1 = side view; 2 = ventral view.

Foto 3. Schedel van een pasgeboren *M. primigenius* kalf, ongeveer twee weken oud, PIN 4353-2614, Sevsk, Bryansk. Niet-bewaard gebleven delen zijn met gips gereconstrueerd (wit). 1 = zijaanzicht; 2 = onderaanzicht.

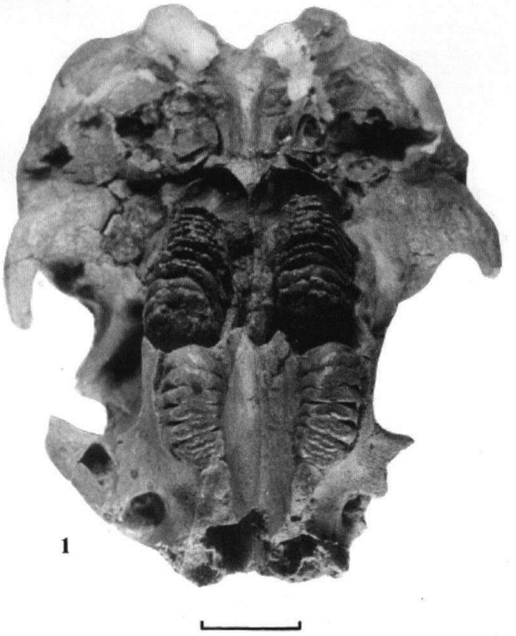


Photo 5. Fragment of a skull of a 10- to 11-months-old calf of *M. primigenius*, ZIN 31771(1), Kostionki 1, Voronezh region. Functional teeth: dp^2 and dp^3, all plates of dp^3 are in wear. 1 = ventral view.

Foto 5. Fragment van een schedel van een *M. primigenius* kalf van tien tot elf maanden oud, ZIN 31771(1), Kostionki 1, Voronezh. Functionele kiezen: dp^2 en dp^3, alle platen van dp^3 vertonen slijtage. 1 = onderaanzicht.

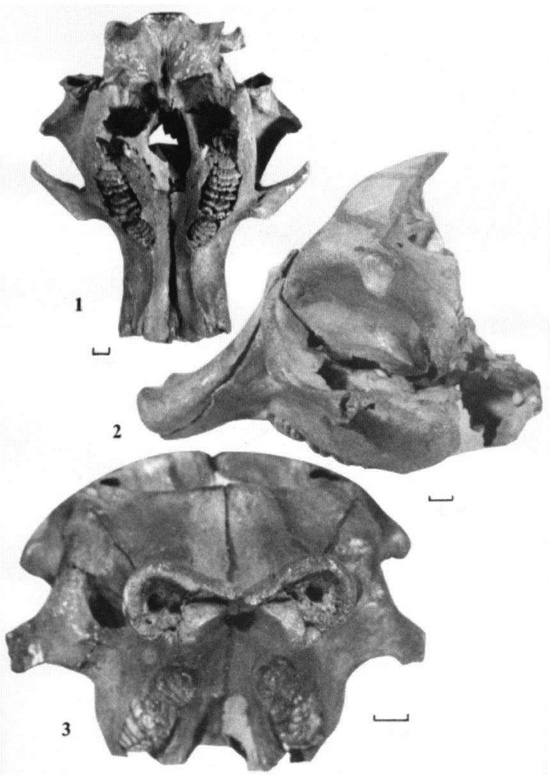


Photo 4. Facial part of the skull of a one-month-old calf of *M. primigenius*, GIN 77, Yamal peninsula. 1 = ventral view; 2 = side view; 3 = alveolar structure.

Foto 4. Aangezichtsdeel van de schedel van een *M. primigenius* kalf van een maand oud, GIN 77, Yamal schiereiland. 1 = onderaanzicht; 2 = zijaanzicht; 3 = tandkas.

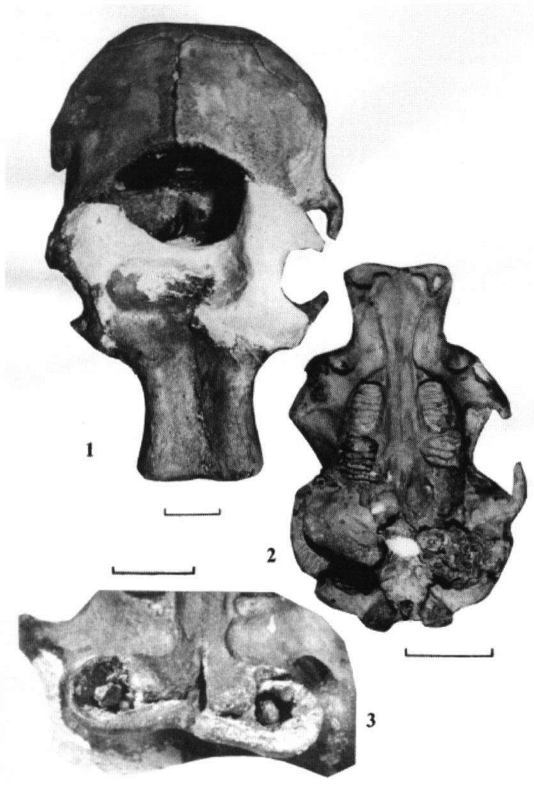


Photo 6. Skull of a calf of one year old of *M. primigenius*, Sevsk, Bryansk region. Functional tooth: dp^3, all plates are in wear. Alveoli of dp^2 persist. In right tusk alveolus the di persist together with I. Non-preserved parts are reconstructed with gypsum (white). 1 = dorsal view; 2 = ventral view; 3 = di and I in tusk alveolus.

Foto 6. Schedel van een jaarling kalf van *M. primigenius*, Sevsk, Bryansk. Functionele kiezen: dp^3, alle platen vertonen slijtage. Tandkassen van dp^2 zijn blijven bestaan. In de tandkas voor de rechter slagtand zit di naast I. Niet-bewaard gebleven delen zijn met gips gereconstrueerd (wit). 1 = bovenaanzicht; 2 = onderaanzicht; 3 = di en I in slagtand-tandkas.

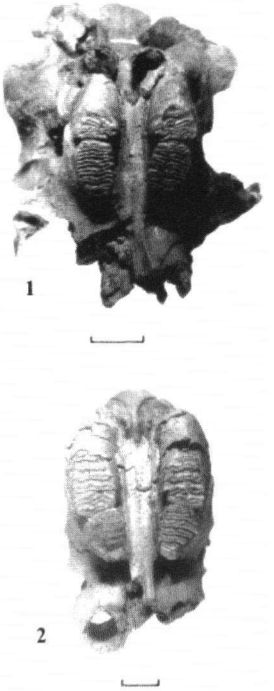


Photo 7. Fragments of skulls of *M. primigenius* calves with functional teeth dp³ and dp⁴, Kostionki 1, Voronezh region, ventral view. 1 = ZIN 31772(2), 2.5-3 years of age; 2 = ZIN 31837, 26-30 months of age.

Foto 7. Schedelfragmenten van *M. primigenius* kalveren met functionele kiezen dp³ and dp⁴, Kostionki 1, Voronezh, onderaanzicht. 1 = ZIN 31772(2), 2,5-3 jaar oud; 2 = ZIN 31837, 26-30 maanden oud.

Photo 8. Lower jaws of foetuses of *M. primigenius* during the last prenatal stage (20-22 months of gestation) from the Russian Plain and Siberia. 1. ZIN 29843, symphyseal part of lower jaw, Elisievichi locality, Bryansk region, dorsal view; 2 = ZIN 28392(4), symphyseal part of lower jaw, Kostionki 1, Voronezh region, side view. Part of the interalveolar crest is destroyed and the root of dp2 open; 3 = ZIN 31661, lower jaw, Malta' locality, Irkutsk region, dorsal view; 4 = same, side view.

Foto 8. Onderkaken van *M. primigenius* vruchten in het laatste stadium van de dracht (20-22 maanden) van de Russische Vlakte en Siberië. 1. ZIN 29843, symphysisdeel, Elisievichi, Bryansk, bovenaanzicht; 2 = ZIN 28392(4), symphysisdeel, Kostionki 1, Voronezh, zijaanzicht. Een deel van de kam tussen de tandkassen is vernield, en de wortel van dp2 is open; 3 = ZIN 31661, onderkaak, Malta', Irkutsk, bovenaanzicht; 4 = idem, zijaanzicht.

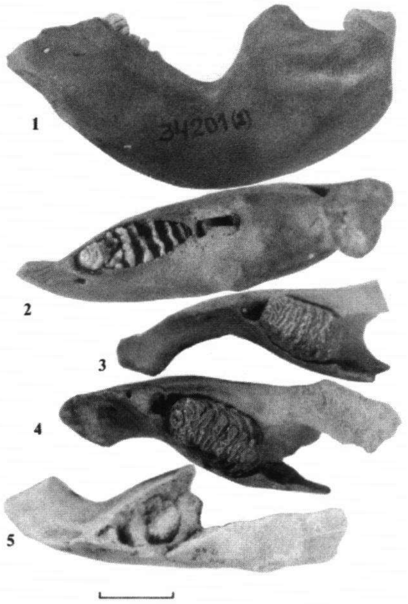


Photo 9. Lower jaws of *M. primigenius* calves of one month (1) and of eight to eleven months (2-5) from the Russian Plain and Siberia. 1 = ZIN 34201(1), Yurebetiyakha river, Yamal peninsula, left ramus, symphyseal part destroyed, side view; 2 = same, dorsal view; 3 = ZIN 34427, Yakutia, right ramus, dorsal view; 4 = ZIN 34426, as (3); 5 = ZIN 28284(2), Kostionki 14, Voronezh region, left ramus, dorsal view.

Foto 9. Onderkaken van *M. primigenius* kalveren van een maand (1) en van acht tot elf maanden oud (2-5) van de Russische Vlakte en Siberië. 1 = ZIN 34201(1), Yurebetiyakha rivier, Yamal schiereiland, linker tak, symphysisdeel is vernield, zijaanzicht; 2 = idem, bovenaanzicht; 3 en 4 = ZIN 34427 en ZIN 34426, Yakutië, rechter takken, bovenaanzicht; 5 = ZIN 28284(2), Kostionki 14, Voronezh, linker tak, bovenaanzicht.

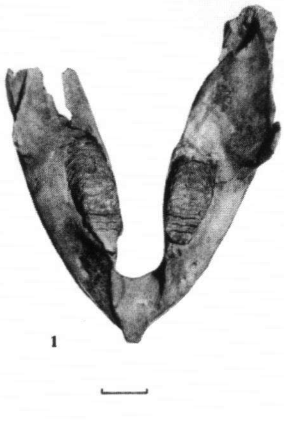


Photo 11. Lower jaw of a calf of 14-18 months of *M. primigenius*, PIN 4353-668, Sevsk, Bryansk region; dorsal view.

Foto 11. Onderkaak van een *M. primigenius* kalf van 14-18 maanden oud, PIN 4353-668, Sevsk, Bryansk; bovenaanzicht.

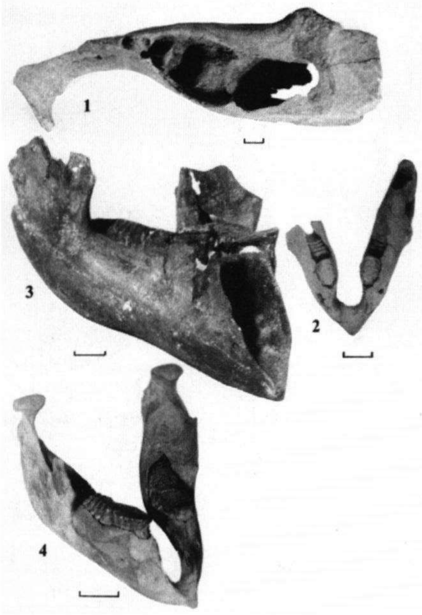


Photo 10. Lower jaws of *M. primigenius* calves from the Russian Plain and Siberia. 1 = PIN 2323-12, Viliny river, Yakutia, right ramus of calf of 8-11 months, dorsal view; 2 = ZIN field mark "Kostionki 1, 1994", Kostionki 1, Voronezh region, jaw of a calf of 11-12 months, dorsal view; 3 = PIN 778(1), Viliny river, Yakutia, jaw of a calf of 14-18 months, side view; 4 = PIN 4531-12, Yakutia, jaw of a calf of 14-18 months, side view.

Foto 10. Onderkaken van *M. primigenius* kalveren van de Russische Vlakte en Siberië. 1 = PIN 2323-12, Viliny rivier, Yakutië, rechter tak van een kalf van 8-11 maanden oud, bovenaanzicht; 2 = ZIN veldnummer "Kostionki 1, 1994", Kostionki 1, Voronezh, kaak van een kalf van 11-12 maanden oud, bovenaanzicht; 3 = PIN 778(1), Viliny rivier, Yakutië, kaak van een kalf van 14-18 maanden oud, zijaanzicht; 4 = PIN 4531-12, Yakutië, kaak van een kalf van 14-18 maanden oud, zijaanzicht.

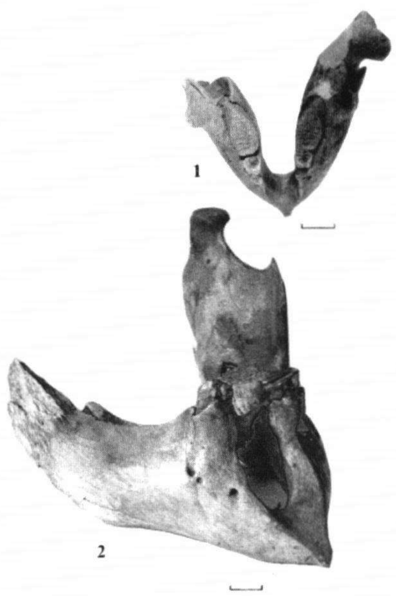


Photo 12. Lower jaws of *M. primigenius* calves from the Russian Plain and Siberia. 1 = ZIN 31836(1), Kostionki 1, Voronezh region, a calf of approx. 3 years; the only known representative of the Elephantinae with simultaneously functioning dp^2, dp^3 and dp^4. Scale bar: 5 cm. 2 = PIN 4531-14, Yakutia, a calf of 3.5-4 years, side view. Scale bar: 2 cm.

Foto 12. Onderkaken van *M. primigenius* kalveren van de Russische Vlakte en Siberië. 1 = ZIN 31836(1), Kostionki 1, Voronezh, een ongeveer drie jaar oud kalf; dit is het enige exemplaar uit de subfamilie Elephantinae met gelijktijdig functionerende dp^2, dp^3 en dp^4 dat bekend is. Maatstreep 5 cm. 2 = PIN 4531-14, Yakutië, 3,5-4 jaar oud kalf, zijaanzicht. Maatstreep 2 cm.

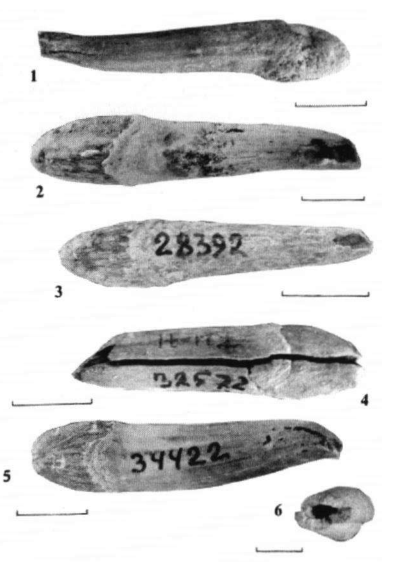


Photo 13. Deciduous tusks (di) of *M. primigenius* calves from the Russian Plain. Scale bar: 1 cm. 1 = ZIN 31372(1), Kostionki 1, Voronez region, left di, lateral view; 2 = ZIN 32572(3), Kostionki 21, right di, lateral view; 3 = ZIN 28392, Kostionki 11, left di, medial view; 4 = ZIN 32572(6), Kostionki 21, left di, medial view; 5 = ZIN 34422, Yudinovo locality, Bryansk region, right di, lateral view; 6 = ZIN 32572(6), Kostionki 21, root ending.

Foto 13. Melkslagtanden (di) van *M. primigenius* kalveren van de Russische Vlakte. Maatstreep 1 cm. 1 = ZIN 31372(1), Kostionki 1, Voronez, linker di, zijaanzicht; 2 = ZIN 32572(3), Kostionki 21, rechter di, zijaanzicht; 3 = ZIN 28392, Kostionki 11, linker di, binnenzijde; 4 = ZIN 32572(6), Kostionki 21, linker di, binnenzijde; 5 = ZIN 34422, Yudinovo, Bryansk, rechter di, zijaanzicht; 6 = ZIN 32572(6), Kostionki 21, wortelpunt.

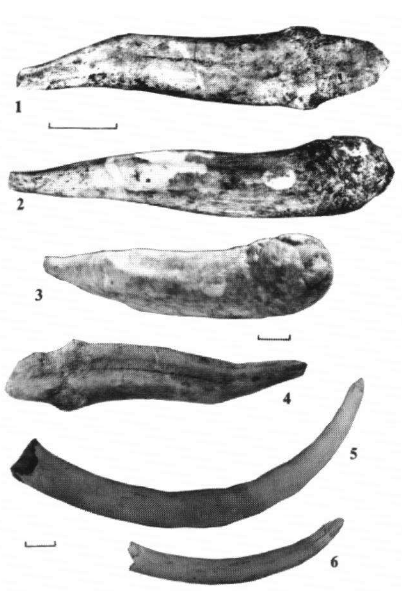


Photo 14. Deciduous (di) and permanent (I) tusks of *M. primigenius*, Sevsk, Bryansk region. Scale bar 1 cm (1-4) and 5 cm (5, 6). 1 = PIN 4353-3240, left di, medial view; 2 = PIN 4353-3241, left di, lateral view; 3 = PIN 4353-3241, left di, medial view; 4 = PIN 4353-3240, left di, lateral view; 5 = PIN 4353-320, right I of an individual of 13-15 years; 6 = PIN 4353-1213, right I of a 4-6 year old individual.

Foto 14. Melk- (di) en blijvende (I) slagtanden van *M. primigenius*, Sevsk, Bryansk. Maatstreep 1 cm (1-4) en 5 cm (5, 6). 1 = PIN 4353-3240, linker di, binnenzijde; 2 = PIN 4353-3241, linker di, buitenzijde; 3 = PIN 4353-3241, linker di, binnenzijde; 4 = PIN 4353-3240, linker di, buitenzijde; 5 = PIN 4353-320, rechter I van een 13-15 jaar oud individu; 6 = PIN 4353-1213, rechter I van een 4-6 jaar oud individu.

Photo 15. First generation teeth dp2 of *M. primigenius* calves from the Russian Plain. 1 = ZIN 28392(1), left dp2, Kostionki 11, Voronezh region, buccal view; 2 = ZIN 34419(29), left dp2, Kostionki 1, buccal view; 3 = same, masticatory surface; 4 = PIN 4353-2614, left dp2, Sevsk, Bryansk region, buccal view; 5 = ZIN 30932, fragment of left part of upper jaw with dp^2-dp^3, Kostionki 1, buccal view; 6 = ZIN 31541(13), right dp2, Kostionki 1, masticatory surface; 7 = same, buccal view; 8 = ZIN 34420(2), right dp2, Kostionki 19, buccal view.

Foto 15. Eerste generatie kiezen (dp2) van *M. primigenius* kalveren van de Russische Vlakte. 1 = ZIN 28392(1), linker dp2, Kostionki 11, Voronezh, wangzijde; 2 = ZIN 34419(29), linker dp2, Kostionki 1, wangzijde; 3 = idem, kauwvlakte; 4 = PIN 4353-2614, linker dp2, Sevsk, Bryansk, wangzijde; 5 = ZIN 30932, fragment van linker deel van een bovenkaak met dp^2-dp^3, Kostionki 1, wangzijde; 6 = ZIN 31541(13), rechter dp2, Kostionki 1, kauwvlakte; 7 = idem, wangzijde; 8 = ZIN 34420(2), rechter dp2, Kostionki 19, wangzijde.

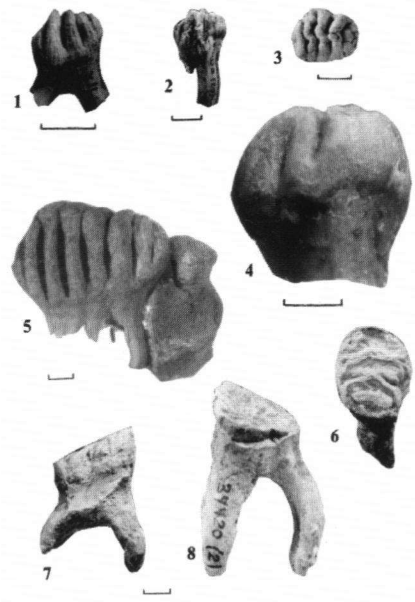


Photo 16. First generation teeth dp_2 of *M. primigenius* calves from Elisievichi locality, Bryansk region. 1 = ZIN 34421, left dp_2, masticatory surface; 2 = same, buccal view; 3 = ZIN 34419(31), right dp_2, lingual view; 4 = same, masticatory surface; 5 = PIN 4353-2615, left dp_2, buccal view.

Foto 16. Eerste generatie kiezen (dp_2) van *M. primigenius* kalveren uit Elisievichi, Bryansk: 1 = ZIN 34421, linker dp_2, kauwvlakte; 2 = idem, wangzijde; 3 = ZIN 34419(31), rechter dp_2, tongzijde; 4 = idem, kauwvlakte; 5 = PIN 4353-2615, linker dp_2, wangzijde.

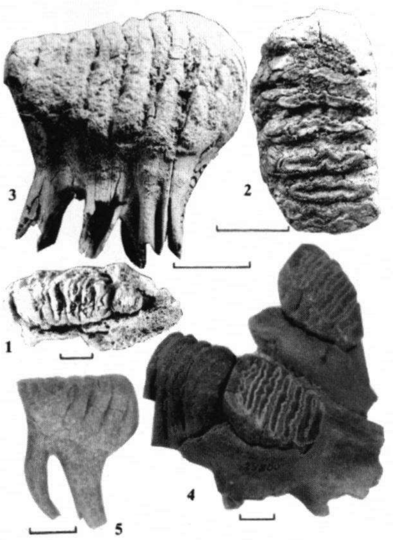


Photo 17. Second generation teeth dp^3 and dp_3 of *M. primigenius* calves from Central Russia. 1 = ZIN 34381, Yudinovo locality, Bryansk region, dp^3 of a calf of approx. 10 months, right fragment of the upper jaw, masticatory surface; 2 = ZIN 30929(1), Yudinovo locality, right dp_3 of a calf of 11-12 months, masticatory surface; 3 = same, lingual view; 4 = ZIN 29880, dp^3 in a fragment of an upper jaw of a calf of 1.5-2 years, Elisievichi locality, Bryansk region, masticatory surface; 5 = ZIN 28284(1), left dp_3 of a calf of 10-12 months, Kostionki 14, Voronezh region, buccal view. Scale bar: 2 cm.

Foto 17. Tweede generatie kiezen (dp^3 en dp_3) van *M. primigenius* kalveren van Centraal Rusland: 1 = ZIN 34381, Yudinovo, Bryansk, rechter fragment van de bovenkaak met dp^3 van een ongeveer tien maanden oud kalf, kauwvlakte; 2 = ZIN 30929(1), Yudinovo, rechter dp_3 van een 11-12 maanden oud kalf, kauwvlakte; 3 = idem, tongzijde; 4 = ZIN 29880, dp^3 in een bovenkaaksfragment van een 1.5-2 jaar oud kalf, Elisievichi, Bryansk, kauwvlakte; 5 = ZIN 28284(1), linker dp_3 van een 10-12 maanden oud kalf, Kostionki 14, Voronezh, wangzijde. Maatstreep 2 cm.

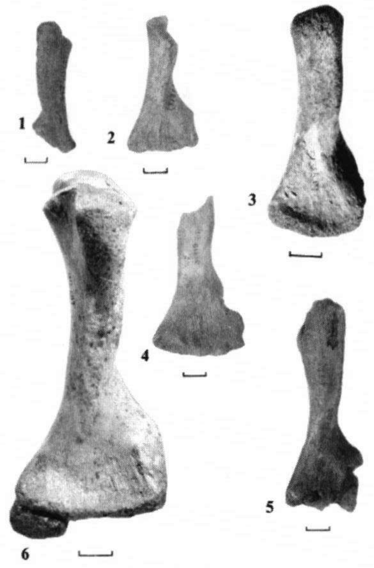


Photo 18. Humeri of juvenile *M. primigenius* from Kostionki 1 (1, 3, 4, 5) and Kostionki 21 (2), Voronezh region, compared to a humerus from Sevsk, Bryansk region (6); front view. All, except for 1, are left humeri. Scale bar: 2 cm. 1 = ZIN 31740(2), foetus of 14-16 months; 2 = ZIN 32572(1), same; 3 = ZIN 34386(3), foetus of 15-18 months; 4 = ZIN 34419(17), newborn calf; 5 = ZIN 20564(54), calf of 1-2 weeks; 6 = PIN 4353-2658, same.

Foto 18. Opperarmbeenderen van ongeboren en pasgeboren *M. primigenius* kalveren van Kostionki 1 (1, 3, 4, 5) en Kostionki 21 (2), Voronezh, vergeleken met een opperarm van Sevsk, Bryansk (6); vooraanzicht. Alle, behalve 1, zijn linker opperarmen. Maatstreep 2 cm. 1 = ZIN 31740(2), ongeboren vrucht van 14-16 maanden; 2 = ZIN 32572(1), idem; 3 = ZIN 34386(3), idem, van 15-18 maanden; 4 = ZIN 34419(17), pasgeboren kalf; 5 = ZIN 20564(54), kalf van 1-2 weken oud; 6 = PIN 4353-2658, idem.

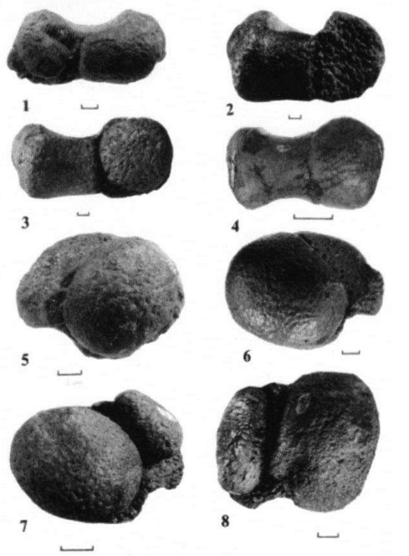


Photo 19. Distal and proximal epiphyses of humeri of *M. primigenius* calves from Sevsk, Bryansk region, distal surface. 1-4 = distal epiphyses, posterior surface of shaft upward; 5-8 = proximal epiphyses, posterior surface of shaft downward. Scale bar 1 cm (1-6) and 2 cm (7, 8). 1, 5 = PIN 4353-2658, right humerus of a newborn of 1-2 weeks; 2, 6 = PIN 4353-713, left humerus of a calf of one year; 3, 7 = PIN 4353-496, left humerus of a calf of 3-4 years; 4 = PIN 4353-62, right humerus of an individual of 6-7 years; 8 = PIN 4353-745.

Foto 19. Bovenste en onderste groeischijven van opperarmbeenderen van *M. primigenius* kalveren uit Sevsk, Bryansk, onderkant. 1-4 = onderste groeischijven, achterzijde van de schacht boven; 5-8 = bovenste groeischijven, achterzijde van de schacht onder. Maatstreep 1 cm (1-6) en 2 cm (7, 8). 1, 5 = PIN 4353-2658, rechter opperarm van een pasgeboren kalf van 1-2 weken; 2, 6 = PIN 4353-713, linker opperarm van een jaarling; 3, 7 = PIN 4353-496, linker opperarm van een kalf van 3-4 jaar oud; 4 = PIN 4353-62, rechter opperarm van een kalf van 6-7 jaar oud; 8 = PIN 4353-745, idem.

Photo 20. Humeri of *M. primigenius* calves of different ages from Sevsk, Bryansk region. Scale bar 2 cm (1, 2) and 5 cm (3, 4). 1 = PIN 4353-2658, right humerus of a newborn; 2 = PIN 4353-713, left humerus of a calf of one year; 3 = PIN 4353-496, left humerus of a calf of 3-4 years; 4 = PIN 4353-745, right humerus of a calf of 6-7 years.

Foto 20. Opperarmen van *M. primigenius* kalveren van verschillende leeftijden uit Sevsk, Bryansk. Maatstreep 2 cm (1, 2) en 5 cm (3, 4). 1 = PIN 4353-2658, rechter opperarm van een pasgeboren kalf; 2 = PIN 4353-713, linker opperarm van een jaarling; 3 = PIN 4353-496, linker opperarm van een kalf van een jaar of drie-vier; 4 = PIN 4353-745, rechter opperarm van een kalf van een jaar of zes-zeven.

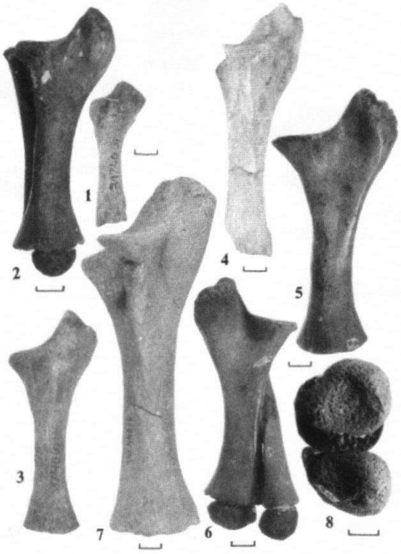


Photo 21. Ulnas of *M. primigenius* calves from Kostionki 1, Voronezh region (1, 3, 4, 7) and from Sevsk, Bryansk region (2, 5, 6, 8). Scale bar: 2 cm. 1 = ZIN 31740(3), right ulna of foetus of last prenatal stage (20-21 months), medial view; 2 = PIN 4353-2659, right ulna (with radius) of a newborn of 1-2 weeks old, medial view; 3 = ZIN 31740(5), left ulna of a calf of approx. one month, lateral view; 4 = ZIN 34419(13), left ulna of a calf of approx. one year, lateral view; 5 = PIN 4353-878, right ulna of a calf of one year, medial view; 6 = PIN 4353-499, left ulna (with radius) of a calf of 3-4 years, medial view; 7 = ZIN 31744(4), right ulna of a calf of 6-7 years, lateral view; 8 = PIN 4353-877, left ulna (with radius) of a calf of 3-4 years, distal view.

Foto 21. Ellepijpen van *M. primigenius* kalveren van Kostionki 1, Voronezh (1, 3, 4, 7) en van Sevsk, Bryansk (2, 5, 6, 8). Maatstreep 2 cm. 1 = ZIN 31740(3), rechter ellepijp van een ongeboren kalf van 20-21 maanden, binnenzijde; 2 = PIN 4353-2659, rechter ellepijp (met spaakbeen) van een pasgeboren kalf van 1-2 weken, binnenzijde; 3 = ZIN 31740(5), linker ellepijp van een kalf van ongeveer een maand oud, buitenzijde; 4 = ZIN 34419(13), linker ellepijp van een jaarling, buitenzijde; 5 = PIN 4353-878, rechter ellepijp van een jaarling, binnenzijde; 6 = PIN 4353-499, linker ellepijp (met spaakbeen) van een kalf van 3-4 jaar oud, binnenzijde; 7 = ZIN 31744(4), rechter ellepijp van een kalf van 6-7 jaar oud, buitenzijde; 8 = PIN 4353-877, linker ellepijp (met spaakbeen) van een kalf van 3-4 jaar oud, onderzijde.

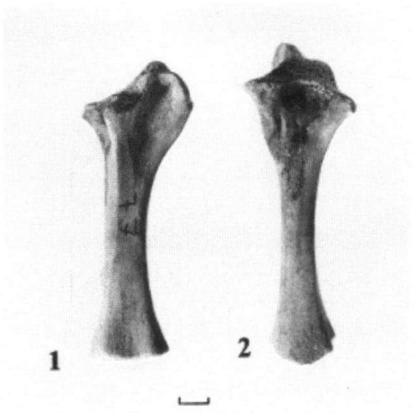


Photo 22. Right ulna of a *M. primigenius* calf of approx. one month, GIN 77, Yamal Peninsula: 1 = lateral view; 2 = front view. Scale bar = 2 cm.

Foto 22. Rechter ellepijp van een *M. primigenius* kalf van ongeveer een maand oud, GIN 77, Yamal schiereiland: 1 = zijaanzicht; 2 = voorzijde. Maatstreep 2 cm.

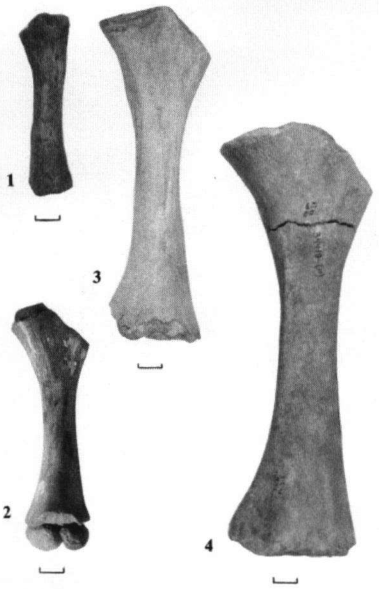


Photo 23. Femora of foetuses and calves of *M. primigenius* from Kostionki 1, Voronezh region (1, 3, 4; scale bar 2 cm) and from Sevsk, Bryansk region (2; scale bar 10 cm), anterior surface. 1 = ZIN 31740(6), right femur of a foetus of 16-18 weeks; 2 = PIN 4353-2698, left femur of a calf of 1-2 weeks; 3 = ZIN 34419(12), left femur of calf of approx. one month; 4 = ZIN 34419(11), left femur of a calf of approx. 1.5 years.

Foto 23. Dijbeenderen van ongeboren en jonge *M. primigenius* kalveren van Kostionki 1, Voronezh (1, 3, 4; maatstreep 2 cm) en van Sevsk, Bryansk (2; maatstreep 10 cm), voorzijde. 1 = ZIN 31740(6), rechter dijbeen van een ongeboren vrucht van 16-18 weken; 2 = PIN 4353-2698, linker dijbeen van een kalf van 1-2 weken oud; 3 = ZIN 34419(12), linker dijbeen van een kalf van ongeveer een maand oud; 4 = ZIN 34419(11), linker dijbeen van een kalf van ongeveer 1,5 jaar oud.

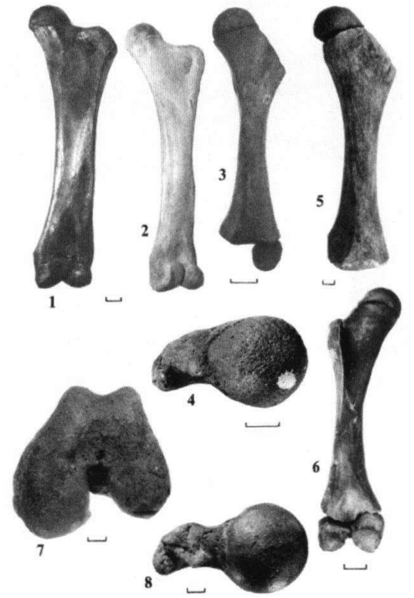


Photo 24. Left (5) and right (1-3, 6-8) femora of *M. primigenius* of different ages from Sevsk, Bryansk region. Scale bar 2 cm (4, 5, 7, 8), 5 cm (1, 2, 3) and 10 cm (6). 1 = PIN 4353-2792, adult individual (probably male) of over forty years of age, posterior view; 2 = PIN 4353-2795, adult female of over thirty-five years of age, posterior view; 3 = PIN 4353-552, calf of one year old, anterior view; 4 = PIN 4353-333, medial ossification center of proximal epiphysis (shaft: PIN 4353-552) of a calf of one year old, distal view; 5 = PIN 4353-419, calf of 3-4 years, anterior view; 6 = PIN 4353-48, individual of 6-7 years, posterior view; 7 = same, distal epiphysis, distal view; 8 = same, proximal epiphysis, proximal view.

Foto 24. Linker (5) en rechter (1-3, 6-8) dijbeenderen van *M. primigenius* van verschillende leeftijden uit Sevsk, Bryansk. Maatstreep 2 cm (4, 5, 7, 8), 5 cm (1, 2, 3) en 10 cm (6). 1 = PIN 4353-2792, volwassen individu (waarschijnlijk mannelijk) ouder dan veertig jaar, achterzijde; 2 = PIN 4353-2795, volwassen vrouwtje, ouder dan vijfendertig jaar, achterzijde; 3 = PIN 4353-552, jaarling kalf, voorzijde; 4 = PIN 4353-333, binnenste verbeningscentrum van bovenste groeischijf (schacht: PIN 4353-552) van een jaarling kalf, onderzijde; 5 = PIN 4353-419, drie tot vier jaar oud kalf, voorzijde; 6 = PIN 4353-48, zes tot zeven jaar oud jong dier, achterzijde; 7 = idem, onderste groeischijf, onderzijde; 8 = idem, bovenste groeischijf, bovenzijde.

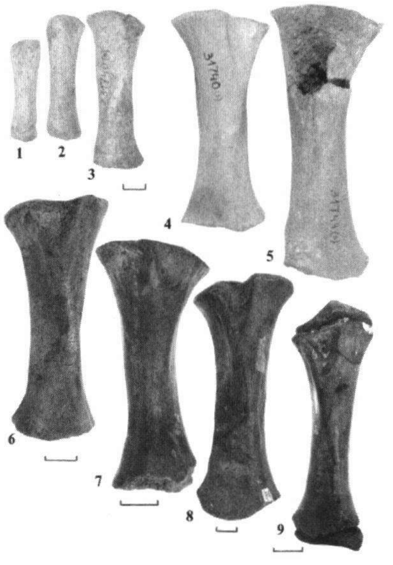


Photo 25. Tibias of foetuses and calves of *M. primigenius* from Kostionki 16, Voronezh region (1-5) and Sevsk, Bryansk region (6-9), anterior surface, left (1, 5, 7) and right (2, 3, 4, 6, 8, 9). Scale bars: 2 cm (1-8) and 5 cm (9). 1 = ZIN 31740(7), foetus of 12-16 months; 2 = ZIN 34419(16), foetus of 16-19 months; 3 = ZIN 31740(9), foetus of the last prenatal stage or a newborn; 4 = ZIN 31740(8), one-year-old calf; 5 = ZIN 31744(6), four-years-old calf; 6 = PIN 4353-2703, newborn of 1-2 weeks (with radius); 7 = PIN 4353-1709, one-year-old calf; 8 = PIN 4353-873, calf of 3-4 years; 9 = PIN 4353-625, calf of 6-7 years.

Foto 25. Scheenbeenderen van ongeboren vruchten en kalveren van *M. primigenius* van Kostionki 16, Voronezh (1-5) en Sevsk, Bryansk (6-9), voorzijde, links (1, 5, 7) en rechts (2, 3, 4, 6, 8, 9). Maatstrepen 2 cm (1-8) en 5 cm (9). 1 = ZIN 31740(7), vrucht van twaalf tot zestien maanden; 2 = ZIN 34419(16), vrucht van zestien tot negentien maanden; 3 = ZIN 31740(9), vrucht gedurende laatste stadium van de dracht of pasgeboren; 4 = ZIN 31740(8), jaarling kalf; 5 = ZIN 31744(6), kalf van vier jaar oud; 6 = PIN 4353-2703, pasgeboren kalf van een tot twee weken oud (met spaakbeen); 7 = PIN 4353-1709, jaarling kalf; 8 = PIN 4353-873, kalf van drie tot vier jaar oud; 9 = PIN 4353-625, jong dier van zes tot zeven jaar oud.

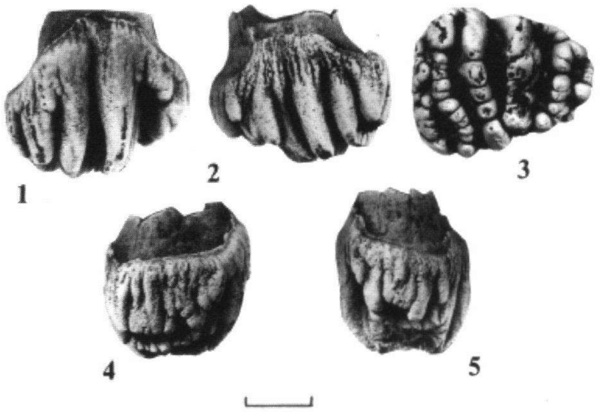


Photo 26. First generation tooth dp2 of *Archidiskodon gromovi*, GIN 300/13, Chapry locality, Rostov region. 1 = buccal view; 2 = lingual view; 3 = masticatory surface; 4 = medial view; 5 = distal view. Scale bar: 1 cm.

Foto 26. Eerste generatie kies dp2 van *Archidiskodon gromovi*, GIN 300/13, Chapry, Rostov. 1 = wangzijde; 2 = tongzijde; 3 = kauwvlakte; 4 = voorzijde; 5 = achterzijde. Maatstreep 1 cm.

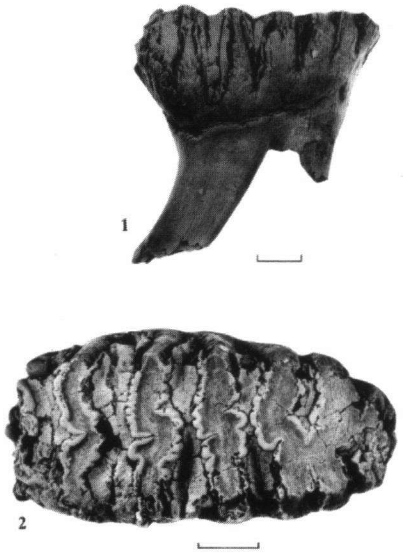


Photo 28. Second generation tooth dp_3 of *Archidiskodon gromovi*, GIN 29071, Kobyakova Balka locality, Aksaisk, Rostov region. 1 = masticatory surface; 2 = lingual view. Scale bar: 1 cm.

Foto 28. Tweede generatie kies dp_3 van *Archidiskodon gromovi*, GIN 29071, Kobyakova Balka, Aksaisk, Rostov. 1 = kauwvlakte; 2 = tongzijde. Maatstreep 1 cm.

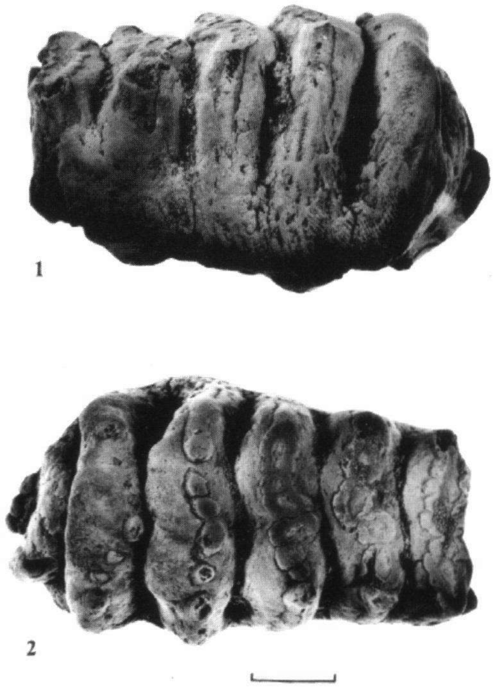


Photo 27. Second generation tooth dp3 of *Archidiskodon gromovi*, GIN 300/124, Chapry locality, Rostov region. 1 = lingual view; 2 = masticatory surface. Scale bar: 1 cm.

Foto 27. Tweede generatie kies dp3 van *Archidiskodon gromovi*, GIN 300/124, Chapry, Rostov. 1 = tongzijde; 2 = kauwvlakte. Maatstreep 1 cm.

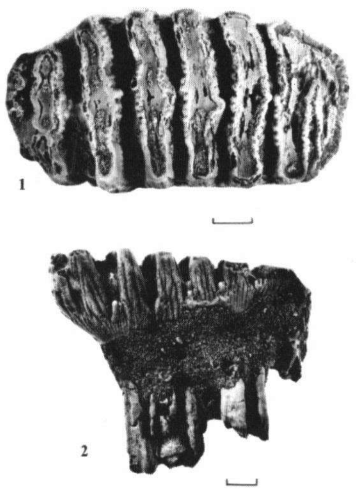


Photo 29. Third generation tooth dp_4 of *Archidiskodon gromovi*, GIN 30012, Liventovsky quarry, Rostov region. 1 = masticatory surface; 2 = lingual view. Scale bar: 1 cm.

Foto 29. Derde generatie kies dp_4 van *Archidiskodon gromovi*, GIN 30012, Liventovsky groeve, Rostov. 1 = kauwvlakte; 2 = tongzijde. Maatstreep 1 cm.

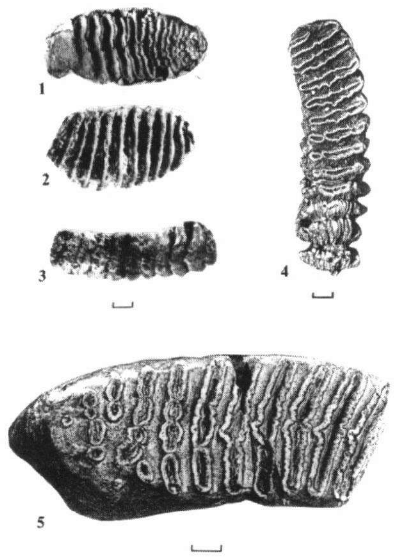


Photo 30. Second generation teeth M3 of elephants from the Pliocene and Pleistocene of Eurasia: 1-3 (*Archidiskodon gromovi*) from Garutt & Baigusheva (1981), 4 and 5 (*M. trogontherii*) from Sorghel (1903: table 1, fig. 10) and Adam (1988: 20, fig. 5) resp.; masticatory surface (1, 3-5), buccal view (2). Scale bar: 2 cm. 1 = ZIN 31216, left M3, Morskaya locality, Rostov region; 2 = GIN 270/10, right M3, Liventsovsky quarry, Rostov region; 3 = ZIN 31217, left M3, same locality as (4); 4 = right M3, Mauer locality, Germany; 5 = right M3, Pasipler locality, Erzerum, Turkey.

Foto 30. Tweede generatie kies M3 van olifanten van het Plioceen en Pleistoceen van Eurazië: 1-3 (*Archidiskodon gromovi*) uit Garutt & Baigusheva (1981), 4 and 5 (*M. trogontherii*) uit Sorghel (1903: tabel 1, fig. 10) en Adam (1988: 20, fig. 5) resp.; kauwvlakte (1, 3-5) of wangzijde (2). Maatstreep 2 cm. 1 = ZIN 31216, linker M3, Morskaya, Rostov; 2 = GIN 270/10, rechter M3, Liventsovsky groeve, Rostov; 3 = ZIN 31217, linker M3, zelfde vindplaats als (4); 4 = rechter M3, Mauer, Duitsland; 5 = rechter M3, Pasipler, Erzerum, Turkije.

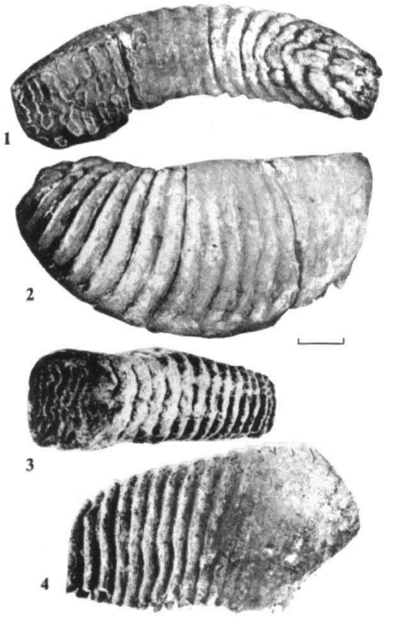


Photo 31. Second generation teeth M3 of *M. trogontherii* from Kolkotova Balka locality, Tiraspol, Moldavia (Dubrovo, 1981). 1 = TPI, right M_3, masticatory surface; 2 = same, buccal view; 3 = OPS 1641, left M^3, masticatory surface; 4 = same, buccal view. Scale bar: 5 cm.

Foto 31. Tweede generatie kies M3 van *M. trogontherii*, Kolkotova Balka, Tiraspol, Moldavië (Dubrovo, 1981). 1 = TPI, rechter M_3, kauwvlakte; 2 = idem, wangzijde; 3 = OPS 1641, linker M^3, kauwvlakte; 4 = idem, wangzijde. Maatstreep 5 cm.

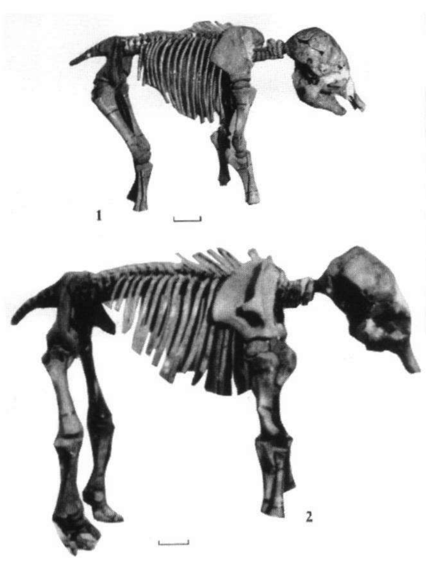


Photo 32. Mounted skeletons of *M. primigenius* calves from Sevsk, Bryansk region. 1 = newborn of one to two weeks old, PIN 4353-2614 to -2717; 2 = a one-year old calf, PIN 4353-211 to -217, -507, -570 to -573, -709 to -716, -810, -817, -873 to -880, -884 to -887, -894 to -907, -922 to -965. Scale bar: 10 cm.

Foto 32. Gemonteerde skeletten van *M. primigenius* kalveren uit Sevsk, Bryansk. 1 = pasgeboren kalf van een tot twee weken oud; 2 = een jaarling kalf. Voor nummers, zie Engelstalig onderschrift. Maatstreep 10 cm.

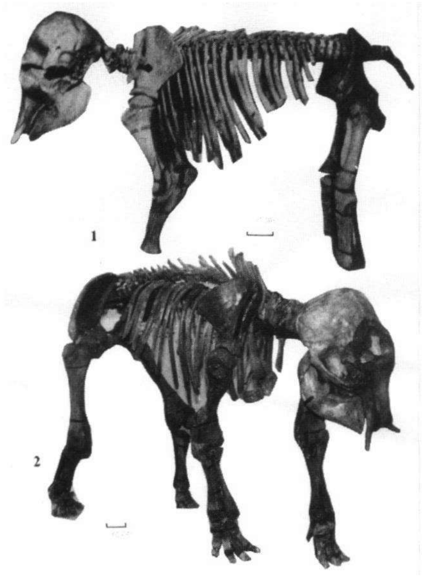


Photo 33. Mounted skeletons of *M. primigenius* from Sevsk, Bryansk region. 1 = a calf of 3-4 years, PIN 4353-447 to -585; 2 = an individual of 6-7 years, PIN 4353-14, -55, -110, -119, -121, -122, -139, -147, -248 to -257, -260, -283, -340, -356, -370 to -372, -384, -386 to -391, -605, -610 to -623, -633, -634, -639 to -647, -649, -651, -652, -661, -663, -664, -670, -678, -690, -732 to -735, -751, -752, -768, -776, -799, -909, -990 to -994, -1061, -1062, -1071, -1076, -1325. Scale bar: 10 cm.

Foto 33. Gemonteerde skeletten van *M. primigenius* uit Sevsk, Bryansk. 1 = kalf van drie tot vier jaar oud; 2 = jong dier van zes tot zeven jaar oud. Voor nummers, zie Engelstalig onderschrift. Maatstreep 10 cm.

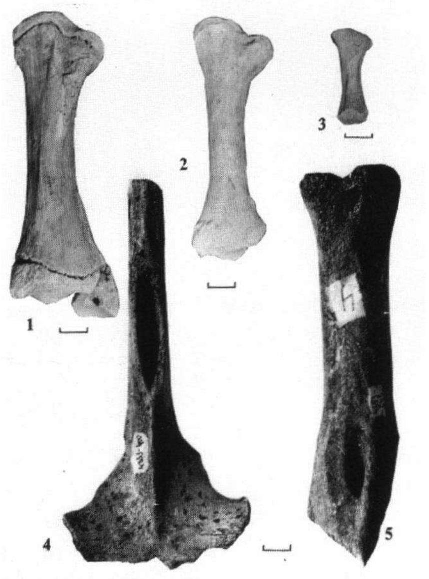


Photo 35. Remains of *M. primigenius* from Sevsk, Bryansk region. 1 = PIN 4353-1495, left tibia of a subadult individual (proposedly, male) with unfused epiphyses, front view; 2 = PIN 4353-1240, left tibia of an adult small-sized female of over 35 years, with completely fused epiphyses, front view; 3 = PIN 4353-1709, right tibia of a calf of one-year old, dorsal view; 4 = PIN 4353-400, perforated dorsal spine of a thoracic vertebra of a calf of 1.5 years, dorsal view; 5 = PIN 4353-51, same, of an individual of 6-7 years.

Foto 35. Resten van *M. primigenius* uit Sevsk, Bryansk; alle van voren gezien. 1 = PIN 4353-1495, linker scheenbeen van een bijna volwassen dier, waarschijnlijk een stier, met nog niet vergroeide groeischijven; 2 = PIN 4353-1240, linker scheenbeen van een vrij kleine volwassen koe, ouder dan vijfendertig jaar, met volledig vergroeide groeischijven; 3 = PIN 4353-1709, rechter scheenbeen van een jaarling kalf; 4 = PIN 4353-400, geperforeerd doornuitsteeksel van een borstwervel van een anderhalf jaar oud kalf; 5 = PIN 4353-51, idem, van een jong dier van zes tot zeven jaar oud.

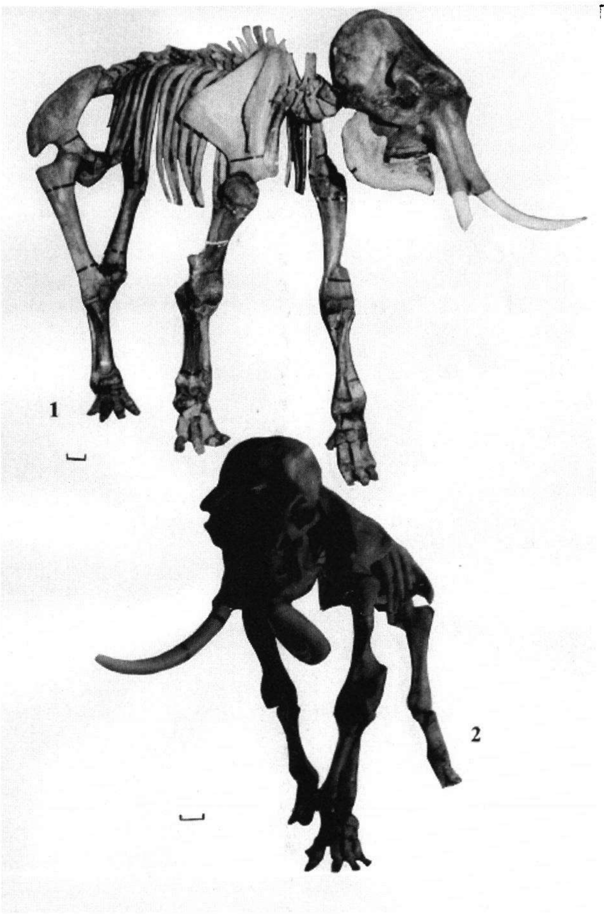
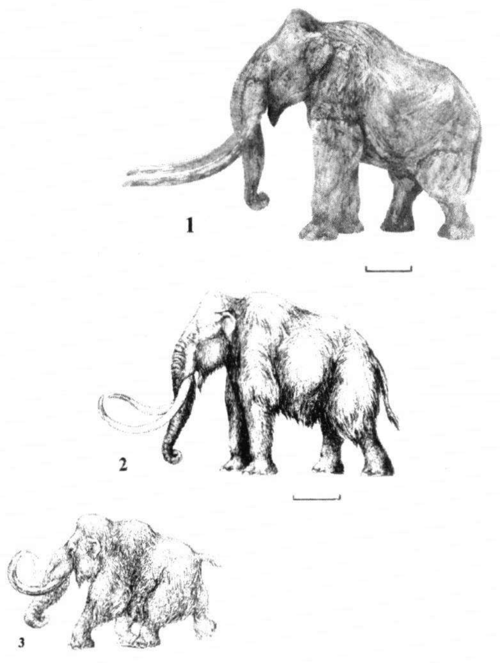


Photo 34. Mounted, incomplete skeletons of *M. primigenius* from Sevsk, Bryansk region. 1 = female of 16-17 years; 2 = an adult, proposedly male. Numbers of specimen 1 are: PIN 4353-4, -5, -8, -9, -24, -34, -39, -52, -54, -56, -60, -61, -86, 43531-02, 43531-19, -20, -23 to -27, -31, -32, -39, -42, -92, 43532-21, -27, -42, -44, -45, -47, -48, -50, -51, -65, -68, -75, -80, -86, -70, -90, 43533-16, -27, -32, -67, -68, -74, -75, 43534-04, -12, -13, -16, -17, -19, -27, -29, -30, -36, 43535-87, -93, 4353601, 43537-10, -24, -37, -72, -82, -84, -93, -94, 43538-08, -12, -22, -27 to -29, -32, -51, -57, -58, -61, -62, 43539-69, -84, -85, -96, 435310-04 to -06, -09, -12, -13, -20, -23, -45, -60, -63, -68, -77, -79, -86, -95, 435311-39, -71, -75, 435312-22, -27, -52, -55, -98, 435314-53, -54, -62, -69, 435315-55, -56, -99 to -435316-01, -34, -70, -74, -98, 435317-54, -57, -77, -82, 435318-59, -62, 435319-35, -41, -58, -89, -92, -95 to -98, 435320-00 to -02, -31, -85, -86, -91, 435321-50, -67, -76, -97, -98, 435323-31, 435324-48, -72, -75, 4353-2611, -2821, -2939, 435330-10, -27, -52, -69, 435331-18, -21, -37, -56, -71, -72, -76, 435332-30, -35, -36, 435333-59, -63, -72, -43, 435335-68, -73. Numbers of specimen 2 are: PIN 4353-314, -704, -728, -977, 435310-03, -15, -82, 435311-13 to -17, -19 to -21, -30, -37, -38, -51, -57, -68 to -70, -72, 435312-11, -54, -57, -59, 435313-37, -52, -67, -91, 435314-13, -20, 435315-30, -35, -37, -84, 435316-02, -20 to -22, -33, -41, -44, -47, -49, -51, -52, -59, -60, 435317-24, -94, 435318-66 to -68, -91, 435319-85 to -87, -99, 435320-28, -34, -38, -46, -50, -84, 435321-37, -49, -54, 435323-02, -03, -21, -34, -91, -93, 435325-08, -09, -10, -67, -89, 435327-27, -36, -43, -44, -45, -85, 435328-20, -25 to -30, -35, -36, -38 to -40, -55, -78, -89, -92, -99 to 435329-11, -38, -56, 435330-11, -12, -15, -24, -28, -46, -49, -53, -54, -81, -84, -86, -91, 435331-08, -12, -94, -435332-46 to -48, -50 to -52, -65, -66, 435333-36, -39, -40, -61, -64, -71, -75, 435334-01, -02, -07, -08, -44, 435335-01, -37, -45, -59, -65, -66, -70, 43533-689, -837.

Foto 34. Gemonteerde, incomplete skeletten van *M. primigenius* uit Sevsk, Bryansk. 1 = vrouwtje van zestien tot zeventien jaar oud; 2 = volwassen dier, waarschijnlijk mannelijk. Voor nummers zie Engelstalig onderschrift

Photo 36. A reconstruction of the mammoth-like elephant lineage (Garutt, 1987). 1 = *Archidiskodon;* 2 = *M. trogontherii;* 3 = *M. primigenius*. Scale bar: 1 m.

Foto 36. Een reconstructie van de evolutie mammoetachtige olifanten (Garutt, 1987). 1 = *Archidiskodon;* 2 = *M. trogontherii;* 3 = *M. primigenius*. Maatstreep 1 m.



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