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New data on the morphology of a foetal mammoth (*Mammuthus primigenius*) from the Late Pleistocene of southwestern Siberia

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Abstract

Twenty-six bones and fragments of bones belonging to a *Mammuthus primigenius* (Blumenbach, 1799) foetus have been discovered in osteological material coming from the late Pleistocene site of Shestakovo, Chebulinsk area, Kemerovo Province. The age of the site is estimated as 24,000–20,000 years BP (Karginian–Sartanian). The stage of intra-uterine development of the foetus can be estimated as 19–20 months. This foetal skeleton is the most complete of all known foetus materials belonging to this species.

1. Introduction

Ten bones and fragments of bones belonging to foetal *Mammuthus primigenius* Blumenbach, 1799 at different stages of intra-uterine development have been recorded previously from various localities in the Russian Plain and Siberia (Kuzmina and Maschenko, 1999; Maschenko, 2002). In 1993, the author identified a fragment of foetal mammoth skeleton in the site of Shestakovo, Chebulinsk area, Kemerovo Province. The absolute age estimated by ^{14}C from the mammoth bones and bones of the late Pleistocene *Equus caballus* and *Rangifer tarandus* at the site is 24,000–20,000 years (Okladnikov and Molodin, 1981; Derevianko et al., 2000). This foetus skeleton is the only quasi-complete foetal skeleton of this species known. It is represented by 26 bones and fragments of bones, with only the pelvis missing. The material described in this paper gives an exceptional opportunity to describe the development of the skeleton in *M. primigenius* during late prenatal stages and discuss features of early ontogeny in this species.

2. Material and methods

Twenty-six bones and fragments of bones belonging to the same foetal skeleton were discovered by the Institute of Archaeology and Ethnography of the Siberian Branch of the Russian Academy of Sciences (IAE, Novosibirsk) during the field season of 1977. The material was discovered in the second cultural layer of the site (Derevianko et al., 2003) within the area of seven excavation quadrants. Most of the material came from quadrants 4B and 5B. Among the bones preserved there are: *humerus* (right) (Sh-77, q 4C); small fragment of the *ulna* (right) (Sh-77, q 5C); *femur* (left) (Sh-77, q 5B); *tibia* (left) (Sh-77, q 4B); *scapula* (left) (Sh-77, q 4C); a fragment of lower jaw (Sh-77, q 6 D); fragmentes of *squama occipitalis* (left and right) (Sh-77, q 4B); three spinal processes of thoracal vertebras (Sh-77, q 3C, 3D); *corpus vertebra* of a lumbar vertebra (Sh-77, q 4D); 13

Abbreviations: q, quadrant; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg; GIN, Geological Institute of the Russian Academy of Sciences, Moscow; Sh, Shestakovo site—abbreviation for field numbers in the Institute for Archeology and Ethnography (IAE) of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk

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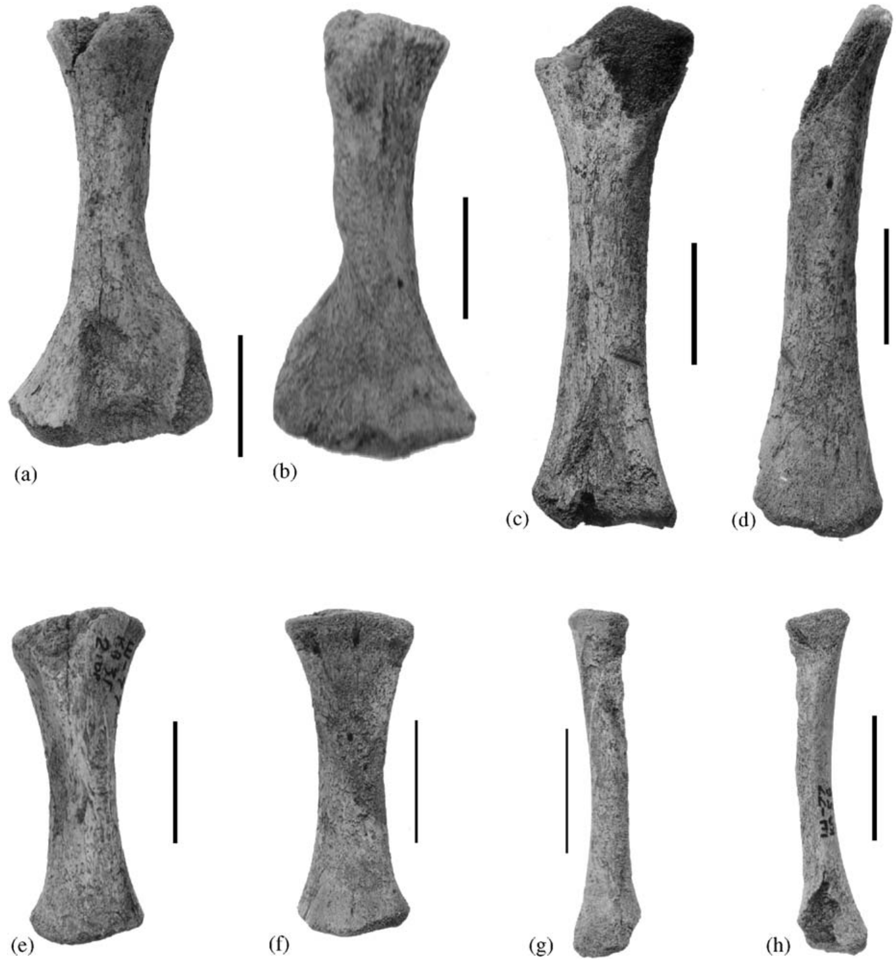

Fig. 1. Bones of an incomplete skeleton of a *M. primigenius* foetus in the last prenatal stage (ca. 20–21 months of pregnancy), Shestakovo Locality, Chebula District, Kemerovo Region: a—right *humerus*, field mark: IAE, Sh-77, 4C,—posterior surface; b—anterior surface; c—left *femur*, field mark: IAE, Sh-77, 4B,—anterior surface; d—medial surface; e—left *tibia*, field mark: IAE, Sh-77, 3D,—anterior surface; f—posterior surface; g—right *radius* field mark: IAE, Sh-77, 5B,—anterior surface; h—posterior surface. Scale bar: 5 cm.

ribs and their fragments (Sh-77, q 4B, 5B) (Figs. 1 and 2). All bones were damaged, probably by the Paleolithic man during carcass butchering.

The following material has been used for comparison:

1. Fragments of mammoth foetus at different stages of intra-uterine development and fragments of a skeleton of a mammoth calf 1-month old, from the site of Eliseevichi (Bryansk Province), housed in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN): *humerus* (right) (ZIN 34386(3), 32572 (1), 20564(54)); *humerus* (right) (ZIN N34386 (5)); *tibia* (left) (ZIN 34386(4)); a fragment of *scapula* (right) (ZIN 34386(10)); *tibia* (right) (ZIN 31740, 31740 (9), 34201 (2)). The absolute age of this material, assigned by ^{14}C, is about 17,000 years (Paleolith of the USSR, 1984).
2. Fragment of a foetal *femur* coming from the site Chotylevo (Bryansk Province), housed in the Zoological Institute of the Russian Academy of Sciences (ZIN 34385). The absolute age (by ^{14}C) is about 24,000 years (Paleolith of the USSR, 1984). A complete foetal *femur* (ZIN 31740 (6)) is housed in the Zoological Institute of the Russian Academy of Sciences.
3. Fragment of a mammoth calf *humerus* from North Russia (PIN 2069–100). Newborn mammoth calf *scapula* (PIN 4353–2658), *humerus* (PIN 4353–2658) and *radius* (PIN 4353–2659) and a 1-year-old calf *scapula* (PIN 4353–881) from the Sevsk locality (Bryansk Province). This material is housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).
4. *Femur* (left) (PIN 4353–3242), *femur* (right) (PIN 4353–3242) and *humerus* (left) of a mammoth foetus (PIN 4353–3243) from the Sevsk locality (Bryansk Province) housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). Absolute age (by ^{14}C) is about 14,000 years (Maschenko, 1992).

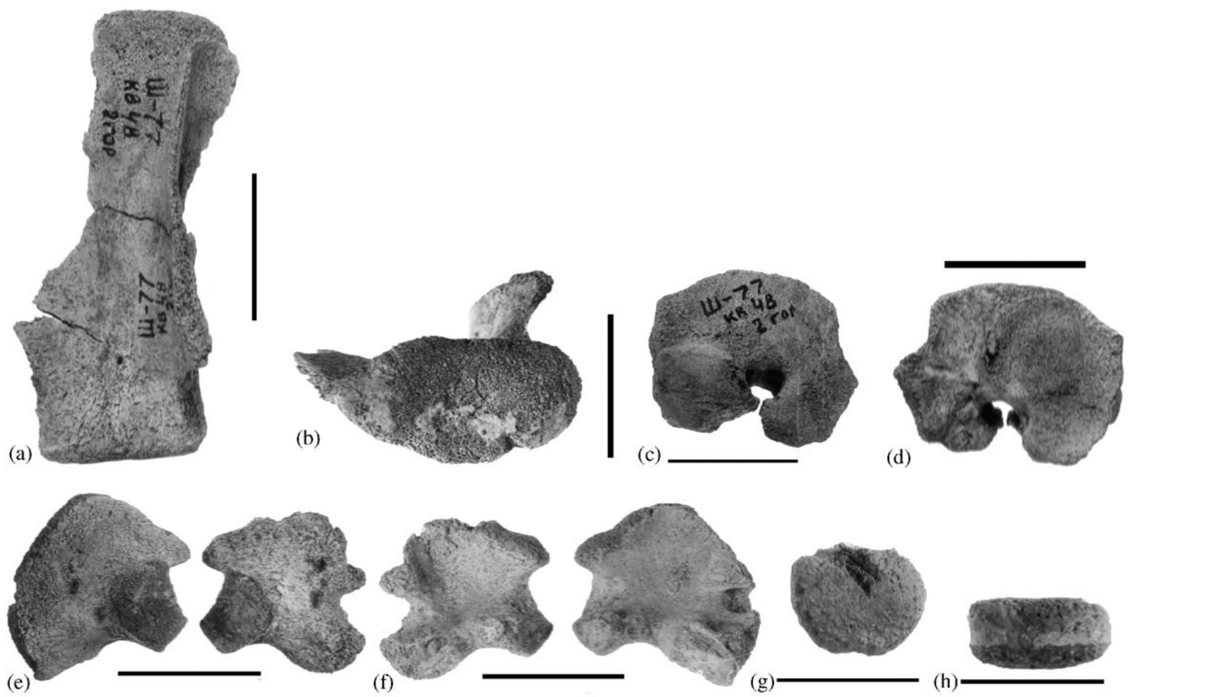

Fig. 2. Bones of an incomplete skeleton of a *M. primigenius* foetus in the last prenatal stage (ca. 20–21 months of pregnancy), Shestakovo Locality, Chebula District, Kemerovo Region: a—right *scapula*, field mark: IAE, Sh-77, 5B,—lateral surface; b—glenoid cavity. c—left *squamosum*, field mark: IAE, Sh-77, 4B,—lateral surface; d—inner surface. e—lower part of the occipital bone (*exoccipitale*), field mark: IAE, Sh-77, 48,—outside surface; f—inner surface; g—thoracic vertebrae (*corpus vertebra*) field mark: IAE, Sh-77, 3D,—cervical surface; h—ventral surface. Scale bar: 5 cm.

5. Bones of mammoth calves (newborn to 1-year old) housed in the Paleontological Institute of the Russian Academy of Sciences (PIN, collections 301 and 4353) and in the Geological Institute of the Russian Academy of Sciences, Moscow (GIN, collection 77).

The stage of intra-uterine development of each foetus was estimated by comparison of sizes and degree of development of foetal bones with similar characteristics of newborn calves from the Sevsk locality and by comparison with modern elephant calves (Tikhonov and Khrabri, 1989; Kuzmina, 1999; Vereshchagin and Tikhonov, 1999; Maschenko, 2002). Individual ages of these calves can be rather precisely estimated by tooth generation (dP2) and degree of tooth development and wear, as well as by some other osteological characteristics of mammoth calves (Roth and Shoshani, 1988). Data are also available on the development of recent elephant foetuses (Deraniyagala, 1955; Frade, 1955; Ananthanarayana and Mariappa, 1988; Beyer et al, 1990). Statistical data on size variation of newborn babies of *Elephas maximus* Linnaeus and *Loxodonta africana* Blumenbach (Stenley, 1943) have been also used. It is possible to recognize size variation in leg bones of newborn calves and mammoth foetuses in the last prenatal stages (Maschenko, 2002).

Pregnancy duration in *M. primigenius* can be considered similar to that reported for recent *E. maximus* and *L. africana* (Sikes, 1966, 1971; Haynes, 1991). Not only pregnancy duration but also some other physiological characteristics of recent African and Asiatic elephants are often extrapolated to mammoths (Agenbroad, 1990; Haynes, 1990), based on the close systematic position of *M. primigenius* and *E. maximus*, similarity of some of their morphological features, and identity of *E. maximus* to *L. africana* in some aspects of ethology. Taking into account all the data available, the stage of intra-uterine development of the foetus from Shestakovo can be estimated as 19–20 months, and pregnancy duration in *M. primigenius* as 21–22 months.

Mammoths differed from recent elephants in showing strongly seasonal birthing as in almost all animals inhabiting areas with long winters. Calves of *M. primigenius* were born in spring and summer, as has been proven by examinations of baby mammoth carcasses from the Kolyma River and the Yamal peninsula, for which both individual age and season of death have been evaluated (Vereshchagin, 1981; Tikhonov and Khrabri, 1989; Vereshchagin and Tikhonov, 1999).

3. Description

3.1. *Radial bone (radius) (IAE, Sh-77, q 5B) (Figs. 1g, j and 3a,b)*

Diaphysis is preserved, and it is rather straight in comparison with diaphyses of young and adult animals.

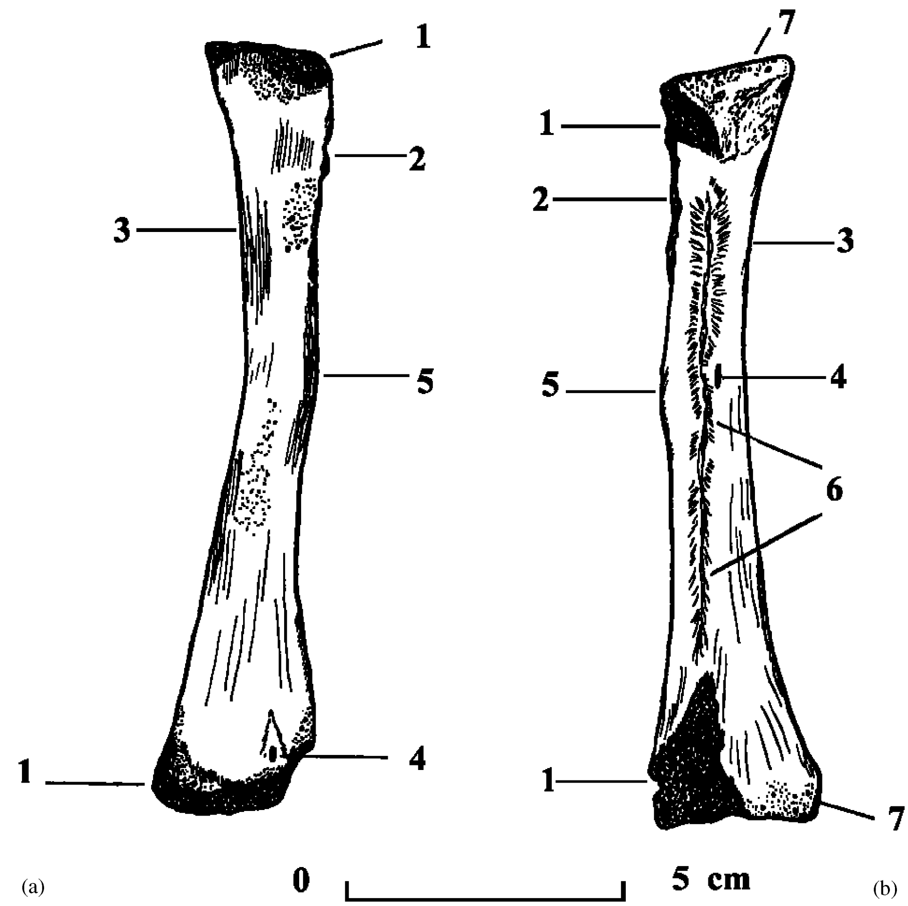

Fig. 3. Right *radius* of a *M. primigenius* foetus in the last prenatal stage (20–21 months of pregnancy), specimen field mark: IAE, Sh-77, 5B, Shestakovo Locality, Chabula District, Kemerovo Region: a—anterior surface; b—posterior surface. Scale bar: 5 cm. 1—damaged areas of bone; 2—*margo posterior*; 3—*margo anterior*; 4—*foramen nutricium*; 5—*tuber radii* usually referred to the area of attachment of *musculus biceps*; 6—the rough tract of margo interosseus; 7—substantia spongiosa on diaphyseal endings.

Proximal and distal parts of the *radius* are less massive than in the *radius* of newborn mammoth calves. The foetal diaphysis, compared to those of adult animals, is relatively short and thick.

The proximal part of the diaphysis is narrower than its lower distal part and has the same proportions as the diaphysis of a newborn mammoth calf (Table 1). The whole diaphysis is flattened in the anterior–posterior direction and has an oval contour. Relief on diaphysis in areas of attachment of large muscles is not pronounced. Posterior margin of the diaphysis (*margo posterior*) in its upper quarter is acute, forming a crest. Although roughness for the attachment of the biceps is not pronounced, one can observe a small tuber (*tubirositas biceptalis radii*) in the area of its future localization. This area is relatively less displaced toward the upper margin of the diaphysis, compared to subadult and adult individuals (PIN 4353–2618).

On the inner margin of the diaphysis *(margo interosseus*) one can see relief looking like a vertical tract of roughness situated along the middle part of the diaphysis. In later stages of ontogeny, this roughness can form a crest separating the front part of the bone from its inner margin.

The external surface of the *radius* is more convex, the inner, more flattened. The distal part of the foetal diaphysis is longer than its proximal part, as in newborn calves, subadults and adult individuals. The smallest diameter of the diaphysis is located 21 mm from the proximal margin of this bone.

Most probably the rate of growth of ends of the radius was higher than the rate of growth in the length of the diaphysis during the last few stages of prenatal ontogeny and the few first months of postnatal ontogeny in *M. primigenius*. For later portions of postnatal ontogeny, the rate of increase in diaphysis length was higher than the rate of growth of its ends in traverse and longitudinal directions.

The outer layer of the bone (*substantia compacta*) preserved on various parts of the diaphysis is thinner than in young and adult individuals. The inner part of the diaphysis is filled with *substantia spongiosa*. Elements (trabeculae) of the upper layers of *substantia spongiosa* are oriented along the longitudinal axis of the

Table 1
Measurements (mm) of *radius* of foetuses and calves of mammoths (*M. primigenius*)

Measurement	IAE Sh-77, 3B—foetus, last stage of pregnancy	PIN 4353–2659—newborn
1. Maximal diaphyseal length	137	164
2. Transverse/anteroposterior diameters of distal end of diaphysis	30/—	46/27
3. Transverse/anteroposterior diameters of proximal end of diaphysis	26/16.5	33/18
4. Minimal transverse/anteroposterior diameters of diaphysis	15.5/11	18/—
Ratio 2/1	0.21	0.28
Ratio 4/1	0.18	0.21
Ratio 6/1	0.11	0.10
Ratio 4/2	0.86	0.72

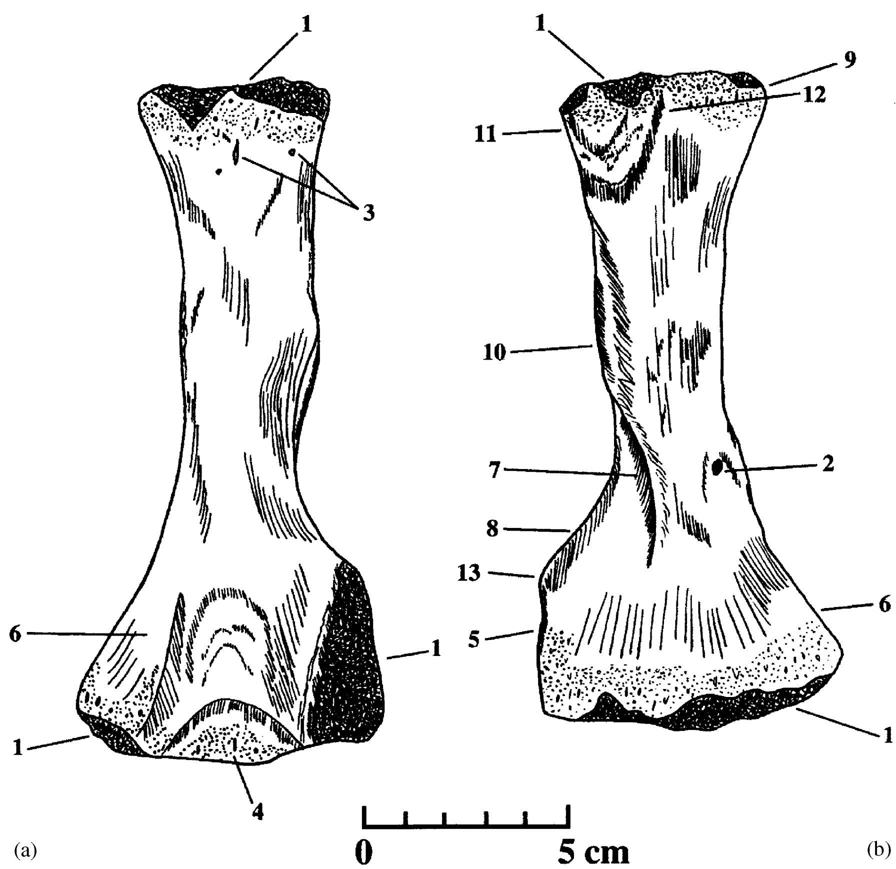

Fig. 4. Right *humerus* of an incomplete skeleton of a *M. primigenius* foetus in the last prenatal stage (ca. 20–21 months of pregnancy), specimen field mark: IAE, Sh-77, 4C, Shestakovo Locality, Chebula District, Kemerovo Region: a—posterior surface; b—anterior surface. Scale bar: 5 cm. 1—damaged areas of diaphysis; 2—*foramen nutricium*; 3—small nutritive foramina on the proximal end of the diaphysis; 4—*fossa olecrani*; 5—*epicondylus lateralis*; 6—*epicondylus medialis*; 7—delta-shaped crest (*crista tuberculi majoris*); 8—*crista epicondyli lateralis*; 9—*tuberculum minus*; 10—*tuberositas deltoidea;* 11—*tuberculum majus*; 12—*sulcus intertubercularis*; 13—tuber localized in proximal part of lateral epicondyle.

diaphysis. The medullary cavity (*cavum medullare*) cannot be observed on damaged parts of the bone.

In spite of the fact that the outer layer of the bone is damaged, it is possible to see that *substantia compacta* is better developed in the middle part of the diaphysis. On the ends of the diaphysis this layer is friable and has many small openings and pores indicating incomplete development of this part of the bone (Figs. 1g, h, and 3a, b).

On the surface of the bone, as preserved, one can see two nutrient foramina (*foramen nutricium*) (Figs. 3b and 4). The foramen on the distal end of the outer anterior surface of the diaphysis is oval in shape, 1.5×0.9 mm in size and located 12 mm distal and of the diaphysis. The foramen on the posterior surface of the bone is about 1 mm in diameter and is located in the notch, near its lower edge. The notch formed by this foramen is 5 mm in length and 1 mm in width.

On the *radius* diaphysis of a mammoth calf 1 month in age (GIN 77), *foramen nutricium* is located only in the lower part of the anterior surface of the diaphysis. The number and contour of this kind of foramen on other available specimens are variable. The surface of the proximal end of the diaphysis is inclined, medial margin being located higher than the lateral one. The foetal diaphysis has no pronounced torsion of the proximal end of the diaphysis relative to its lower end. In newborn baby mammoths (PIN 4353–2659, 1233), such torsion is already better pronounced, and it is especially clear and sometimes very strong in adults, as one can see on specimen PIN 4353–625.

3.2. Shoulder bone (humerus) (IAE, Sh-77, q 4B) (Figs. 1a, b and 4a, b)

The diaphysis is similar in shape and the main proportions to that of calves and adults. The upper third of the diaphysis widens in the anterior–posterior direction the lower third is flattened in an anterior–posterior direction and widens in a transverse direction (Fig. 4). Proximal and distal ends of the diaphysis are flattened, and the length of the bone can be evaluated roughly (Table 2).

The diaphysis narrows progressively starting from the level of the *tuberculum ectocondiloideum* and acquires an oval shape. Starting from the beginning of *crista deltoidea* the proximal part of the diaphysis starts to turn relative to the distal part of the diaphysis, the anteroposterior diameter of the diaphysis becoming greater than its transverse width. The degree of torsion is about 80°. This differs from the diaphysis of adults and calves by less pronounced development of the *tuberculum ectocondyloideum* and by the *crista epycondyli lateralis* forming a more acute angle with the longitudinal axis of the diaphysis (in adults this angle is about 50°).

The *tuberculum ectocondyloideum* in the foetal *humerus* is relatively closer to the distal end of the diaphysis than in subadults and adults (Fig. 4b-13). The point of minimum width of the diaphysis, where the *crista epicondyli lateralis* stops, is located relatively higher than in juveniles and adults, i. e., the part of the diaphysis that is higher than this point seems to be longer in adults (PIN 4353–630).

The deltoid crest (*crista deltoidea*) is pronounced to the same degree as in newborn and adults. It starts at a distance of 59 mm from the distal end of the diaphysis and goes upwards, partly covering the lateral surface of the bone. In some parts it has additional roughened relief. The *tuberositas deltoidea* is clearly pronounced (Fig. 4b, 10), and on the diaphysis of the foetal *humerus* it represents the clearest trace of muscle attachment. This roughness starts almost at the top of the *crista deltoidea*. Edges of the lateral and medial epicondyles are situated at different levels, the level of the medial epicondyle being 18 mm higher.

The surface of the lower third of the diaphysis is almost completely destroyed; the *substantia compacta* in this area is about 1.5 mm thick and consists of 5–6 sublayers underlain by *substantia spongiosa*.

There are no visible nutrient foramina on the anterior surface of the lower part of the diaphysis. A rather large

Table 2
Measurements (mm) of of *humeri* foetuses and calves of mammoths (*M. primigenius*)

Measurements	ZIN 32572 (1)	IAE Sh-77, 4B	ZIN 31744 (1)	ZIN 34419(17)	ZIN 20564 (54)	PIN 4353–2658
Diaphyseal length	—	168(?)	—	—	—	204
Mediolateral diameter of the distal end of diaphysis	62	80	78	80	70(?)	98
Anteroposterior diameter of the distal end of diaphysis	19(?)	35	29	21	28	46
Shortest mediolateral diameter of diaphysis	20	26.5	30	25	24	34
Anteroposterior diameter of the proximal end of diaphysis	—	63	—	—	54(?)	81
Mediolateral diameter of the proximal end of diaphysis	—	48	—	—	—	61
Height from the end of *crista epicondylus lateralis* to the distal end of diaphysis	46	52	59(?)	56	60(?)	50
Individual age	Foetus (beginning (?) of the second year of pregnancy)	Foetus (last period of pregnancy)	Newborn 1 week (?)	Newborn 1 week (?)	Newborn 1 week (?)	Newborn 1 week (?)

nutrient foramen (4 × 2 mm) is located somewhat below the level of the beginning of the *crista deltoideum*. Such a location for this foramen is also common for most subadults and adults, but, on the *humerus* of a newborn calf from Sevsk (PIN 4353–2616), this foramen is absent.

The surface of the compact layer observed on non-damaged parts of the bone is smooth and has a microtexture consisting of vertical lines situated almost parallel to each other, visible to the naked eye. Such a texture has not been observed on bones of the adults studied (PIN 4353–3242, 2801,2804,2811,2813,2814, 1140,1136, 1135, 286).

The diameter of the proximal end of the diaphysis is relatively large compared to other parameters of the bone. The *tuberculum minus* can be observed in the upper portion of the diaphysis, but damage to the bone prevents evaluation of its size. *Sulcus intertubercularis* (= *fossa bicipis* by Zalensky, 1903) is weakly pronounced. Its depth does not exceed 2.5 mm. The bottom of this fossa where *musculus biceps* is attached has no relief like that seen on the newborn calf (PIN 4353–2658, 2161).

The proportions of the proximal part of the foetal diaphysis (transversal and longitudinal diameters) are different from those of adults. Diameter is noticeably greater than transversal diameter, but in adults these dimensions are usually almost equal (PIN 4353–875, 2658, ZIN 34386(3)). In spite of bone damage, one can see that the head of the *humerus* (*caput humeri*) had an oval shape. Its size could be about 39 × 34 mm. The long axis of the head of *humerus* is oriented in a medial–lateral direction. The head of the *humerus* is located close to the lateral margin of the proximal end and 10 mm away from the medial margin.

Three nutrient foramina can be observed on the posterior surface of the proximal end of the bone (Fig. 4a-3). Two of them are semicircular in shape, with diameters of about 1 mm and the third is situated in a furrow in the outer layer of bone 4 × 1 mm in size. A rather large nutrient foramen (1 × 1 mm) is located also on the lateral surface of the proximal edge of the diaphysis, 28 mm from its top.

Location of smaller nutrient foramina as well as a number of large nutrient foramina on newborn calf bones can be somewhat variable, but they are always concentrated near the ends of the diaphysis, in the growth zone. Nutrient foramina in the foetal and newborn calf *humerus* are left by the largest blood vessels situated in the cartilaginous growth zone. Small foramina disappear quickly after the cartilage in the growth zone has been replaced by bone, but larger foramina stay longer (Romer and Parsons, 1992). A permanent nutrient foramen for an artery is always located on the anterior surface of the diaphysis at the level of the deltoid crest (Fig. 4b, 2).The cubital fossa (*fossa olecrani*) is not deep, has no clear boundaries (Fig. 4a, 4), and is pronounced.

3.3. Shoulder blade (scapula) (IAE, sh-77, 4B) (Figs. 2a, b and 5a, b)

The *margo cervicalis* is damaged, and the *margo thoracalis* is destroyed (Table 3). The proximal margin of the *scapula* is flattened as in subadult and newborn individuals and unlike that of adults has no clear convexity. The epiphyses of the *scapula* in mammoths and elephants fuse rather late, also most probably ossifites late, and until 6–7 years of age remain completely cartilaginous. It has been noticed that in the series of skeletons of calves of various ages from the Sevsk locality (collection PIN 4353) ossified epiphyses of the *scapula* are only reported for animals older than 6–7 years (Maschenko, 2002). The scapular crest (*spina scapulae*) is oriented almost perpendicular to the profile of the articular surface (in lateral view), its base being displaced toward the anterior margin of the *scapula*. The ventral margin of the scapular crest is located about 24 mm above the articular cavity margin. It has been noticed that two groups can be recognized in scapulae of calves and young individuals (6–9 years old) based on the location of scapular crests: a group with the scapular crest strongly displaced toward the anterior margin, with the base of the crest being located close to the articular cavity margin, and a group with the scapular crest located rotated away from the anterior margin of scapula and from the articular cavity margin (Kuzmina and Maschenko, 1999). These differences could be connected with changes in scapular proportions with age. Scapulae of individuals older than 2–3 years belong to the second group, and foetal scapulae, to the first group.

Widths of the scapular neck and articular cavity are almost equal. The scapular tuber (*tuber scapulae*) on the anterior margin of the articular cavity of the foetal *scapul*a is not formed yet. The articular cavity margin is straight, but not bow shaped as in young and adult individuals (PIN 4353–562, ZIN 32572, 31740(10), 34418, 31835(1), 34419(2)). In newborn calves it is slightly concave and the neck (*collum scapula*) is narrower than the glenoid cavity (*cavitis glenoidalis*) width. This part of the scapula in 1-year-old calves reaches the same proportions as in adult individuals (PIN 4353–881).

An articular cavity with an insignificant depression (3–4 mm) in its central part and an almost straight margin represents an important characteristic of the foetal *scapula*. In newborn calves the *scapula* (PIN N4323–2657) articular cavity is deeper and has a curved margin.

The scapular crest is noticeably inclined toward the plane of the blade of the *scapula* and in its lower third

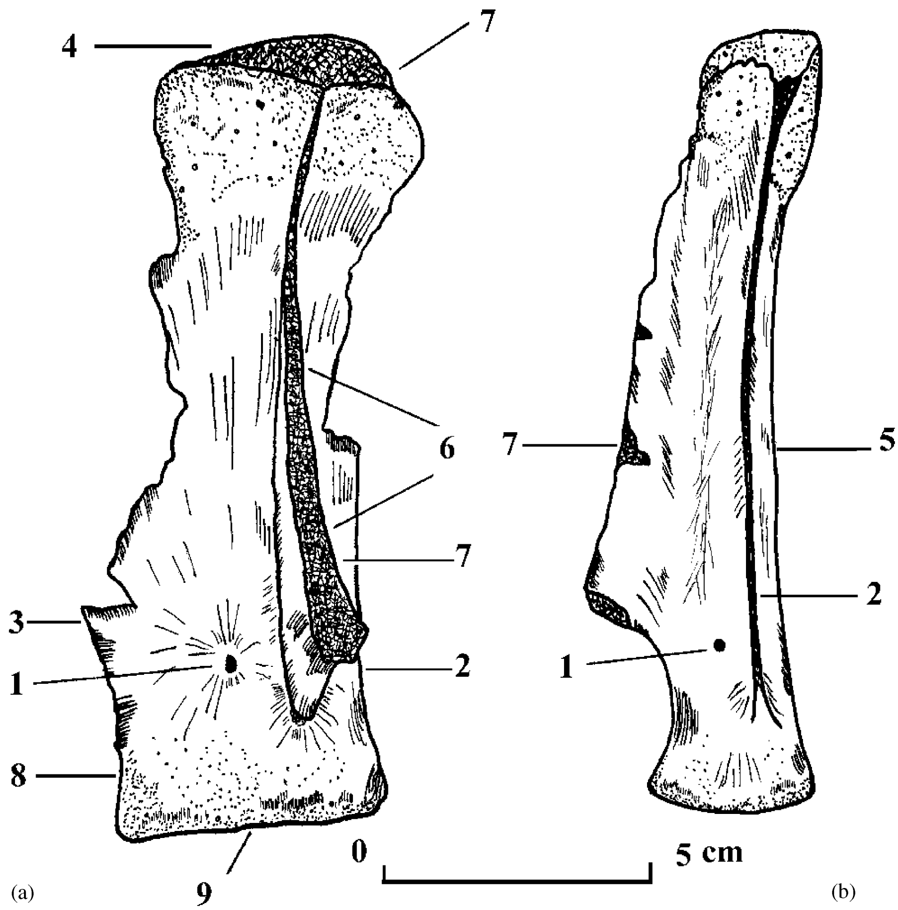

Fig. 5. Right *scapula* of an incomplete skeleton of a *M. primigenius* foetus in the last prenatal stage (ca. 20–21 months of pregnancy), specimen field mark: IAE, Sh-77, 5B, Shestakovo Locality, Chebula District, Kemerovo Region: a—lateral surface; b—anterior surface. Scale bar: 5 cm. 1—*foramen nutricium*; 2—*margo cervicalis*; 3—*margo thoracales*; 4—*margo vertebralis*; 5—mesial surface; 6—spina scapulae; 7—damaged areas of shoulder blade; 8—scapular neck; 9—*cavitas* glenoidalis.

Table 3
Measurements (mm) of *scapula* of a foetus and calves of mammoths (*M. primigenius*)

Measurements	IAE Sh–77, 4B	PIN 4353–2658	ZIN 31740 (10)	PIN 4353–881
Maximal length	146.5	185	192	238
Length to the middle of the glenoid cavity	145.5	179	188	233
Maximal width	—	157	197	220
Width/depth of neck of the scapula	55/-	68/26	73/31	88/32
Width/length of the glenoid cavity	55/29	78/40	76/40	94/51
Length of scapular crest	119	143	150	136
Ratio of the length of scapular crest to maximal length	0.81	0.77	0.78	0.57
Ratio of the width of the glenoid cavity to maximal length	0.38	0.42	0.40	0.40
Ratio of the width of the neck of the scapula to maximal length	0.37	0.42	0.38	0.40
Individual age	Foetus (last period of pregnancy)	Newborn—1 week (?)	Calf 3–4 months (?)	Calf, 1 year

forms an angle of 50°. This angle increases toward the upper margin of the scapula and close to its top reaches 90°. The scapular crest in two-thirds of its length, from the glenoid cavity to the top of the scapula, is parallel to the anterior border. The upper third of the scapular crest is deflected forward to the anterior border. The preserved part of the crest is 22 mm wide, and its minimum thickness near the base is 6 mm.

The outer layer is dense in the central part of the scapula. The lower (glenoid cavity) and upper parts (vertebral and thoracic margin) of the scapula have porous surfaces, and the *substantia compacta* there has another texture (Fig. 5a). There were probably 6–7 nutrient foramina, 1×1 mm in diameter, near the upper margin of the scapula, but poor preservation of this part of the bone preclude accurate data.

The maximum thickness of the upper margin of the scapula (about 16 mm) is near the base of the scapular crest; thickness decreases evenly toward the anterior and posterior margins. There is one big nutrient foramen (3×1 mm in size) behind the scapular crest in the lower part of the scapula, 30 mm above the border of the glenoid cavity (Fig. 5a, 1). Another nutrient foramen (1×1 mm in size) is located in front of the scapular crest near the anterior margin of the scapula. It is directed toward the base of the scapular crest and is 28 mm above the border of the glenoid cavity.

The inner surface of the foetal scapula is curved less than in scapulae of young individuals (PIN 4353–501,323). Only the area close to the articular surfaces is noticeably curved. In the upper part of the inner surface of the scapula there is a small longitudinal crest, located close to the posterior margin of the scapula. The position of this crest corresponds to the origin of *musculus cerratus ventralis* in adults (Gambaryan and Rukhkyan, 1974).

The main difference between foetal, newborn and subadult individuals in the proportions of the scapula is in the length of the scapula relative to the width of the articular cavity (or width of the neck of the *scapula*) ratio. The foetal *scapula* is relatively short and has a relatively wide glenoid cavity. Adults have longer scapulae and narrower glenoid cavities than the foetus and newborn individuals (Table 3). Another difference is in the scapular length to scapular width ratio. In calves younger than one year, length and width of the scapula are rather close. In subadult and adult animals scapulae become longer. The foetus had the shortest and the widest scapula (PIN 4353–2657, 881, 501; ZIN 31740(10)).

3.4. Thigh (femur) (IAE, Sh-77, q 5B) (Figs. 1c, d and 6a, b)

The upper part of the diaphysis is damaged; only its anterior wall is preserved. The lower posterior part is also damaged: the outer layer (*substantia compacta*) is damaged, especially in its middle part, where it to thin, less than 1 mm in thickness.

The diaphysis is similar in shape to femora in newborn individuals (PIN 4353–2698, 2702, 1844, 2507). The middle part of the diaphysis is oval in transverse section, the proximal part is dilated in the mediolateral direction, and the distal part in the anteroposterior. The diaphysis is curved in an upper third in the anteroposterior direction. Such a curvature can be observed in femora of some newborn calves and calves younger than 1 year (ZIN 34419(10), PIN 4353–552).

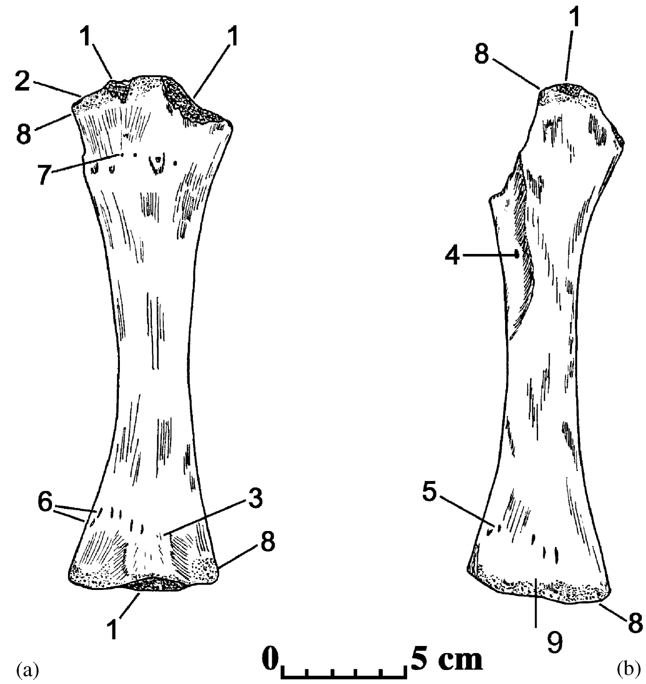

Fig. 6. Right *femur* of an incomplete skeleton of a *M. primigenius* foetus in the last prenatal stage (ca. 20–21 months of pregnancy), specimen field mark: IAE, Sh-77, 4B, the Shestakovo Locality, Chabula District, Kemerovo Region: a—anterior surface; b—medial surface. Scale bar: 5 cm. 1—damaged area of *femur* with *substantia spongiosa*; 2—*trochanter major;* 3—protrusion of the anterior surface of distal end of diaphysis over presumptive *trochlea patellaris*; 4—permanent *foramen nutricium*; 5—grooves of small nutritive foramina on the posterior surface of diaphysis; 6—grooves of small nutritive foramina on posteromedial surface of distal end of diaphysis; 7—small nutritive foramina on anterior surface of proximal end of diaphysis; 8—compact layer on the diaphyseal end; 9—*fossa trochanterica*.

The anterior surface of the distal part of the diaphysis is much more convex than the posterior surface. One can see on it a convexity that in subadult and adult animals becomes a base for the *trochlea patellaris*. Minimum width of the diaphysis is about its middle, like in femurs of calves and young animals (Table 4). Starting from its middle the diaphysis increases evenly in width upwards and downwards.

The trochanteric fossa (*fossa trochanterica*) in the foetus from Shestakovo is developed to the same degree as in the newborn baby (PIN 4353–2698). This structure can be observed already on the femur of a foetus no older than 10 months (PIN 4353–3243). The greater trochanter (*trochanter major*), as one can judge according to its preserved part, has the same proportions as in newborn and subadult animals (PIN 4353–2453, 1844, 419, 403). In a foetus of 10 months (PIN 4353–3243) it is

Table 4
Measurements (mm) of *femur* of foetuses and calves of mammoths (*M. primigenius*)

Measurements	ZIN 31740 (6)	IAE Sh-77, 5b	ZIN 34419(10)	PIN 4353–2698	ZIN 34201 (4)	PIN 4353–552
Transverse/longitudinal diameters of head of the femur	27/24	—	48/40	51/-	50/48	74/69
Mediolateral diameter of the distal end of diaphysis	36	60.5	63	80	72	96
Anteroposterior diameter of the distal end of diaphysis	32	49	53	62	54	81
Shortest mediolateral diameter of diaphysis	24	29.5	33	40	32	47
Shortest anteroposterior diameter of diaphysis	19	28	27	34	24	41
Maximal diaphyseal length	156	208(?)	226	250	245	310
Longitudinal/transverse diameter of the neck of *femur*	26/35	—	33/51	45/59	36/52	53/70
Diaphyseal length (to trochanter major)	143	183	198	210.5	211	270
Individual development stage	Foetus (last stage of pregnancy)	Foetus (last stage of pregnancy)	Newborn	Newborn	Calf, 1 month (?)	Calf, 1 year

already outlined and looks like a thin and narrow plate. And already at this stage of inter-uterine development the femur diaphysis is similar in shape and main proportions to that of adults.

A large (4.3×2.9 mm) and permanent nutrient foramen is located on the inner (medial) surface at the base of the upper third of the diaphysis at a distance of 73 mm from the top of the trochanteric fossa. On femora of all foetal, newborn, subadult and adult individuals studied, this foramen is located in the same part of the diaphysis.

Five nutrient foramina, no more than 1 mm in diameter, are located on the anteromedial surface of the distal part of the diaphysis in the upper parts of furrows that are 6–10 mm in length and 1–2 mm in width. These furrows are oriented along the long axis of the bone and are located 22–31 mm from the lower margin of the diaphysis (Fig. 6a, 6; Fig 6b, 5).

Six nutrient foramina of the same size are located on the anterior surface of the proximal part of the diaphysis in the lower parts of furrows 5–6 mm in length and 2–3 mm in width. These furrows are located 30–33 mm below the upper margin of the diaphysis.

On the femur of a newborn calf (PIN 4353–2698) nutrient foramina are located in a similar way but are fewer in number (2–3) and longer in size than on the foetal femur from Shestakovo site. One can suppose that the presence and level of development of these foramina are indicative of the intensity of growth processes during the last months of pregnancy and the period just after birth.

3.5. Tibia (IAE Sh-77, q 3C) (Figs. 1e, f and 7a, b)

The tibia is the most completely preserved bone of the foetus skeleton described. There is insignificant damage on the upper and lower edges of the diaphysis (Fig. 7b, 7). *Substantia compacta* is strongly damaged on the posterior surface of the diaphysis. Measurements are given in Table 5.

The crest of the *tibia* (*crista tibiale*) marked by roughness on the anterior surface of the diaphysis. It starts at the level of the border of the tuberosity of the tibia (*tuberositas tibiae*) and goes downward upon the surface of the diaphysis, progressively deviating toward the medial side of the bone, but does not reach its lower border. On the tibia of the newborn calf (PIN N4353–2703) this crest is already better developed and reaches the lower border of the diaphysis. It too noticeably deviates toward the inner side of the bone. The crest of the tibia in young and adult individuals is more vertical.

Transverse width of the tuberosity of the tibia is greater than its vertical height (Table 5). The tuberosity looks like a depression with very gentle slopes narrowing downwards. Its lower border forms the tubercle from which the crest of the tibia starts. In newborn calves and individuals younger than 3 years, the transverse width of the *tuberositas tibiae* is normally less than its vertical height (PIN 4353–2703, 1709, 870). The character of the tuberosity in all specimens mentioned is about the same.

The lateral border of the upper part of the epiphysis is higher than the medial border similar to the epiphysis of a newborn calf (PIN 4353–2609, 2793). The difference in the degree of inclination and in height between lateral and medial borders of the proximal edge of the diaphysis of the tibia of the newborn calf is greater than in the tibia of the foetus described; for a 1-year-old calf (PIN 4353–1709) this difference is greater than for the newborn. The pattern of inclination of these surfaces toward each other typical for adults develops, most probably, after 3 years. In individuals 6–7 years old from the Sevsk locality (PIN 4353–625) the pattern is like that in adults.

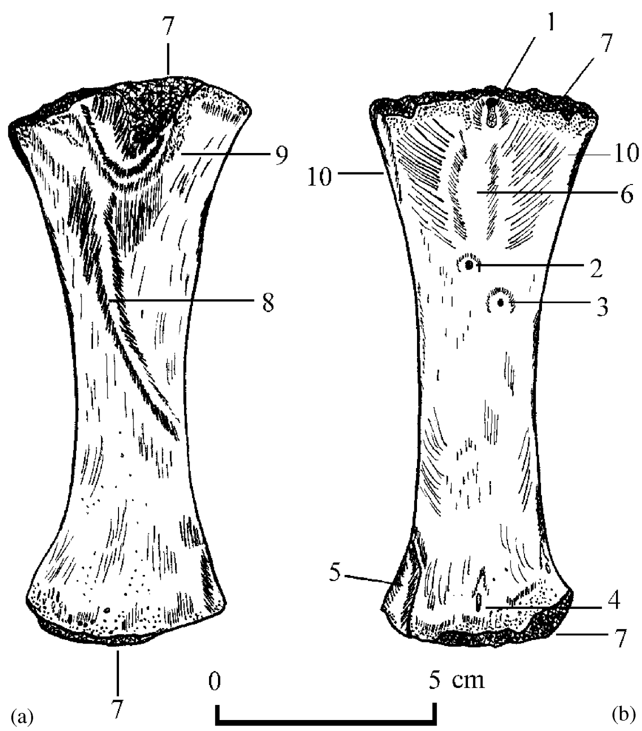

Fig. 7. Left *tibia* of *M. primigenius* foetus of last prenatal stage (20–21 months of pregnancy), specimen field mark: IAE, Sh-77, q 4®, the Shestakovo Locality, Chabula District, Kemerovo Region: a—anterior surface; b—posterior surface. Scale bar: 5 cm. 1—proximal *foramen nutricium*; 2—middle *foramen nutricium*; 3—distal *foramen nutricium*; 4—depression near distal end of diaphysis; 5—*sulcus malleolaris*; 6—concavity of posterior surface of diaphysis; 7—damaged areas of bone; 8—*crista tibiale*; 9—*tuberositas tibia*; 10—crests of lateral and medial edges of posterior surface of diaphysis usually referred to as *linea muscularis*.

There are no visible nutrient foramina on the anterior surface of the diaphysis of the specimen described. The upper quarter of the posterior surface of the diaphysis is concave. It is separated from the lateral and medial sides of the bone by crests (*linea muscularis*) (Figs. 7b and 10). These crests are developed similarly both on the foetus and in the newborn calf (PIN 4353–2703) tibia, with low, rounded tops. They do not differ in shape from *linea muscularis* on tibiae of subadult and adult individuals (PIN 4353–870, 625, 1625, 2153). During later ontogenesis *linea muscularis* become higher and have thin, acute tops. The development of the adult form for these structures started about the age of one year.

On the posterior surface of the diaphysis one can observe three rather large nutrient foramina. The largest one (5×2 mm) has an oval contour and is located 4 mm below the upper border of the diaphysis. In one newborn calf (PIN N4353–2703) it is located similarly. On tibiae of other newborn calves (PIN 4353–2355, 2162, 2699) similar nutrient foramina near the proximal border of the diaphysis are absent.

The intermediate nutrient foramen (2.5×2 mm) is located 44 mm far below the proximal border of the diaphysis and 74 mm above its distal border, and the lower nutrient foramen (2.5×1.5 mm) is located 56 and 62 mm from the proximal ends and distal borders of the diaphysis, respectively. The number of nutrient foramina in the middle part of the posterior surface of diaphyses could vary from 1 to 3. But studies of *tibiae* of more advanced calves (PIN 4353–1709, 870) demonstrated that only the intermediate nutrient foramen was consistently present. On tibiae of newborn and subadult animals it occupies almost the same position as on the foetal *tibia*.

There are a few smaller nutrient foramina located in rows along the distal border of the posterior surface of the diaphysis. Their position, shape and function are the

Table 5
Measurements (mm) of *tibiae* of foetuses and calves of mammoths (*M. primigenius*)

Measurements	ZIN 31740	IAE Sh-77, 3g	ZIN 31740 (9)	PIN 4353–2703	ZIN 34201 (2)	PIN 4353–1709
Maximal diaphyseal length	135	127.5	146	160	156	184
Transverse/anteroposterior diameters of proximal end of diaphysis	52/36(?)	51/39	57/48	69/51	66/65	88/63
Minimal anteroposterior/transverse diameters of diaphysis.	29/25	25/25	33/27	34/27	33/26	40/35
Transverse/anteroposterior diameters of distal end of diaphysis	38(?)/37	43.5/34	47/37(?)	60/42	66/45	63(?)
Individual age	Foetus, last stage of pregnancy	Foetus, last stage of pregnancy	Newborn (?)	Newborn	Newborn	Calf, 1 year

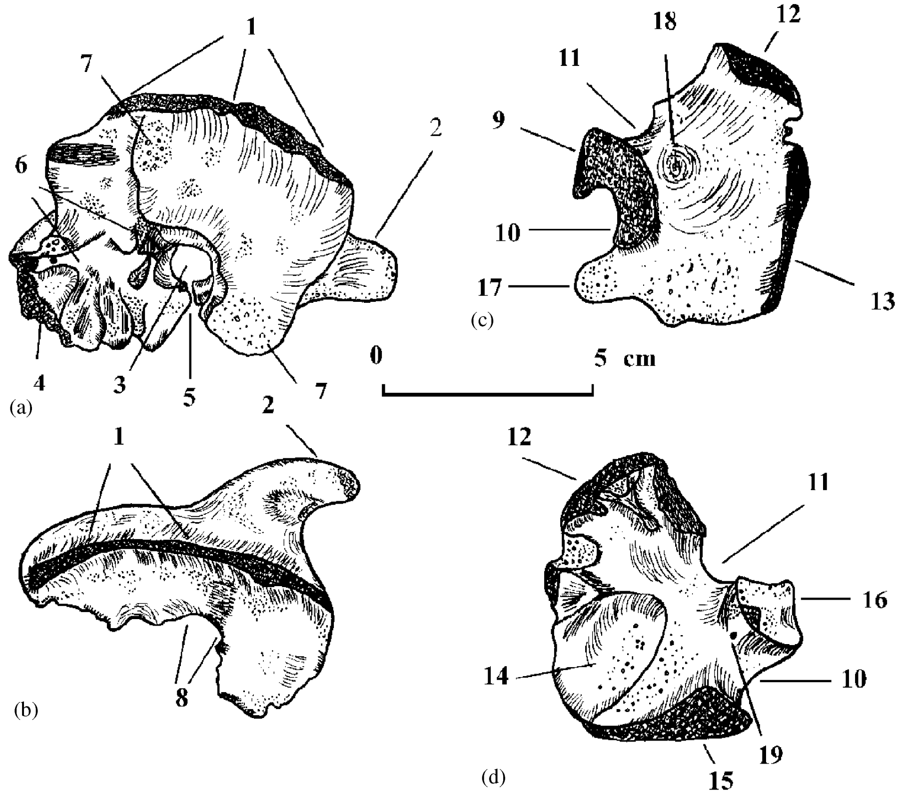

Fig. 8. Left *squamosum* of an incomplete skeleton of a *M. primigenius* foetus in the last prenatal stage (ca. 20–21 months of pregnancy), specimen field mark: IAE, Sh-77, 4B, the Shestakovo Locality, Chebula District, Kemerovo Region: a—lateral surface; b—upper view. Scale bar: 5 cm. 1—edge facing to *parietale*; 2—*processus zygomaticus*; 3—porus acusticus externus; 4—edge facing to *exoccipitale*; 5—ossis meatus auditorius squamosum; 6—relief of inner surface; 7—substantia spongiosa; 8—notch for the *nervus facialis*. Left *exoccipetale* of an incomplete skeleton of a *M. primigenius* foetus in the last prenatal stage (ca. 20–21 months of pregnancy), specimen field mark: IAE, Sh-77, 48, Shestakovo Locality, Chebula District, Kemerovo Region: c—outside surface; d—inner surface. Scale bar: 5 cm. 9—*condylus occipitalis*; 10—*foramen occipetale magnum*; 11—*foramen jugulare*; 12—edge facing to *squamosum*; 13—damaged area of *exoccipetale*; 14—relief of inner surface; 15—edge facing to *supraoccipetale*; 16—edge facing to *pars basilare*; 17—protrusion closing the *foramen occipitale magnum*; 18—oval fossa; 19. *foramen nutricium*.

same as for small nutrient foramina in the distal part of the femur and other bones described above.

The *sulcus malleolaris* is outlined on the medial surface of the distal margin of the diaphysis (Figs. 7b and 5). It is developed to the same extent as on the *tibia* of a newborn calf (PIN 4353–2703).

3.6. Fragment of the temporal bone with external acoustic meatus (squamosum, meatus acusticus externus) (IAE, Sh-77, q 4B) (Figs. 2c, d and 8a, b)

The size of the preserved fragment of the temporal bone *squamosum* is 75–67 mm. On the upper side of this fragment is the part that contacts the lower part of the parietal bone (*os parietale*). The temporal process of the zygomatic arch (*processus zygomaticus*) is also preserved. The thickness of the fragment of the temporal bone in its upper and anterior parts is about 4 mm; in its posterior and lower parts it is much thicker. The processes closing the external acoustic meatus do not come into contact and the gap between them is about 2 mm. The outer size of the external acoustic meatus (*meatus acusticus externus*) is 12 × 14.5 mm. The *meatus* is somewhat posterior and is not perpendicular to the longitudinal axis of the skull. The external acoustic meatus in a newborn calf (PIN N4353–2614) is oriented the similarly. On the inner surface of the temporal bone it has an oval shape and is 13.5 × 9.5 mm in size. The posterior margin of temporal process of the zygomatic arch starts from the anterior margin of the external acoustic meatus. The temporal process of the zygomatic arch is oriented at an angle of 45 degrees to the surface of the temporal bone. The vertical and transverse diameters of the *processus zygomaticus* at its base are 22 and 19 mm, respectively.

The zygomatic arch (*arcus zygomaticus*) in the foetus from Shestakovo locality, newborn calf mentioned above and individuals younger than 1 year (PIN N4353–2919,872) probably consists of two ossified parts–the temporal process of the zygomatic arch (*processus zygomaticus*) and the postorbital process (*processus postorbitalis*) the jugal bone. In individuals younger than one year, these ossified parts, most probably, are separated by non-ossified cartilage. Eales

(1926) indicates that in the foetus of the African elephant (*L. africana*) at the beginning of the second year of pregnancy, these parts are connected by the already ossified jugal bone (*jugale*), and already at this early stage of embryonic development they form together the zygomatic arch. The structure and shape of both processes in the baby skulls at our disposal (PIN 4353–2614, 933; ZI N 31661) indicate that at least during the first month of life the jugal bone was not ossified. Jugal bones belonging to individuals younger than 1 year have also not been discovered among 20 specimens of jugal bones from the Sevsk locality (PIN 4353) or the material from other localities (GIN 77 Jamal; ZIN 31661 (Mal'ta Site), ZIN 31771(1) (Kostenki Site)). This could prove the hypothesis that the zygomatic arch in mammoths completely ossifies after birth.

Two sutures on the zygomatic arch are indicated for the foetus of *L. africana* (Eales, 1922): the shorter one in the area of contact between the jugal and the maxilla and the longer one (*sutura jugosquamosal*)—between the zygomatic process of the squamosal and the jugal bone. Both sutures persist for a long time during the postnatal period, the second one being present during the whole life. On processes of temporal bones of the newborn calf (PIN N4353–2614) and 1-year-old calf (PIN N4353–933) the second suture is very weak.

The complicated relief on the posterior part of the inner surface of the temporal bone of the foetus from Shestakovo is related bound to the attachment there of the *petrosum* and *tympanicum* and to the traces of elements of the inner ear that are not preserved. Near the posterior margin of the inner acoustic meatus there is the areola 6×4.5 mm in size showing the relief composed of longitudinal grooves. The anterior upper third of the inner surface of the temporal bone has no relief and is slightly concave. All the outer layers of the bone are friable and porous.

The notch for the facial nerve (*nervus facialis*) is preserved on the lower surface of the temporal bone. It has the same location as in calves of *E. maximus* (Boas and Simon, 1925).

Although the margins of the temporal bones that are oriented toward the upper part of the occipital bone (*supraoccipitale*) and toward the parietal bone (*os parietale*) are destroyed, the shape of the posterior margin of the temporal bone, as well as the temporal bone of a newborn calf (PIN 4353–2919), indicates that the posterior part of the temporal bone, lower posterior part of the parietal bone and lower lateral margin of the *supraoccipitale* do not contact, the mastoid fontanel (*fonticulus mastoideum*) being situated in this area.

The outer surface of the temporal bone is rather well preserved. The outer layer almost everywhere has a porous structure. Nine openings of nutrient foramina 1 mm in diameter are located just above the level of the external acoustic meatus, between the middle of the base of the *processus zygomaticus* and the anterior margin of the external acoustic meatus.

3.7. Lower part of the occipital bone (exoccipitale) (IAE, Sh-77, 4B) (Figs. 2e, f and 8c, d)

The lower part of the occipital bones consists of separate left and right parts. Fusion of these parts of the *exoccipitale* and *supraoccipitale* probably takes place at the end of the second year of life (Maschenko, 2002).

This description is based on the left part of the *exoccipitale* (Fig. 8c and d), the maximum size of which is 58×65 mm. The length of the condyle (*condyli occipitalis*) is 22 mm, and the width, 19 mm. The width of the surface of the lower part of the occipital bone facing the *pars basilare* is 23 mm. The reconstructed size of the greater occipital foramen (*foramen occipitale magnum*) is about 24×20 mm. In the newborn calf (PIN 4353–2614) the maximum size of the left *exoccipitale* is 89×72 mm, the length of the condyle is 37 mm, and its width is 25 mm. The width of the surface oriented toward the *pars basillare* is 30 mm; the size of the greater occipital foramen is 30×38 mm.

On the surface oriented toward the *perioticum* there is a notch forming the back wall of the opening of the jugular foramen (*foramen jugulare*) (Fig. 8c, 11). An oval pit (Fig. 8c, 18) also characteristic for babies and adults (PIN 4353–2614, 933, 3557) is located higher than this foramen, closer to the occipital condyle (*condylus occipitalis*). Most probably this pit served for the attachment of some large muscle.

The process bordering the great occipital foramen on top is relatively long (Fig. 8c, 17). In the newborn calf (PIN 4353–2614) and in a 1 year old (PIN 4353–933) the inner parts of these processes join each other at one point only, or do not join all, but their inner ends approach each other very closely. In both cases they are separated by the process of the upper part of the occipital bone (*supraoccipitale*) oriented toward the great occipital foramen. In calves of *E. maximus* this process is less long and does not separate processes of the *exoccipitale* bordering the upper margin of occipital foramen. Instead, these processes come into contact, forming a suture aligned with the axis of the great occipital foramen.

On the inner surface of the margin of the *exoccipitale* oriented toward the temporal bone, there is relief related to the attachment of the margin of the *petrosum* in this area. The marginal parts of the outer and inner surfaces of the bone have a porous outer layer, but the marginal portions are denser, with *substantia compacta* normally developed. One large nutrient foramen 1.5 mm in diameter is located on the inner surface of the bone below the basial margin of the occipital condyle (Fig. 8d-19).

Table 6
Measurements (mm) of fragments of ribs of the foetus (*M. primigenius*) from the Shestakovo locality

Measurements	1 right	4 right	8 (9?) right	12–14 (?) right	12–15 (?) right	15–16 (?) right
Anteroposterior diameters of middle part of corpus costae	14	11.5	—	7	7	7.2
Transverse diameters of middle part of corpus costae	6	5.5	—	4.8	4.5	5.5
Transverse/anteroposterior diameters of diaphysis collum costae	10/7.5	13/6	11.5/7.5	6/6	6/6	8/6.5
Maximal diameter of the rib head	7	—	—	7	7	7.5

3.8. *Ribs (costae) (Iae, Sh-77, 4B, 5B) (Table 6)*

Seven fragments of ribs with heads (*caput costae*) and eight small fragments without heads are preserved. The better preserved fragments belong to the 1st, 4th, 8–9th, 12–14th, and 14–16th right ribs and the 12–15th, and 14–16th left ribs.

The first right rib is the most complete. It has a flattened, dilated distal end and a bifurcated proximal end. The tubercle of the rib (*tuberculum costae*) and the head of the rib (*caput costae*) are about the same size. The proportions of the neck of the rib (*collum costae*), the head of the rib and the tubercle of the rib of the foetus are close to proportions of the first rib of adult individuals. The presence of a nutrient foramen 1 mm in diameter on the posterior surface of the rib, 14 mm below the top of the head of the rib, is an individual characteristic of this specimen. There are no similar nutrient foramina on the first rib of the newborn calf from Sevsk (PIN 4353–2679) or on the other specimens at our disposal. On the other ribs of the foetus and newborn calf, the nutrient foramina (if present) are located near the upper ends of ribs near their posterior surface.

The maximum distance between the outer border of the head of the rib and the outer border of the tubercle of the rib is about 20 mm. The depth of the hollow between the head and the tubercle is 5 mm. The transverse (6.5 mm) and longitudinal (7 mm) diameters of the tubercle are close to the size of the head of the rib. In the specimen from Shestakovo the length of the rib along the chorda is 95 mm. The rib of the newborn calf (PIN 4353–2679) has the same proportions, but is bigger. On specimen PIN N4353–2493 the maximum distance between the border of the head and the outer border of the rib is 28 mm, the diameter of the head is more than 8 mm, the depth of the hollow between the head and the tubercle is 5.5 mm, the width and thickness of the neck of the rib are 8 and 7.5 mm, respectively and the length of the rib along the chorda (between the head and the distal end of the rib) is 123 mm.

The smaller size of the head compared to the size of the tubercle in the foetus distinguished it from the first rib of the newborn calf. In the latter, the head of the rib is almost twice the size of the tubercle. The same proportions are characteristic for adult individuals (PIN 4353–4114, 3246).

3.9. *Vertebrae (IAE, Sh-77, 3d, 4d) (Figs. 2g and j)*

Four fragments of the *throracal vertebrae* represented by the body of a 23rd–24th thoracic vertebrae (*corpus vertebra*) and spinous processes of 3rd, 4th–6th and 13th–15th thoracic vertebrae.

The body of the basilar vertebra has the shape typical of the vertebrae of this part of the vertebral column. The upper surface is flat with a hollow in the middle, and the lower is almost semicircular. The maximum thickness of the body is located in the middle of its width. There is a small waist in the middle of the lower margin. The anterior and posterior surfaces have a tubercular outer layer with many nutrient foramina. The epiphyses adjoining the anterior and posterior surfaces of the body of the vertebra are probably completely cartilaginous. Ossification of epiphyses, as one can judge on the material from Sevsk develops in mammoths no earlier than at an age of 6–9 years.

The stripe-like area of the outer surface characterized by more dense and non-porous texture extends around the lower surface of the body of the vertebra on its side and is slightly depressed into it. The vertebrae of the newborn calf (PIN 4353–2928, 1562, 3000) have a similar texture on anterior, posterior and lateral surfaces.

The width of the body of the foetus basilar vertebra is 47 mm, i.e. much greater than its height (36.5 mm). The ratio of these parameters −0.78-together with features of the shape of this vertebra indicates that it is most probably the third basilar vertebra. In the newborn calf (PIN N4353–2643) the second basilar vertebra is 43 mm in width and 32 mm in height (ratio 0.74). In both adults and calves, the height of basilar vertebrae from the first to the fourth increases relative to their width. The thickness of the bodies of basilar vertebrae also increases. In the foetus it is 23.5 mm, and in the specimen from Sevsk, 18 mm. The anterior surface of the basilar vertebra of the foetus is narrower and slightly more convex than the posterior surface.

The length of the fragment of the spinous process of the 3rd vertebra is 67 mm, and its end measures

13×8.5 mm in width and thickness. The lower surface of this fragment is flattened, the upper, convex. The width of the spinous process is almost constant. The length of the spinous process of the newborn calf (PIN N4353–2821) is 102 mm, and of its end measures 16×12 mm in width and thickness. It differs from the fragment of the spinous process of the foetus by its narrower middle part (minimum width is 10 mm at a point 43 mm from the end of the spinous process). The different shapes of spinous processes of 3rd vertebrae of these two individuals can be explained by variabilities in shape of spinous processes in all parts of the vertebral column of elephants and many mammals. In mammoths, the spinous process of the 3rd thoracic vertebra is the longest one and the most massive, and in the foetus skeleton described here it can be easily recognized.

The length of the fragment of the spinous process of the 4th-6th thoracic vertebra is 55 mm, the reconstructed width from the outer borders of the transverse processe (*processus transversus*), 40 mm, and the minimum width, 12 mm. The lower surface is slightly concave, the upper slightly convex. The crest extends along the long axis of the spinous process on its outer surface. The right anterior articular process (*processus articularis superior*), with its facets is preserved. The width of the notch between the right and left articular processes is 9.5 mm, and its depth (from the anterior border of the anterior articular process to the beginning of the spinous process), 11 mm. The posterior articular processes (*processus articularis posterior*) in mammoths are confluent with the spinous process. They look like a widening of the spinous process.

Both posterior articular facets (*facies articularis inferior*) are preserved. Their size is 10.5×7 mm, and their long axes are oriented along the spinous process. For the specimen described, these facets are bordered by small crests.

The proportions of this spinous process are the same as the proportions of the 6th vertebra of a newborn calf (PIN 4353–2630), but the size is different. The minimum width of the spinous process of the 6th vertebra of the newborn baby is 12 mm, the width between the outer borders of transverse processes, 60 mm. The crest extending along the outer surface is shorter, starts at the border of the notch between the right and left anterior articular processes and is 20 mm in length. The crest on the spinous process of the foetus is longer. The depth of the notch is 8 mm, its width, 7 mm. The facets on the anterior and posterior articular processes are almost identical in size.

The length of the fragment of the spinous process of the 13th–15th thoracic vertebra as well as the reconstructed width between the outer borders of the transversal processes, 42 mm. The maximum anteroposterior diameter of the right transverse process is 13 mm. The width of the notch between the anterior articular processes is 7 mm, and the facet on the anterior right articular process is very small, 3×3 mm in size. The size of the facet on the posterior articular processes is 8×6.5 mm. The spinous process is oval in contour. There is a crest extending along its long axis on its upper surface.

The change in contours of the transversal sections of spinous processes in later ontogenetic stages represents the most important difference between the foetus and subadult (PIN 4353–518) and adult (PIN 4353–640) individuals. With age, the concavity of the lower surface of the spinous process, as well as the absolute size of the facet-bearing parts of the anterior articular processes, increases. It is possible to conclude that already in late prenatal stages, the anterior and posterior articular processes of the mammoth foetus become almost completely co-ossified with the bases of transverse processes and with the base of the spinous process.

4. Conclusions, remarks and discussion

The stage of intra-uterine development of the foetus from Shestakovo most probably corresponds to 19–20 months, i.e. to the late stage of pregnancy. Available data on the size of embryos and newborn calves of recent elephants can be extrapolated to mammoths to assist to evaluating their pregnancy duration. Most probably it lasted about 19–22 months (in *L. africana* and *E. maximus* it is 19–23 months). Some features of ethology typical for elephants and recently discovered in *M. primigenius* indicate the possibility of such extrapolation. Both elephants and mammoths have family groups consisting of females with calves (Maschenko, 2002), separate from groups of adult males of various ages (Agenbroad, 1990).

In newborn calves of late Pleistocene *M. primigenius* the shoulder height of the body varies within the limits of 700–800 mm. These data have been obtained from reconstructing of the height of the newborn calves using the skeletons excavated in Sevsk (PIN N4353–2619–2404) (Maschenko, 1992, 2002). The shoulder height of newborn calves of *E. maximus* varies from 760–950 mm (Stenley, 1943), i.e. in mammoth newborn calves they were smaller than in the Asiatic elephant.

Reconstruction of body height in shoulder has been based on the total length of *humerus* and *ulna* and the length of *scapula* for legs of the newborn calf from Sevsk (Maschenko, 2002). The reconstructed length of the *humerus* and *ulna* is 360–370 mm. The length of the *femur* and *tibia* is 390–430 mm. The total length of *humerus*, *ulna* and *scapula* is about 575 mm. The height of the body of this calf, evaluated with due regard to muscular tissue, general construction of articulations in mammals, and proportions of the distal parts of extremities in babies of recent elephants, did not exceed 800 mm. Another newborn mammoth calf from this locality (PIN N4353) could have been about 750 mm in shoulder height.

The length of the *humerus* and *ulna* (length of the ulna is reconstructed approximately, based on the length of the *radius*) of the foetus from Shestakovo could be about 335–355 mm. This also includes the length of the epiphyses that looked like oval ossifications not adherent to the diaphyses. They are formed in the cartilage, around centers of ossification. In recent elephant substitution of cartilage, by bone around the centers of ossification of epiphyses begins at the end of the first year of pregnancy. The total length of *humerus*, *ulna* and *scapula* in the fetus described is about 485–495 mm. The foetus body height reconstructed most probably could be about 665–685 mm. A foetus of *L. africana* at the same intra-uterine stage (about 20 months) is 780 mm in height, but in this species newborn calves are generally even bigger than in *E. maximus* (body height in shoulder up to 1090 mm) (Beyer et al., 1990).

Among the bones (ZIN 31744(1),34419(17),3449(10), 34201(4),31744(5)) of the mammoth calves from late Pleistocene localities it is possible to recognize the bones of newborn calves and foetuses (ZIN 32572(2),31740(6), 31740(7),34419(16),31740(9)), even at the late prenatal stages. In newborn calves, length of *humerus* ranges within the limits of 185–200 mm, the length of *ulna*, 170–180 mm, the length of *femur*, 240–250 mm, the length of *tibia*, 145–150 mm. The long bones of smaller size can be considered to be the bones of foetuses. In some cases these data can be corrected because in mammals (including Proboscidea) the size of a newborn calf depends on a complex of physiological data. Thus, the first baby delivered by female is always 10–15% smaller than others (Sikes, 1971). However, as a whole, the data given above cover these individual factors.

It should be noticed that the ossification of long bone diaphyses of mammoth foetus (as well as recent elephant foetuses) takes place rather early, at the end of the first year of pregnancy (9th–11th month). That is why one finds foetus bones that are similar to bones of adult animals in their proportions and shape, but very small in size. At the Sevsk locality, the smallest of all known foetus bones have been discovered: *humerus* and *femur* 65 and 72 mm long, respectively (PIN 4353–3241, 3242) (Maschenko, 2002).

Not only absolute size, but also some other morphological characteristics, help separate bones of foetuses and newborn calves. These characters mainly reflect changes taking place during this period of ontogeny. Among the most general characteristics of this kind, known also in other groups of mammals, is the relief on diaphyses associated with muscle attachments. In young and adult individuals muscle attachments look like well-developed crests, grooves, pits, etc., but this relief is absent or very weak in the foetus. Thus, in the foetus, crests on the surface of diaphyses are manifested at best as surface roughness. The outer layers of foetal diaphyses have a texture somewhat different from that of a newborn calf. In a newborn calf, the outer compact layer of bone (*substantia compacta*) is developed to the same extent over the whole surface of the diahpysis. Its thickness in the middle of the diahpysis is not less than 1.5 mm. A slight decrease in thickness and a somewhat looser structure can be observed only at the very ends of the diaphysis adjacent to the growth zone between the diaphysis and the partly ossified epiphyses. In a mammoth foetus, even in the last prenatal stage, the compact layer is thinner. It is well developed in the central part of the diaphysis but very thin and loose near its ends. The growth zone differs from that in the newborn not only in the area between epiphyses and diaphises, but also near the ends of the diaphyseis. The presence here of nutrient foramina for blood vessels in the growth zone at the ends of diaphyses is typical for the foetus. These foramina are 1–2 mm in diameter and 12–18 in number on the anterior and posterior part of each end of a diaphysis. In the newborn there are always fewer foramina on the ends of the diaphyses (no more than 2–3) or, more often, they are completely absent. In calves that are one year old, foramina on the ends of the diaphysis are always absent. It is possible to conclude that the internal stage of development and growth of diaphyses in mammoths stops during the first month of life. Subsequent increase in the length of the diaphysis takes place in the growth zone between the diaphysis and epiphyses.

In the middle portion of foetal diaphyses are additional nutrient foramina. As a rule, they are located near the main nutrient foramen that operates during the entire life of an individual. They are 1.5–2 mm in diameter and 2–4 in number. Newborn calves already have only the main nutrient foramen in the middle portion of the diaphysis and very rarely an additional one, 1 mm in diameter.

Long bones of foetuses limbs differ strongly in proportions from long bones of newborn calves. They look more massive and relatively shorter in the former, if one compares the ratio of the length of the diaphysis and its minimum width.

The medullary cavities (*cavum medullare*) in the long bones of foetuses and newborn calves are probably absent. In mammoths and recent elephants medullary cavities, if present, appear only after the first year of life following a long period of skeleton growth and attainment of large size.

The description of the skeleton of an *M. primigenius* foetus from the Shestakovo locality and its comparison with skeletons of newborn calves from other Late Pleistocene localities offers an opportunity to discuss for the first time some important aspects of late prenatal and early postnatal stages of osteological development in this species. Recognition of the limits of size variability in mammoth foetuses and newborn calves is one of the most important results. This together with other characteristics mentioned in the description provide further ground for extrapolating data on the physiology of recent elephants to *M. primigenius*.

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