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The Steppe Elephant *Mammuthus trogontherii* (Pohlig) from the Irtysh Region Near Omsk

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Abstract—A Pleistocene elephant skeleton was found in 1989 in the alluvial beds of the Tobolsk age on the Om River near the village of Ust'-Tarka (Ust'-Tarkskii District, Novosibirsk Region). The forelimbs and some thoracic and caudal vertebrae are not preserved. Judging from the heavy wear of M3/m3, this animal was about 50–60 years of individual age. The skeleton is about 3.5 m high at the withers. The geological age of the beds enclosing the skeleton and its morphological features suggest that it should be assigned to *Mammuthus trogontherii*.

Keywords: Steppe elephant, morphology, skeleton proportions, Middle Pleistocene, Western Siberia

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INTRODUCTION

Three skeletons of ancient elephants have been recorded in the West Siberian Plain. All of them are confined to the basin or valley of the Irtysh River. A skeleton found on the Om River (right tributary of the Irtysh) at the village of Ust'-Tarka is the first record of the steppe elephant skeleton in Western Siberia. In 1993, the second skeleton was found on the Irtysh River at the village of Chembakchino Hunty–Mansi Autonomous Region (Kosintsev et al., 2004); and the third skeleton was found in 2002 on the Irtysh River at the town of Pyatiryzhsk of the Pavlodar Region (Shpansky et al., 2008a). In the skeleton from Pyatiryzhsk, the skull is not preserved and, in the specimen from Chembakchino, the skull is only represented by several fragments. The skeleton from Ust'-Tarka has a well-preserved skull, which is important for the study of morphology and evolution of Pleistocene elephants in Western Siberia. This skeleton is described in the present study.

The skeleton was excavated by seasonal workers in the summer season of 1989 in the river channel. Approximate coordinates of the record are 55°32′ N, 75°41.5′ E (Fig. 1). Initially, as the skeleton was taken from a sand layer rich in water, it was probably complete. Subsequently, bones of the forelimbs (except for three wrist bones) have been lost. Due to I.E. Grebnev's efforts, the preserved part of the skeleton was brought to the Institute of Archeology and Ethnography of the Siberian Branch of the Russian Academy of Science, Novosibirsk (IAE) in 1990. At present, the reconstructed and mounted skeleton of the steppe elephant is exhibited in the hall of IAE (Fig. 2).

TAPHONOMY AND GEOLOGY

Direct data on the burial conditions of the skeleton in question are absent, although it is possible to judge certain burial conditions from the bone preservation. The bones are heavy, mineralized considerably; the surface is impregnated with manganese hydroxide for up to 1–2 mm of depth. The surface of some bones was initially covered with a cemented sandy cover, which stripped gradually off in the course of drying. It is plausible that the elephant cadaver was buried rather rapidly under a fine-grain sand layer at the border of the river channel. The skull preserved with tusks and lower jaw suggests that the cadaver was not transported for a long distance.

A.V. Shpansky investigated the presumable locality in 2002. The section, where the specimen was found had not been investigated, because it was completely turf-covered. The nearest outcrop is located on the right bank of the Om River, 2.5 km (along a straight line) downstream from the village of Ust'-Tarka. The distance from the point of skeleton finding is several hundred meters. The following beds are recognized downward in the section: (1) soil (0.3 m thick); (2) yellowish brown fine-grain, horizontally thin-layer, dense sand; in the upper part, sand passes into siltstone, with rare vertical fracturing; in the lower part, sand is medium-grained, encloses shells of the freshwater mollusk *Ame-*

soda asiatica (Marthens, 1874) and carbonate nodules (7.0 m thick); (3) brown with light blue spots, thin-interbedding clays, containing abundant carbonate concretions (6.0 m of exposed thickness).

The lower part of the outcrop was closed by a landslip and turf-covered, about 20 m thick. A similar texture of Quaternary deposits is observed in high terraces throughout the lower reaches of the Om River. It is probable that the elephant skeleton comes from a terrace base, where clays of Bed 3 are underlain by sand of the Tobolsk Horizon of the Middle Neopleistocene.

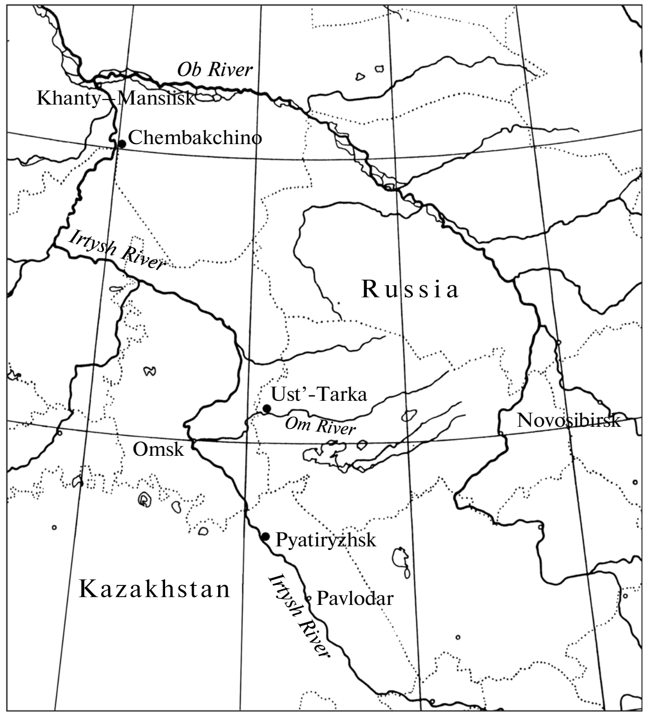
MATERIAL AND METHODS

Specimen IAE, no. 18, skeleton of male *Mammuthus trogontherii* Pohlig, including a skull with tusks, lower jaw, seven cervical and 15 thoracic vertebrae (vertebrae 6–8 and 19 are lost), 29 ribs, sternum, last lumbar vertebra, sacrum, pelvis, both hind limbs, including almost all skeletal foot elements. Caudal vertebrae are not preserved.

The skull and lower jaw were measured following the method developed by Dubrovo (1960) and supplemented by some measurements of vertebrae (Shpansky et al., 2008a) (Fig. 3) and long limb bones (Baigusheva and Garutt, 1987). The generation of functioning molars is determined following Sher and Garutt (1985). The sex is determined based on the long diameter of tusks and pelvic structure, following Lister (1996b). In long limb bones of the steppe elephant, sexual dimorphism is poorly pronounced (Shpansky et al., 2008b). The ranges of measurements of the scapulae and long limb bones of males and females overlap considerably (Fig. 4). Only the indices of pelvic bones (Table 10) calculated according to Lister (1996b) differ distinctly. Since the skeleton is mounted, it was impossible to measure or describe the bones of feet and some vertebrae. Some skull measurements are approximate, because its rostral part (premaxillae) was reconstructed.

Published and original data on nine skeletons of *M. trogontherii* and also one skeleton and two skulls of *M. trogontherii chosaricus* Dubrovo were used for comparison (Table 1).

As the taxonomic position of the elephant from Ust'-Tarka was determined, we followed the point of view traditional for Russian researchers concerning the recognition of two genera among Euroasian mammoth-like elephants, *Archidiskodon* Pohlig, 1885 and *Mammuthus* Brookes, 1828 (Garutt, 1998; Garutt and Tikhonov, 2001; Baygusheva and Titov, 2012). The analysis of morphological skull characters is based on published data on *A. meridionalis*, specimen SM, no. 14120 from the town of Georgievsk (Garutt and Safronov, 1965) and Italy: specimen IGF, 1054 from Upper Valdarno (Palombo and Feretti, 2005); from Sauvignon (Reggiani and Sala, 1994). The material of *M. primigenius* includes a skull (specimen PM TGU,



● Localities of *Mammuthus trogontherii Pohlig*

Fig. 1. Geographical position of localities of steppe elephant skeletons within the West Siberian Plain.

no. 1/54) and lower jaws (specimens PM TGU, nos. 1/34 and 1/56).

The following abbreviations are used in the present study: (AMZ) Azov Reserve Museum, Azov, Russia; (IAE) Institute of Archeology and Ethnography of the Siberian Branch of the Russian Academy of Science, Novosibirsk, Russia; (IEI) Museum of Archeology and Ethnography of the Institute of Ethnographic Studies of the Ufa Scientific Center of the Russian Academy of Science, Russia; (MP PGPI) Museum of Nature of the Pavlodar State Pedagogical Institute, Pavlodar, Kazakhstan; (PM OGU) Paleontological Museum of Odessa State University, Ukraine; (PIN) Paleontological Museum of the Borissiak Paleontological Institute of the Russian Academy of Science, Moscow, Russia; (PM TGU) Paleontological Museum of Tomsk State University, Tomsk, Russia; (TOKM) Tomsk Regional Museum, Tomsk, Russia; (KhM) "Museum of Nature and Man," Khanty-Mansiisk, Khanty–Mansi Autonomous Region, Yugra, Russia; (IGF) Museo di Geologie e Paleontologia, Universita di Firenze, Italia; (SM) Stavropol State Historical and Cultural and Nature–Landscape Reserve Museum, Stavropol, Russia. The symbol "C" preceding a measurement in the tables designates that it is incomplete; The upper and lower molars of the last generation are designated M3 and m3, respectively.

Fig. 2. A skeleton of the steppe elephant *Mammuthus trogontherii*, specimen IAE, no. 18; Novosibirsk Region, Ust'-Tarka; Middle Neopleistocene; mounted and exhibited in the hall of the Institute of Archeology and Ethnography of the Siberian Branch of the Russian Academy of Science (Novosibirsk).

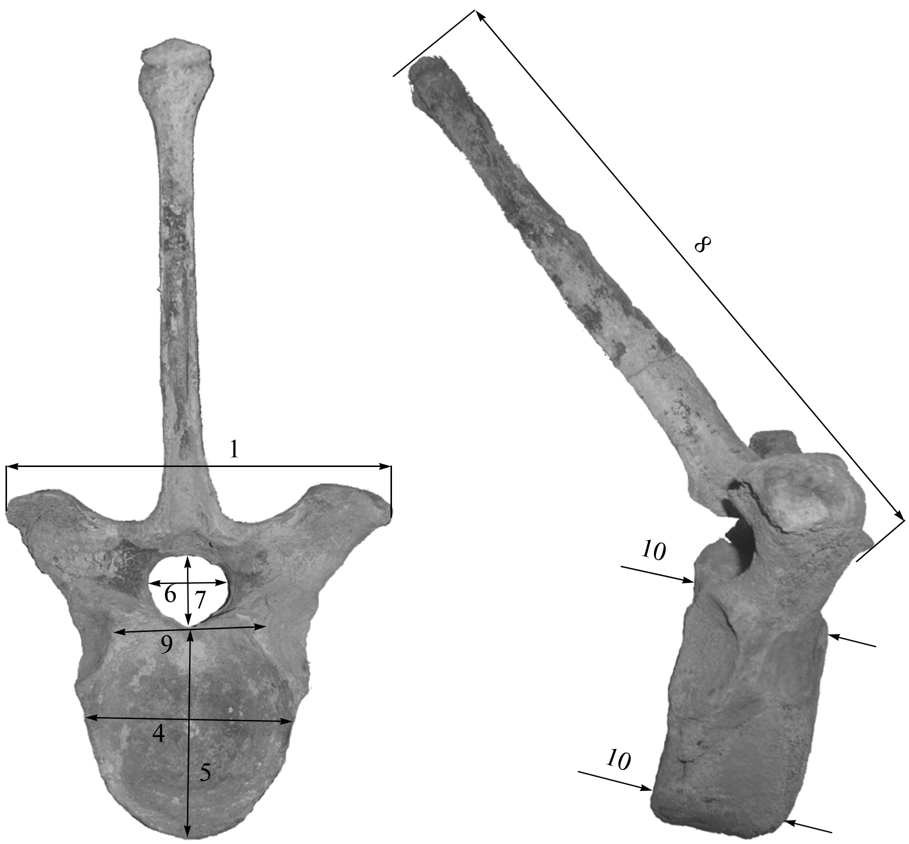


Fig. 3. Scheme of measurements of the thoracic vertebrae of the steppe elephant (after Shpansky et al., 2008a): (1) greatest width at transverse processes; (2, 4) cranial and caudal width of vertebral centrum; (3, 5) cranial and caudal height of vertebral centrum; (6, 7) cranial width and height of spinal canal; (8) neural spine length along anterior edge; (9) minimal width at articular rib fossae cranially anf caudally; (10) vertebral centrum length doesallt and ventrally.

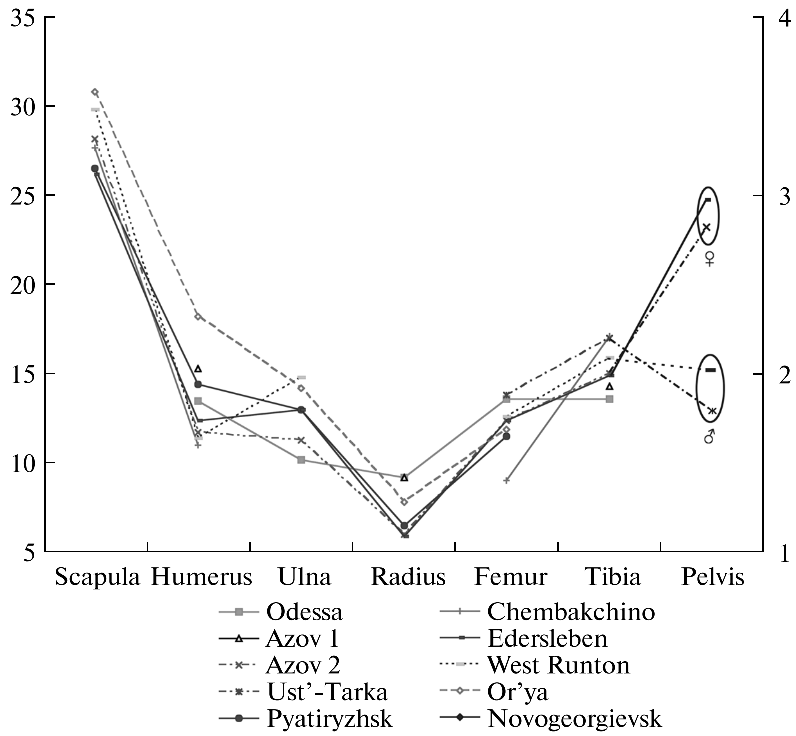


Fig. 4. Relationships of the extent of gracefulness of limb bones of steppe elephants (in the scapula, the ratio of the neck width to the greatest bone length is used; in other bones, the ratio of the diaphyseal width to the greatest length; the data are marked using the left scale; for the pelvis, the index 3 : 5 (Table 10) is used, marked using the right scale).

DESCRIPTION

Skull (Pl. 10, figs. 1, 2; Table 2) without tusk alveoli. The occiput apex and occipital crest is rounded in transverse outline. The occipital plane is convex and smoothly anteriorly rounded in the upper one-third. The occipital condyles project significantly beyond the occipital plane. The skull is high (for measurements and ratios, see Table 2). The forehead surface is slightly concave in the sagittal plane. The forehead is rather wide. The zygomatic arch is positioned at an angle of 105° to the occipital plane in projection on the sagittal plane. The angle of inclination of the forehead plane relative to the premaxillary surface is 150°. Skull width at ptojections is greater than zygomatic width and greatest occipital width. The nasal process is triangular, with a sharpened lower edge, slightly projects above the level of the frontal surface. The nares are semilunar, with the lateral edge extending strongly downwards. The lower edge of the nares is slightly short of reaching the orbital midline. In *Archidiskodon*, the nares are located in line with the upper orbital border (Baigusheva and Garutt, 1987). The skull measurements of the elephant from Ust'-Tarka are inferior to that of the Azov 1 skull and superior to that of *M. trogontherii chosaricus* (Garutt, 1972; Shpansky, 2000) (Table 2).

The lower jaw (Pl. 10, figs. 3, 4; Table 3) has massive horizontal rami strongly widened in the middle part. The mental protuberance is long, flattened in the sagittal plane, and pointed. The lower jaw of the female from the Azov 2 locality has a short mental protuberance (Baigusheva, 2001). The anterior ends of the crista mentalis are well pronounced, ridgelike, with a relief surface. The left horizontal ramus has two large mental foramina, which are located under the anterior edge of the alveolus of m3. The right ramus has one larger mental foramen. The horizontal ramus measured along the anterior alveolar edge is much deeper than that measured along the posterior edge. The distance between the lateral edges of the articular heads is less than the width between the lateral surfaces of jaw corners. In *M. trogontherii*, the ratio of these measurements is 89–90% (Table 3). The lower jaw of the male from Azov 1 shows an inverse relation. Baigusheva and Garutt (1987, table 2) provide a considerably overestimated measurement (in our opinion, by 200 mm) of "the distance between the external edges of jaw angles" (820 mm), which does not correspond to the value provided by these authors for the ratio of this measurement to the distance between the edges of heads of the articular processes (101.2%).

The teeth belong to the last generation, M3/m3 (Pl. 10, figs. 3, 5; Tables 4, 14). All plates are worn; the talons are at the initial wear stage; several anterior plates are already lost. The enamel plates are wide, anterior and posterior walls of the plates are moderately worn, positioned parallel to each other; the spaces between them are very small. The enamel is

Table 1. Skeletons of mammoth-like elephants involved in comparison

Locality (reference)	Depository, no.	Sex	Geological age
Mammuthus trogontherii (Pohlig 1885)			
Khadzhibeiskii estuary, Odessa, Ukraine (Yatsko, 1948)	PM OGU	Male	Early Neopleistocene
Novogeorgievsk, right bank of Dnieper River, Ukraine (Zakrevs'ka, 1935)	Not specified	Female	Not specified
Kagal'nitskii quarry, Azov, Rostov Region (Baigusheva and Garutt, 1987)	AMZ no. KP-21081	Male	Not specified
Kagal'nitskii quarry, Azov, Rostov Region (Baigusheva and Titov, 2010)	AMZ no. KP-28689	Female	Early stage of Tiraspol Assemblage, MQR6-5
Ust'-Tarka, Om River, Novosibirsk Region (original data)	IAE, no. 18	Male	Tobolsk horizon, ca. 400 ka
Pyatiryzhsk, Irtysh River, Pavlodar Region, Kazakhstan (Shpansky et al., 2008a)	MP PGPI no. P2002.1149	Male	Tobolsk horizon, ca. 400 ka
Chembakchino, Irtysh River, Khanty-Mansi Autonomous Region (Kosintsev et al., 2004)	KhM-10398	Male	Second part of Early Neopleistocene, 550–600 ka
Gelsenkirchen, Westfalen, Germany (Siegfried, 1956)	Geology Museum, Münster	Male	Saale-Vistula Interglacial, beginning of Middle Neopleistocene, ca. 400 ka
Edersleben, Germany (Garutt and Nikolskaya, 1988)	Sangerhausen	Female	Beginning of Early Neopleistocene, ca. 700 ka
West Runton, Norfolk, Great Britain (Lister and Stuart, 2010)	Museum of Norfolk Life, no. 1992.36; 1996.181	Male	ca. 700 ka
Mammuthus trogontherii chosaricus (Dubrovo 1966)			
Starokudashevo, Or'ya River, Bashkiria (Garutt, 1972)	IEI, OF-909	Female	Dnieper horizon, ca. 300 ka
Chernyi Yar, Volgograd Region (Dubrovo, 1966)	PIN, no. 4874	Male	Dnieper horizon, ca. 300 ka
Town of Asino, Chulym River, Tomsk Region (Shpansky, 2000)	TOKM, no. 10300/3	Male	Samara horizon, ca. 300 ka

coarsely plicate; in the lower teeth, it is thicker than in the upper teeth. In the crowns of M3, nine plates are preserved. Right m3 retains seven plates and left m3 has eight. The crown of the right tooth is somewhat more raised above the alveolus; the left tooth is lower by 0.5–1.0 cm. The upper teeth are located in accordance with them; the right tooth projects from the alveolus to a lesser extent than the left tooth, thus, compensating the difference in height of m3.

The alveolar parts of tusks about 1.5 m of length are preserved. The tusks are circular in cross section, about 270 mm in diameter in the alveolar part and 860 mm in circumference at the alveolar edge.

The total length of mounted cervical vertebrae is 500 mm. The wing width of the atlas of the elephant from the Ust'-Tarka locality is less than that of elephants from Azov and Pyatiryzhsk (Table 5). The neural arch is horizontal, has a sinusoidal longitudinal concavity on the caudal side. The dorsal arch has crestlike tubercles, which are particularly well developed in the lateral parts. The vertebra is relatively high, the ratio of the vertebral height to greatest width at the wings is 59.3% (in the males from Azov 1 and Pyatiryzhsk, it is 58.6 and 48.4%, respectively). In the middle of the ventral arch, the vertebra has a well-developed tubercle, the apex of which is displaced caudally relative to the transverse plane.

Epistropheus (or axis) (Table 6). The crest on the neural arch is divided by a deep sagittal notch and narrows cranially. The bases of the lateral parts of the cranial articular facets overhang transverse foramina. The caudal facet is slightly concave, widely oval. The spinal

Explanation of Plate 10

Figs. 1–5. *Mammuthus trogontherii* (Pohlig 1885), specimen IAE, no. 18; Novosibirsk Region, Ust'-Tarka; the middle Neopleistocene, the Tobolsk horizon: (1) skull, anterior view; (2) skull, lateral view; (3) lower jaw, right lateral view; (4) lower jaw, dorsal view; (5) right upper M^3, view of masticatory surface.

Plate 10

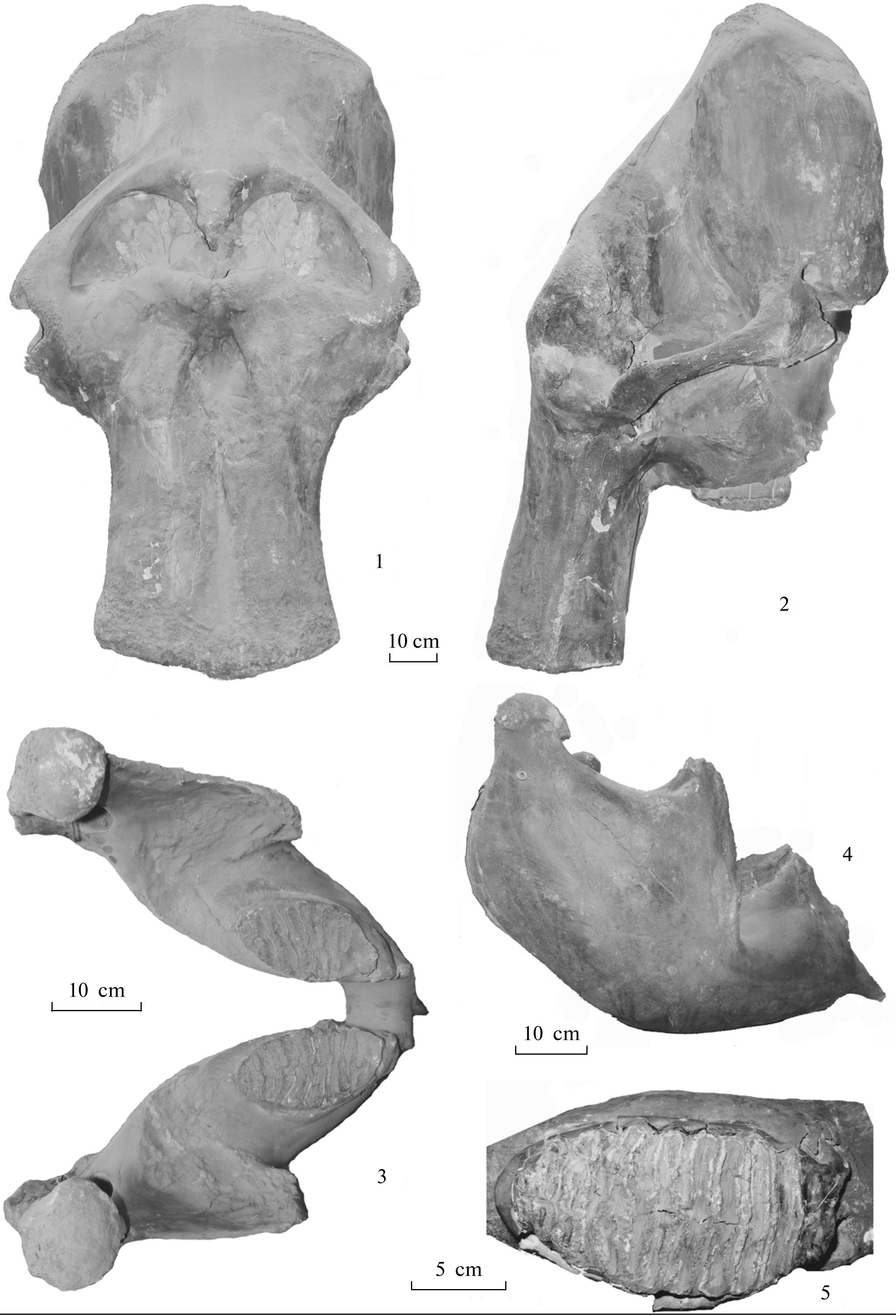


Table 2. Skull measurements of *Mammuthus trogontherii* (Pohlig, 1885)

No.	Measurements (mm) and indices (%)	*M. trogontherii*			*M. trogontherii chosaricus*		
		Ust'-Tarka, specimen IAE, no. 18	Azov 1, specimen AMZ, KP-21081 (Baigusheva and Garutt, 1987)	Gelsenkirchen (Siegfried, 1956)	Or'ya, OF-909 (Garutt, 1972)	Asino, TOKM, no. 10300/3 (Shpansky, 2000)	Chernyi Yar, specimen PIN, no. 4874 (Dubrovo, 1966)
1	Skull length: distance from anterior orbital border to occipital condyles inclusive	840	695	780	600	775?	680
2	Parietal length: from apex to anterior edge of premaxillae	1450	C1910	1220	1190	1390	1390
3	Condylobasal length: from upper (posterior) edge of occipital condyles to lower (anterior) edge of premaxillae	1140	1440		1020	1061	1100
4	Forehead length: from apex to lower edge of nasals (in projection on midline)	670					
5	Forehead length along with nares: from apex to lower edge of nares	700	965	533	C580	580	570
6	Length of premaxillae: from lower edge of nares to lower end of premaxillae	850	962	750		812	870
7	Nares (greatest width × greatest height)	630 × 158	c700	504 × 144	470 × 160	460 × 195	532 × 155
8	Zygomatic width: greatest skull width at zygomatic arches	790	1050		700		785
9	Greatest occipital width	835	1056	780	676	C760	805
10	Width of premaxillae, upper: at level of lower edge of infraorbital foramina (along with processes of maxillae)	495	640	420	430	350	456
11	Greatest occipital width at lower edge: between external edges of tusk alveoli at lower rostrum end	—	731	670	464	~560	530
12	Minimum forehead width: minimum distance between crests bordering temporal fossae	430	640?	360	310	310	
13	Tusk diameter at alveolar edge (internal alveolar diameter)	270	215 × 174	160	(146)	(165)	191
14	Distance from skull apex to masticatory molar surface along perpendicular to this surface	1050	C1100	850	790	1020?	996
15	Occipital depth: from uppermost point of occiput to lower side condyle	680	C670		480	645	598
16	Position of condyle: distance from upper condylar edge to posterior edge of masticatory surface of upper molar along edge	565				515	
17	Minimum depth of the zygomatic	54			83	56.5	71
18	Length of zygomatic arch	300	C580		402	480	446
19	Anterior palatal width: distance between molar alveoli at anterior edges	~97				54	
20	Posterior palatal width: distance between molar alveoli at posterior edges	~150				119	
21	Skull width at supraorbital processes	870	1040	820	730	680	880
22	Width of occipital condyles	284	225		208	267	226
23	Diameters of foramen magnum, height × width		100 × 72		90 × 82	59 × 83	78 × 83
24	Angle between crest bordering anteriorly lower part of temporal fossa and skull midline	38	55	45		43	
25	Angle of divergence of tusk alveoli	15	22	23		15	
26	Height (14) to length (1) ratio of skull	80.0	63.2	91.8	76.0	75.9	68.3
27	Depth (15) to width (9) ratio of occiput	122.8	157.6		140.8	117.8	134.6
28	Ratio of skull width at supraorbital processes (21) to occipital width (9)	96.0	101.5	95.1	92.6	111.8	91.5
29	Ratio of minimum forehead width (12) to greatest forehead length (5)	61.4	66.3	67.5	53.4	53.4	

Table 3. Measurements of the lower jaw of the steppe elephant *Mammuthus trogontherii* (Pohlig, 1885)

Measurements, mm	Ust'-Tarka, specimen IAE, no. 18	Pyatiryzhsk, specimen MP PGPI P2002.1149 (Shpansky et al., 2008a)	Azov 1, ♂, specimen AMZ, no. KP-21081 (Baigusheva and Garutt, 1987)	Azov 2, ♀, specimen AMZ, no. KP-28689 (Baigusheva and Titov, 2010)	Novogeorgievsk ♀, (Zakrevs'ka, 1935)
Length of horizontal ramus: horizontally at level of molar alveoli (without mental protuberance)	472	480		600?	660
Depth of horizontal ramus along anterior edge of alveolus	240	235		201.5	
The same along posterior edge	169	171	187	158	
Greatest thickness of horizontal ramus	194	180	174	176.5	200
Distance between horizontal rami at anterior internal edge of alveoli	85	70		65	
Greatest distance between buccal surfaces of horizontal rami (at posterior edge)	577	640	620*	620	
Minimum distance between molars, anteriorly	68	67		101.7	90
The same, posteriorly	200	185		310	260
Greatest distance between horizontal rami (externally)	282	275		340	
Symphyseal depth	112	93		113.5	130
Anteroposterior symphyseal diameter (including mental protuberance)	150	160		156.2	
Length of mental protuberance	73	141		72	
Depth of ascending ramus	484	485		C450	470
Greatest diameter of ascending ramus	357		C444		
Length of mental part of lower jaw: from anterior alveolar edge to end of mental protuberance	300		380		
Distance from mental protuberance to posterior side of articular head	780	780	880	C810	
Distance from anterior alveolar edge to posterior side of articular head	515	510	540/600	C490	
Distance between articular heads (internally)	336	393		C345	
The same externally	~520	570	630	C515	
Length × width of articular head	96 × 92	85.6 × 93.5	85 × 115	C84 × C97	
Ratio of distance between articular heads edges to distance between external walls of horizontal rami (%)	~90.1	89.1	101.6	>83.1	
Angle of convergence of lower jaw rami (at external walls)	~70°	60°			

* See the text.

Table 4. Measurements (mm) of molars M3/m3 of *Mammuthus trogontherii* (Pohlig, 1885) from localities of the West Siberian Plain and Europe

Locality, collection no. (reference)	Crown length	Crown width	Crown height	Number of plates	Mean length of plate	Frequency of plates per 10 cm	Enamel thickness
Ust'-Tarka, specimen IAE, no. 18, (M3/m3), dex; sin	*189; 210 / 203; 194	94; 97.5 / 104; 108	–	10 + ? / 8.5; 7.5 + ?	17.4; 18.9 / 21.3; 23.4	6.2; 5.6 / 4.5; 4.3	2.3–[2.7]–3.2 / 2.7–[3.2]–4.0
Pyatiryzhsk, specimen MP PGPI, no. P2002.1149, (m3), dex; sin (Shpansky et al., 2008a)	*215; 225	85.5; 91.2	–	12 + ?; 13 + ?	17.5; 18	6	1.8–[2.5]–3.1
Azov 1, specimen AMZ no. KP-21081, (M3/m3), dex; sin (Baigusheva and Garutt, 1987)	354; 372 / 418	104; 105 / 91	191; 189 / 168	20; 21 / 22	19 / 17	5.3 / 5.9	3.2–1.8 / 2.4–2.2
Azov 2, specimen AMZ no. KP-28689, (M3/m3), dex; sin (Baigusheva and Titov, 2010)	380; 385 / 330	120.5; 120 / 110	210; 204 / 135	22 / 21	16 / 18.74	5.5 / 5.25	2.94 / 3.53
West Runton, specimen 1996.181, M3; 1992.36 m3, dex; sin (Lister and Stuart, 2010)	387; c400 / 430	c118 / 104	196 / 167	22 / 21		6.52 / 5.25	2.7 / 2.0–[2.3]–2.7
Chembakchino, specimen KhM-10398, (M3/M3), dex; sin (Kosintsev et al., 2004)	278 / 315	85.7; 80 / 80	178; 181 / 145.3	20 / 22	13.4; 12.9 / 16.7	7.25; 7.5 / 5.75	– / 1.9
Asino, specimen TOKM, no. 10300/3, (M3), dex; sin (Shpansky, 2000)	*215	98; 102	–	c16	17; 16	7; 7.5	3.0
Chernyi Yar, specimen PIN, no. 4874, (M3/m3), dex; sin (Dubrovo, 1966)	. / 2.58; 252	105; 106 / 98; 97	–	20 / 18		7; 6.5 / 6; 5.5	2.5 / 2.5
Or'ya River, specimen OF-909, (m3), dex; sin (Garutt, 1972)	c190; c195	c84; c75		13 + ?		6.5–8	1.8–2.1

* Incompletely erupting teeth; therefore, measurement concerns accessible part.

canal is wide, trapezoidal, with a widened ventral part. The ventrocaudal edge of the vertebral centrum has a weak depression, which is distinct in the southern elephant (Garutt, 1954).

Table 7 shows measurements of cervical vertebrae 3–7. The third and fourth vertebrae are trapezoidal in outline, with a wider ventral part and narrowed dorsal part. In ventral view, the centrum of these vertebrae is slightly convex. The transverse foramina are oval, extending dorsoventrally. The transverse rib processes (pr. costotransversarius) spread aside and do not descend beyond the ventral part of the vertebral centrum. The spinal canal is triangular, with widely rounded corners.

The **transverse processes** are the largest in the sixth vertebra; they are directed ventrolaterally, considerably projecting beyond the ventral edge of the vertebral centrum. The distal parts of the transverse processes of the sixth vertebra have large tubercles on the caudal side, which are hooked, entering the ventral incisures of transverse processes of the succeeding seventh vertebra. The sixth vertebra has small pathological outgrowths on the ventral side of the transverse processes. The cranial side of both transverse processes has foramina (about 4 cm in diameter) probably formed in connection with lifetime resorption of spongy tissue of the vertebra. The fourth and fifth vertebrae have similar incisures in the same place, although they are less developed (particularly in the fourth vertebra). Similar incisures have previously been recognized in the thoracic vertebrae of the elephant from Pyatiryzhsk (Shpansky et al., 2008a).

The ventral part of the centrum of the seventh cervical vertebra has facets on the caudal side for attachment of the first pair of ribs. The ventral part of the vertebral centrum is strongly widened in the transverse plane and the dorsal part is narrowed. The ventral length of the vertebral centrum is considerably greater than the dorsal length. The spinal canal of the seventh vertebra is also triangular, with concave walls. The width of cervical vertebrae in the region of the transverse processes is identical in all vertebrae from the

Table 5. Measurements (mm) of the atlas of *Mammuthus trogontherii* (Pohlig, 1885)

Measurement	Ust'-Tarka, specimen IAE, no. 18	Pyatiryzhsk, specimen MP PGPI, no. P2002.1149 (Shpansky et al., 2008a)	Chembakchino, specimen KhM-10398 (Kosintsev et al., 2004)	Azov 1, ♂, specimen AMZ, no. KP-21081 (Baigusheva and Garutt, 1987)
Distance between edges of ala atlantis	427	475	C390	457
Greatest height of vertebra	253	230	208.5	268
Distance between external edges of fac. art. cranialis	278	270	243	269
Distance from edge of fac. art. cranialis to edge of ala atlantis		122	76	
Minimum width of canalis vertebralis (in middle part)	60	67.5	64	
Greatest width of canalis vertebralis (in upper part)	93	92	82	94
Height of canalis vertebralis	98	125	101	
Distance between edges of fac. art. caudalis	237	245	199	
Vertebral length at arcus dorsalis	107	95	68	117
Width of arcus dorsalis	172	195	173	167

Table 6. Measurements (mm) of the epistropheus of *Mammuthus trogontherii* (Pohlig, 1885)

Measurement	Ust'-Tarka, specimen IAE, no. 18	Pyatiryzhsk, specimen MP PGPI, no. P2002.1149 (Shpansky et al., 2008a)	Chembakchino, specimen KhM-10398 (Kosintsev et al., 2004)	Azov 1, ♂, specimen AMZ, no. KP-21081 (Baigusheva and Garutt, 1987)	West Runton, specimen 1996.181 (Lister and Stuart, 2010)
Greatest height	328	–	C275	–	326
Greatest width at transverse processes	346			360	374
Width anterior to external edges of transverse foramina	274	–	C208		
Width of anterior articular surface	246	260	209.5	249	240
Height of posterior articular surface	164	170	138	–	–
Width of posterior articular surface	183	200	162	–	–
Height of spinal canal (anteriorly)	61	–	65.5	–	–
Width of spinal canal	73	–	66.2	–	–

second to seventh; with the caudal articular surface gradually increasing in width and the vertebral centrum increasing in height.

The first, fifth, ninth, and 18th thoracic vertebrae are preserved. Vertebrae 9–11 are inaccessible for measurements. The thoracic vertebrae are slightly smaller than those of the skeleton from Pyatiryzhsk (Table 8). The angle of inclination of the neural spines of thoracic vertebrae varies from 15° (first thoracic vertebra) to 45° (15th–18th). The neural spines increase in length from the first to fourth (550 mm) thoracic vertebra (in elephants from Pyatiryzhsk and Novogeorgievsk, the neural spine of vertebra 5 is the longest (555 and 475 mm, respectively); in the southern elephant from Nogaisk, the longest spine is in vertebra 4 (712 mm) (Zakrevs'ka, 1935; Garutt, 1954; Shpansky et al., 2008a). Beginning from vertebra 5, the neural spine decreases in length, becoming 180 mm long in thoracic vertebra 18. The spinal canal changes in shape from almost triangular to oval (from vertebra 5 in caudal direction), with the width exceeding height. In the last thoracic vertebrae, it becomes almost circular. The costal facets and transverse processes are displaced gradually dorsally from the ventral position and

Table 7. Measurements (mm) of cervical vertebrae of *Mammuthus trogontherii* (Pohlig, 1885)

Measurement	Vertebra / locality							
	third	fourth		fifth	sixth		seventh	
	Ust'-Tarka	Ust'-Tarka	Pyatiryzhsk	Ust'-Tarka	Ust'-Tarka	Pyatiryzhsk	Ust'-Tarka	Pyatiryzhsk
Vertebral height from ventral edge of centrum to dorsal surface of prezygapophyses	252	278	C265	310	320	297	C350	305
Greatest width at transverse processes	370	370	C275	370	C365	262	370	380
Height-to-width ratio of vertebral centrum, anteriorly			185/180			200/180		195/195
Height-to-width ratio of vertebral centrum, posteriorly	/185	/186	195/193	/185	/195	200/200	/197	185/175
Height of spinal canal (cranially)			C55			56		63
Width of spinal canal			95			117		132

occupy a dorsolateral position on the vertebral centra after vertebra 5. In the first two vertebrae, the ventral length of the centrum is greater than the dorsal length; in succeeding vertebrae, the dorsal length of the vertebral centra gradually becomes greater than the ventral length and the greatest difference is observed in the last thoracic vertebrae.

The neural spine of the last lumbar vertebra is at most 150 mm long. The ventral side of the vertebral centrum has pathological outgrowths in the shape of spinate and hooked processes, osteophytes. The outgrowths are directed both cranially and caudally, embracing ventrally the cranial part of the sacrum (Pl. 11, fig. 4). The development of osteophytes (bone spurs) is probably connected with the senile degenerative–dystrophic processes in bone tissue of the vertebral centra; however, it is hardly probable that they caused the death of the elephant, because they develop over a rather long time. Similar osteophytes are observed on the vertebrae of the cave bear from Irgik Cave (Tasnadi-Kubacska, 1962).

The sacrum consists of five fused vertebrae. In the dorsal plane, they form a vaulted bend. On the cranial side, the sacrum is 290 mm wide at the wings; on the ventral side, it is 420 mm long; the caudal width at the wings is 210 mm; the total cranial height of the sacrum is 160 mm; the centrum of the cranial sacral vertebra is 110 mm wide; the cranial articular facet of the cranial sacral vertebra is 200 mm wide; the caudal articular facet of the caudal vertebra is 100 mm wide. The sacrum of the female from Azov 2 (AMZ, no. KP-28689), also consisting of five fused vertebrae, is somewhat larger; on the ventral side, it is 432 mm long, 310 mm wide cranially at wings, and 175 mm wide caudally. In the elephant from West Runton, the sacrum includes six fused vertebrae (due to fusion with the first caudal vertebra), so that it is 565 mm long on the ventral side and 322 mm wide at the wings (Lister and Stuart, 2010), which is the greatest value of this parameter. In the steppe elephant from Novogeorgievsk, like the mammoth from the Berezovka River, the number of fused sacral vertebrae is reduced to four (Zalensky, 1903; Zakrevs'ka, 1935).

Seventeen left and 12 right ribs are preserved. The anterior ribs are massive, with gradually expanding distal ends. The medial surface is flattened and the lateral surface is slightly convex. The proximal end is turned medially relative to the sagittal plane. The first rib is 700 mm long and its distal end is 185 mm wide. In the elephant from Ust'-Tarka, ribs curve very weakly and smoothly. One of its longest ribs is the fourth, it is 1000 mm long along the arc chord and 1200 mm long along the curvature (in the elephant from Novogeorgievsk, this parameter is 1210 mm in the ninth rib: Zakrevs'ka, 1935); the rib head is 88 mm in longitudinal diameter.

Two segments of the sternum are preserved; the anterior segment is 360 mm long and 165 mm high anteriorly and 170 mm high posteriorly; its greatest width is 115 mm. The posterior segment is 288 mm long and 147 mm high in the anterior part and 109 mm high posteriorly; the greatest width is 100 mm.

Pelvis (Table 9). The iliac wings are very wide and flat, the ventrolateral edges curve smoothly anteriorly (Pl. 11, fig. 1). The incisure of the acetabulum opens on a flattened surface rather than directly in the oval foramen. The distance from the incisure edge to the edge of the oval foramen is 55 mm. Dubrovo (1982) proposed that this position of the incisura acetabuli is a diagnostic character of *M. primigenius;* however, the same incisure pattern of the acetabulum is characteristic of the elephant from Chembakchino (Kosintsev et al., 2004) and the female from Azov 2 (specimen AMZ, no. KP-28689). The measurements and shape of the ilia and the indices proposed by Lister (1996b) suggest that this is a male skeleton. The indices of the

Table 8. Measurements (mm) of the thoracic and lumbar vertebrae of *Mammuthus trogontherii* (Pohlig, 18)

No. of vertebra	Locality	Measurement									
		1. Width at transverse processes (greatest)	2. Cranial width of vertebral centrum	3. Cranial height of vertebral centrum	4. Caudal width of vertebral centrum	5. Caudal height of vertebral centrum	6. Width of spinal canal (anteriorly)	7. Height of spinal canal (anteriorly)	8. Length of neural spine along anterior edge	9. Minimum width at articular costal fossae (anteriorly/posteriorly)	10. Length of vertebral centrum dorsally/ventrally
I	Ust'-Tarka	390					C84	C59	380		C72/81
	Pyatiryzhsk	C325	187	170	175	175	120?			115/140	60/85
II	Ust'-Tarka	390							480		
	Pyatiryzhsk	410	170	162	160	163	93	77	485	150/150	60/90
	Azov 2, ♀*								485		
III	Ust'-Tarka	360							520		
	Pyatiryzhsk	382	160	160	140	165	88	63?	550	160/155	78/82
	Azov 2, ♀	305	156	152.5	155	156	85	53	440	120/142	65/56
IV	Ust'-Tarka	350							550		
	Pyatiryzhsk	360	145	155	141	162	75	55	540	150/140	85/78
	Azov 2, ♀	315	140	159	159	155	87	35,5	535	141/127	63/63
V	Ust'-Tarka	345							520		
	Pyatiryzhsk	365	148	160	150	165	83	45	555	140/145	90/83
	Azov 2, ♀	295	134	146	161	156	82	78	490	107/102	69/66
XII	Ust'-Tarka								355		
	Azov 2, ♀*								C375		
XIII	Ust'-Tarka								345		80/80
XIV	Ust'-Tarka								330		82/78
	Azov 2, ♀*	224	107	126.5	132	132.5	49	65	365	/76	85/78
XV	Ust'-Tarka	279		138					280?		85/79
	Azov 2, ♀*				154	136				/159	
XVI	Ust'-Tarka	268		143					260		90/82
	Azov 2, ♀		131	138.5	150	138	74	62			99.5/92.5
XVII	Ust'-Tarka	258		130					245		90/81
	Pyatiryzhsk*	C230	132	130	145	130	60	58	310	120/120	90/85
	Azov 2, ♀		135	142	141	143.5		67			89.5/91
XVIII	Ust'-Tarka	235		139					180		104/84
	Azov 2, ♀		129	135	132	147	50	66	222		98/84
V	Ust'-Tarka	315		125					~150		81/
	Azov 2, ♀	299	163	129.5	182	125	106	33			85/92

* Serial number of vertebra is determined approximately.

Table 9. Measurements of pelvic bones of *Mammuthus trogontherii* (Pohlig, 1885)

Measurement (right/left), mm		Ust'-Tarka, ♂, specimen IAE, no. 18	Pyatiryzhsk, ♂, specimen P2002.1149 (Shpansky et al., 2008a)	Chembakchino, ♂, specimen KhM-10398 (Kosintsev et al., 2004)	Azov 2, ♀, specimen AMZ, no. KP-28689
1	Horizontal diameter of glenoid cavities	199		190	190
2	Vertical diameter of glenoid cavities	202	215	195	208
3	Greatest width at ilia (distance between wings)	1550	1700		1820
4	Width between external edges of acetabulum	800	770		
5	The same between internal edges	460	420		500
6	Greatest width of iliac wing	1000/900		840	1050/990
7	Symphyseal length	520			560
8	Length of ischiadic foramen	240	175?	202	237/254
9	Width of ischiadic foramen	110	120?	107	133/127
10	Distance from upper edge of ilium to middle part of glenoid cavity	760		380?	860/790
11	Distance between external edges of ischiadic bones	440	470		600

elephant from Ust'-Tarka differ from that of females from Azov 2 and Edersleben (Fig. 4, Table 10). The pelvis of the elephant from Ust'-Tarka differs additionally from that of females in the flattened wings of the ilia and the straight crest of the iliac wing, as in *M. primigenius;* the pelvis of the male from Azov is not preserved; in the female pelvis from Azov, "... the crest of the iliac wing is convex. The wing surface is rough, concave on both sides" (Baigusheva and Titov, 2010, p. 20). The greater ischiadic foramen (apertura pelvis) is circular; its width is less than the diagonal height measured from the symphysis to the lowermost point of connection with the sacrum. Such a ratio is typical for females, whereas males usually show an inverse ratio. The width of the greater ischiadic foramen could have been limited by the discontinuance of growth of the pubis and ischium at the point of maturity, whereas the foramen height could have increased due to the growth of the ilia (Tikhonov, 1996).

The femora have well adherent epiphyses; the epiphyseal sutures are hardly discernible. The diaphyseal width is considerably greater than the anteroposterior diameter (Table 11). The neck of the head is relatively short and massive, directed medially at an angle of 50°. At the supraglenoid tubercles, the distal end is much wider than the distance between the external edges of the medial and lateral condyles. The articular surface for the patella is wide and slightly concave, somewhat higher on the medial side than laterally.

The tibia are almost straight; in the dorsal plane, the proximal part is trapezoidal, so that the plantar side is wider. The plantar side is concave in the upper one-third, limited laterally by sharp crests (lineae muscularum). The roughness of the tibia is triangular, with a pointed distal end. The main part of the diaphysis is triangular in cross section, with a well-pronounced crest (crista tibiae). The lateral and medial walls are flat; in the proximal part, the medial wall has a small rough depression. The tibiae of the elephant from Ust'-Tarka are relatively short and massive, considerably inferior in absolute length to the bones of males from Azov 1 and Odessa, but superior in the diaphyseal width (Table 11). The lateral articular surface of the proximal epiphysis is positioned much lower

→

Explanation of Plate 11

Figs. 1–4. *Mammuthus trogontherii* (Pohlig 1885), specimen IAE, no. 18; Novosibirsk Region, Ust'-Tarka; Middle Neopleistocene, Tobolsk horizon: (1) pelvis and sacrum, anterior view; (2) left femur with mounted patella, anterior view; (3) distal region of left hind leg, including mounted tibia, fibula, and foot, anterior view; (4) posteriormost lumbar vertebra, with well-developed osteophytes (indicated by arrows), ventral view.

Plate 11

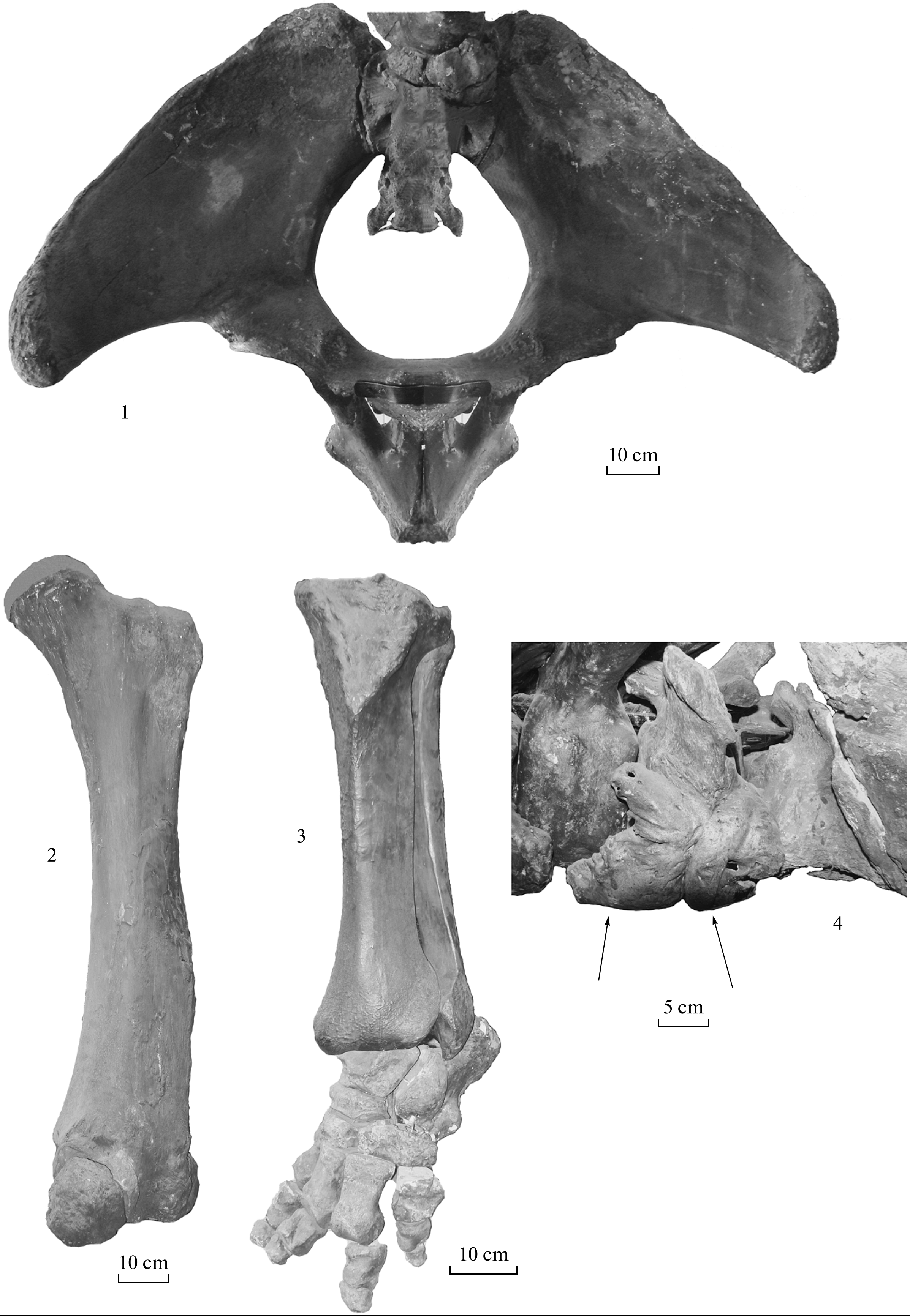


Table 10. Characters of sexual dimorphism in pelvic bones of elephants (after Lister, 1996, modified and supplemented): measurements: (1) greatest width of the pelvis at wings; (2) diagonal height of the greater ischiadic foramen from the symphysis to lower point of connection with the sacrum; (3) maximum horizontal width of the greater ischiadic foramen; (4) width iliac wing from pelvic tubercle to the nearest point of the greater ischiadic foramen; (5) minimum width of iliac neck parallel to anterior plane of the neck

Species, sex, and locality	Measurement, mm					Index					
	1	2	3	4	5	5/1	3/1	3/2	3/4	3/5	2/5
Ahidiskodon meridionalis, ♂, Valdarno, *n* = 3	1600–1880	400–470	440–540	–	251–284	0.141–0.169	0.275–0.287	1.04–1.15	–	1.63–1.95	1.48–1.87
A. meridionalis, ♀, Valdarno, *n* = 2	1300–1380	450	440–470	–	156–170	0.113–0.131	0.319–0.362	0.98–1.04	–	2.76–2.82	2.65–2.88
A. meridionalis, ♂, Rodionovo*	1620	–	452	610	–	–	0.279	–	0.741	–	–
Mammuthus trogontherii, ♂, West Runton	C1760	–	490	–	244	0.139	0.278	–	–	2.01	–
Mammuthus trogontherii, ♂, Ust'-Tarka	1550	520	455	630	253	0.163	0.294	0.88	0.720	1.80	2.06
M. trogontherii, ♀, Azov 2	1820	723	583	610	220; 209	0.121; 0.115	0.320	0.806	0.956	2.65; 2.78	3.28; 3.45
M. trogontherii, ♀, Edersleben	1540	630	570	630	192	0.125	0.370	0.90	0.904	2.97	3.28
M. primigenius, ♂, *n* = 11	1120–1600	330–480	410–510	460–620	182–208	0.133–0.186	0.306–0.384	1.0–1.24	0.788–1.0	1.92–2.64	1.69–2.42
M. primigenius, ♀, *n* = 2	1170–1340	390	440–540	400–452	154–194	0.132–0.145	0.377–0.403	1.13	0.973–1.35	2.78–2.86	2.53

* Initial measurements of pelvic bones of *A. meridionalis*, specimen BX-2120 from Rodionovo are given after Maschenko et al. (2011).

than the medial facet. The facet for the proximal end of the fibula is relatively small, oval.

In the left fibula, the diaphysis is only partially preserved; and in the right counterpart, it is broken. The bones are slightly bent. On the medial side, the distal part of the diaphysis is strongly flattened and expanded in the sagittal plane. The reconstructed right bone is 731 mm long. Its proximal epiphysis is 81 mm wide and 56 mm in sagittal diameter; the diaphysis is 47.5 mm wide in the middle; the distal epiphysis is 78 mm wide and 138 mm in sagittal diameter.

The patella is oval; its cranial surface is gently convex, rough, covered with many small nutrient foramina. The patella of the elephant from Ust'-Tarka is relatively small; it is larger than in the elephant from Chembakchino but considerably smaller than that of large males from Pyatiryzhsk and Azov 1 (Table 12).

SKELETON PROPORTIONS

The skeleton of *M. trogontherii* from Ust'-Tarka mounted on a metal frame shows the following measurements. The length from the anterior surface of the premaxillae to the posterior edge of the ischium is 390 cm. At both the most projecting skull part and the apex of the neural spine of the third thoracic vertebra (at the withers, the highest dorsal point), the skeleton is approximately 350 cm high (Fig. 2). The height of the mounted skeleton at the withers is estimated based on the forelimbs reconstructed using the skeleton of the elephant from Novopetrovsk (specimen PIN, no. 4464; Moscow Region, Istrinskii District), which is similar in size. At the dorsal edge of the pelvis, the mounted skeleton of the elephant from Ust'-Tarka is 293 cm high. The sum of lengths of the foot, tibia, femur, and ilium (from the acetabulum to dorsal edge), is 323 cm. The proportions of the hind limb were calculated based on this parameter, since it allows comparisons with other skeletons, including those not mounted. The difference in the above dimensions follows from the losses in the pelvic and knee articulations and mounting the skeleton in a moving posture (Fig. 2). The hind limb proportions in the elephant from Ust'-Tarka are close to the mean values of steppe elephants. At the sacrum, males are 293–374 cm high and females are 300–342 cm high. The femur length is 40.3% and the tibia length is 24.1%. Small differences are caused by the underestimated distance from the femoral head to the dorsal edge of the ilia (75 cm) and the large foot (the total height of mounted foot bones

Table 11. Measurements of long hind limb bones of *Mammuthus trogontherii* (Pohlig, 1885) from Western Siberia and Eastern Europe

Measurements (mm), indices (%)	Femur							Tibia					
Locality	Ust'-Tarka, IAE, no. 18	Chembakchino, KhM-10398 (Kosintsev et al., 2004)	Pyatiryzhsk, P2002.1149 (Shpansky et al., 2008a)	Odessa (Yatsko, 1948)	Azov 1, ♂ AMZ, no. KP-21081 (Baigusheva and Garutt, 1987)	Azov 2, ♀ AMZ, no. KP-28689 (Baigusheva and Titov, 2010)	West Runton, ♂ no. 1996.181.22 (Lister and Stuart, 2010)	Ust'-Tarka, IAE, no. 18	Chembakchino, KhM-10398 (Kosintsev et al., 2004)	Azov 1, ♂ AMZ, no. KP-21081 (Baigusheva and Garutt, 1987)	Azov 2, ♀ AMZ, no. KP-28689 (Baigusheva and Titov, 2010)	Odessa (Yatsko, 1948)	West Runton, no. 1996.181.27 (Lister and Stuart, 2010)
1. Length	1302	1230	1500	1480	–	1380	1425	777	645	890	825	920	830
2. Diaphyseal width	180	111	172?	202	C230	173	180	132	110.5	127	120	125	132
3. Diaphyseal diameter	115	94	–	112	–	–		119	88	123	107	110	–
4. Greater head diameter	191	–	210	188	230	195	212	283	236	285	266	282	299
5. Transverse head diameter	–	–	–	–	–	–		246		187	217	220	245
6. Width of distal epiphysis	280	243	290	326	340	291	323	206	196	255	221	221	248
7. Transverse diameter of distal epiphysis	306	–	320	–	279	304	308	162	158	172	173	151	183
Index of diaphysis (2 : 1)	13.8	9.0		13.6		12.5	12.6	17.0	17.1	14.3	14.5	13.6	15.9
Proximal index (4 : 1)	–	–	–	–	–	–	–	36.4	36.6	32.0	32.2	30.7	36.0
Distal index (6 : 1)	21.5	19.8	19.3	22.0	–	21.1	22.7	26.5	30.4	28.7	26.8	24.0	29.9

Table 12. Measurements of patella of *Mammuthus trogontherii* (Pohlig, 1885)

Measurement, mm	Ust'-Tarka, specimen IAE, no. 18	Pyatiryzhsk, specimen P2002.1149 (Shpansky et al., 2008a)	Chembakchino, specimen KhM-10398 (Kosintsev et al., 2004)	Azov 1, specimen KP-21081 (Baigusheva and Garutt, 1987)	West Runton, specimen 1995.105 (Lister and Stuart, 2010)
1. Greatest length	148.5	179	143	171	158
2. Greatest width	139	154	112	150	127
3. Greatest diameter	102	112	84	108	–

Table 13. Estimates of skeleton height of steppe elephants based on cylindrical limb bones (mm)

Locality, sex	Humerus (30.4% of skeleton height at withers)		Ulna (23.2% of skeleton height at the withers)		Femur (40.5% of skeleton height at sacrum)		Tibia (24.4% of skeleton height at sacrum)	
	bone length	estimated skeleton height	bone length	estimated skeleton height	bone length	estimated skeleton height	bone length	estimated skeleton height
Novogeorgievsk, ♀	980	3224	850	3664	1210	2988	690	2828
Gelsenkirchen, ♂	1190	3914	950	4095	1300	3210	760	3115
Edersleben, ♀	1066	3507	802	3457	C1277	3153	685	2807
*West Runton, ♂	1240	4079	920	3965	1425	3518	830	3402
Odessa, ♂	1230	4046	980	4224	1480	3654	920	3770
Azov 1, ♂, specimen AMZ, no. KP-21081	1290	4243	c950	4095	1480?	3654	900	3689
Azov 2, ♀, specimen AMZ, no. KP-28689	1160	3816	880	3793	1380	3407	825	3381
Chembakchino, ♂, specimen KhM-10398	1010	3322	C570		1230	3037	645	2643
Pyatiryzhsk, ♂, specimen P2002.1149	1320	4342	940	4052	1500	3704	–	–
Ust'-Tarka, ♂, specimen IAE, no. 18	–	–	–	–	1302	3215	777	3184

* Lister and Stuart (2010) estimated the height at shoulders of the elephant from West Runton with soft tissues as 390 cm.

is 40 cm). In the elephant from Ust'-Tarka, forelimb bones are not preserved; however, based on the ratio of the skeleton height at the withers to the height in the sacral region, which was previously obtained by us (Shpansky et al., 2008b), it is possible to estimate the skeleton height at the withers. In the steppe elephant, this ratio is 1.1 and, hence, as the height at the uppermost point of the pelvis is 323 cm, the height at the withers of the skeleton from Ust'-Tarka is estimated as 355 cm. These measurements are relatively small for males; thus, the elephant from Ust'-Tarka is considerably inferior in size to the giants from Pyatiryzhsk (424 cm high at the withers), Azov 1 (420 cm), West Runton (400 cm), and Gelaineo (389 cm) and superior to females from Novogeorgievsk (339 cm) and Edersleben (Table 13). During the animal's life, the elephant from Ust'-Tarka could have been about 370 cm high at the withers, including soft tissues.

The ribs are only slightly greater in absolute size than ribs of *M. primigenius.* Free forelimb was about

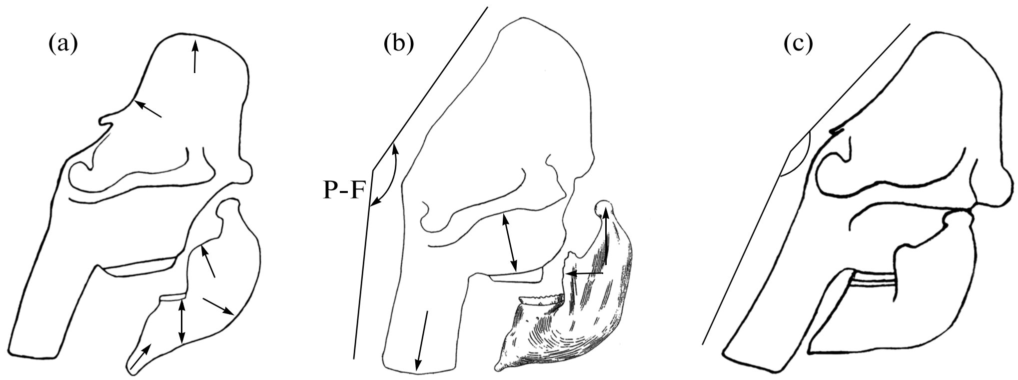


Fig. 5. Comparison of skulls of elephants of the mammoth-like lineage (lateral view): (a) *Archidiskodon meridionalis*, specimen IGF, no. 1054; Italy, Upper Valdarno (Garutt, 1954; Palombo and Feretti, 2005); specimen SM, no. 14120, lower jaw; Georgievsk (Garutt and Safronov, 1965); (b) *Mammuthus trogontherii*, specimen IAE, no. 18; Novosibirsk Region, Ust'-Tarka; specimen PIN, no. 4874, lower jaw; Volgograd Region, Chernyi Yar (Garutt, 1954); (c) *M. primigenius*, neotype ZIN, no. 2710; Taimyr Peninsula (Garutt and Tikhonov, 2001). Arrows show directions of morphological changes in the skull and lower jaw of mammoth-like elephants in phylogeny.

160 cm long (in the male from Azov 1, it is about 180 cm long).

TAXONOMIC POSITION

The taxonomy of mammoth-like elephants is based on dental morphology of the last tooth generation (M3). Additional data for the diagnosis are provided by the morphology of the skull, including lower jaw (Garutt, 1954, 1998; Lister, 1996a). Based on the teeth, it is impossible to determine with certainty the taxonomic position of the elephant from Ust'-Tarka, because they are heavily worn. The controversial question of the assignment of all Euroasian mammoth-like species to the genus *Mammuthus* (according to the West European colleagues) or division into two genera (as is usually accepted by Russian researchers) is beyond the scope of the present study.

The skull and lower jaw morphology of the elephant from Ust'-Tarka is transitional between the genera *Archidiskodon* and *Mammuthus*, as is typical for *M. trogontherii* (Fig. 5). The general questions of the evolutionary trend in changes of the skull and lower jaw of *A. meridionalis, M. trogontherii*, and *M. primigenius* have been investigated in detail (Maglio, 1973; Lister, 1996a). The skull and lower jaw of the specimen considered here (Figs. 5–7) are much closer in morphology to the woolly mammoth: (1) the skull is high and shortened in the sagittal plane, with a tapering apex; (2) the plane of occipital bones is convex; (3) the occipital condyles relatively poorly project beyond the occipital plane; (4) the forehead plane is almost even, its relative width (the ratio of the minimum forehead width to occipital width) is 51.5%, which is characteristic of the genus *Mammuthus*, while in *Archidiskodon*, the relative forehead width is 29–47.1% (Garutt, 1998); (5) the forehead width at the supraorbital processes is greater than the occipital width; (6) the lower edge of the nares is at the level of the orbital midline; (7) the distance between the lateral edges of articular processes of the lower jaw is less than the distance between the lateral walls in the region of jaw angles; (8) the horizontal ramus of the lower jaw is deep, the symphyseal region is short; the ascending ramus is widened in the region of the coronoid process; the crest of the coronoid process is well developed and raised.

The morphology of the premaxilla approaches that of *M. primigenius*; therefore, at the alveolar level, the tusks are directed downwards and, distally, curve anteriorly. In the southern elephant, they are directed ventrally and anteriorly just at the alveolar level. The premaxillae of the elephant from Ust'-Tarka are relatively long; the length-to-width ratio at the level of the infraorbital foramina is 171.7%. In *Archidiskodon*, this ratio is 147.3–176.9% and, in *Mammuthus*, it is 163.5–209.7% (Garutt, 1998). The region near the nares (the proximal end of the premaxillae, particularly the nasal process) and supraorbital processes of *A. meridionalis* strongly project beyond the forehead plane and beyond the nasal surface of the premaxilla, making inflated the middle skull part in projection on the sagittal plane (Figs. 5a, 6a). In *M. trogontherii* and *M. primigenius*, the region near the nares and supraorbital processes is in the forehead plane; at the same time, *M. trogontherii* retains a weak longitudinal concavity on the frontal surface. The nares of *A. meridionalis* are narrowed crescentic, 443–620 mm wide, 71–120 mm high, and the height index is 13.9–21.9%. In *M. trogontherii*, it is relatively high (Table 2), crescentic, but its lateral margins are extended downwards (Pl. 10, fig. 1); the height index is 25.1–28.6%. The nares reach the maximum height in *M. trogontherii chosaricus* (155–195 mm) at 460–532 mm of width; the height index is 29.1–42.4%. In *M. primigenius*, the nares are high, widely oval, with round lateral edges; it is 325–472 mm wide, 80–150 mm high; the height index is 24.2–34.5%. The characteristics listed may

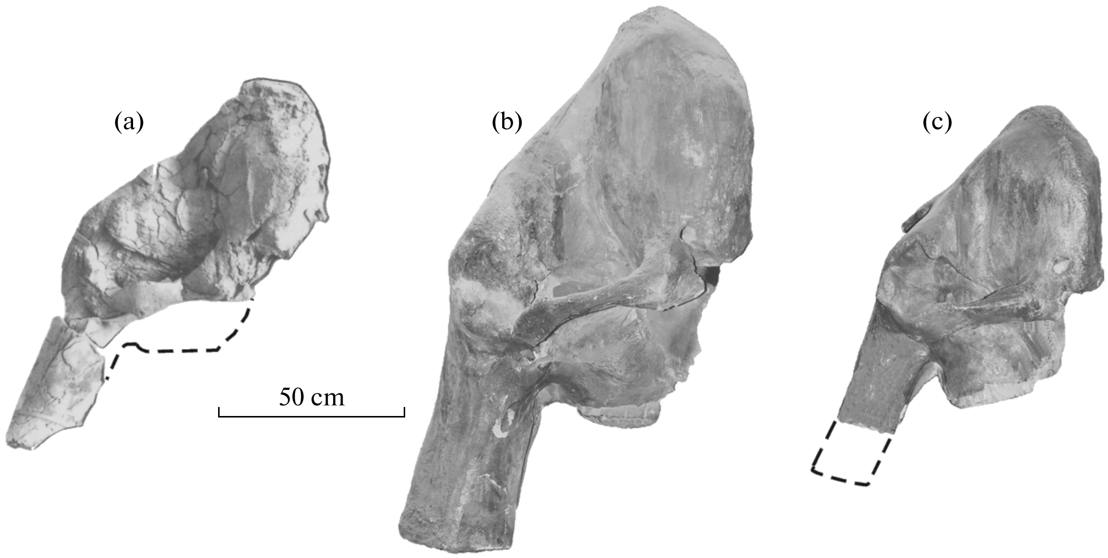


Fig. 6. Skulls of elephants of the mammoth-like lineage, lateral view: (a) *Archidiskodon meridionalis*, Italy, Sauvignon (Regiani and Sala, 1994); (b) *Mammuthus trogontherii*, specimen IAE, no. 18; Novosibirsk Region, Ust'-Tarka; (c) *M. primigenius*, specimen PM TGU, no. 54; Tomsk Region.

result from adaptation to arud climate, with the maximum indices of the nasal opening height in throgonthere elephant, which dwelt during the maximum claxiation and in *M. primigenius* characteristic of the late Late Neopleistocene, with the maximum aridity in the latter half.

A characteristic feature is changes in the lower jaw, i.e., the shortened mental protuberance of the symphysis, accompanied by an increase in the relative depth of the horizontal ramus and expansion of the area of the coronoid process (Figs. 5b, 7b). A significant expansion of the plane of the ascending ramus and rostral displacement of the anterior angle of the coronoid process are similar to that of *M. primigenius.* A distinctive feature of the steppe elephant is the oblique angle of the lower jaw in projection on the sagittal plane, which results in a zigzag line and strong caudal bulge of the upper one-third of the ascending ramus (Fig. 7b).

Table 14 shows the parameters of preserved distal parts of M3/m3.

A straight crest on the iliac wing, which was previously regarded as a diagnostic character of *M. primigenius* (Garutt, 1954; Dubrovo, 1982) is observed in the skeleton of the steppe elephant from Ust'-Tarka and in the elephant *Archidiskodon meridionalis* cf. *gromovi* from northeastern Italy (Reggiani and Sala, 1994). In the southern elephant *A. meridionalis* from Rodionovo, the crest of the iliac wing is gently bent (Maschenko et al., 2011). It should be noted that, in mammoth cubs below three–four years of age, the crest of the iliac wing has a distinct curvature, which is particularly well pronounced in the cubs younger than one year of age (Shpansky and Pecherskaya, 2007).

Table 14. Comparison of teeth in *Mammuthus trogontherii* (Pohlig, 1885) and *Archidiskodon meridionalis* (Nesti, 1825)

	Plate frequency per 10 cm			Enamel thickness, mm		
	M. trogontherii		*A. meridionalis*	*M. trogontherii*		*A. meridionalis*
	Ust'-Tarka, specimen IAE, no. 18	Extreme values in other skeletons (see Table 4)	Shpansky, 1999; Maschenko et al., 2011	Ust'-Tarka, specimen IAE, no. 18	Extreme values in other skeletons (see Table 4)	Shpansky, 1999; Maschenko et al., 2011
M3	5.6–6.2	5.3–6.52	4.5–5.5	2.3–(2.7)–3.2	1.8–(2.7)–3.2	3.0–3.8
m3	4.3–4.5	5.25–6	4.5–5	2.7–(3.2)–4.0	2.0–(2.5)–3.53	2.5–4.0

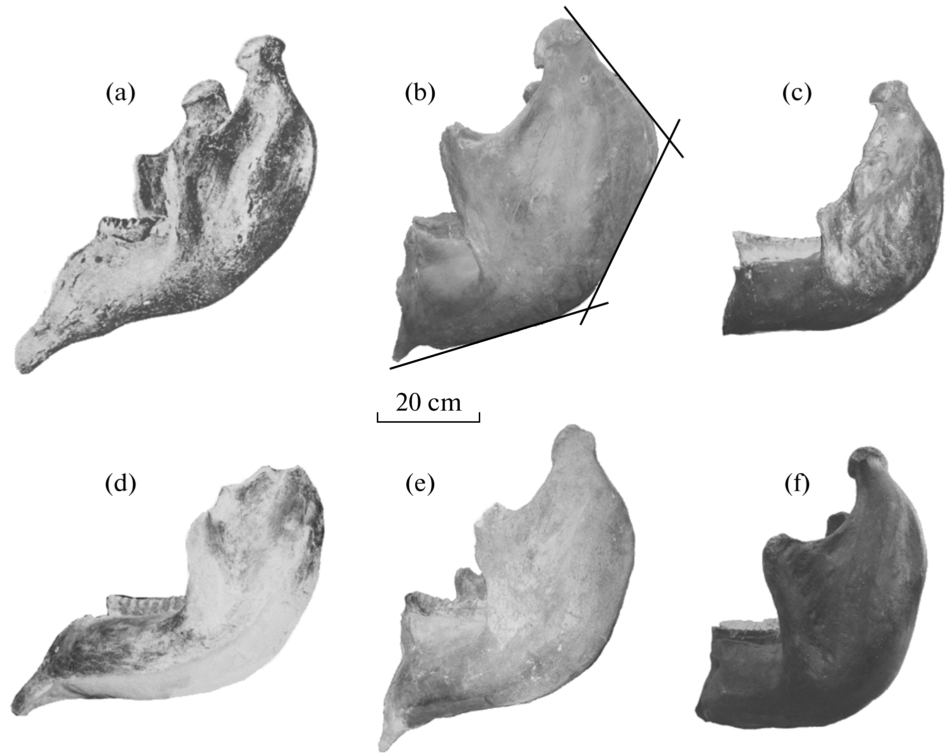


Fig. 7. Lower jaws of mammoth-like elephants, buccal view: (a, d) *Archidiskodon meridionalis*: (a) specimen SM, no. 14120; Georgievsk (Garutt and Safronov, 1965); (d) Italy, Oriolo (Palombo and Ferretti, 2005); (b, e) *Mammuthus trogontherii*: (b) specimen IAE, no. 18; Ust'-Tarka; (e) specimen MP PGPI, no. 2002.1149-1; Pyatiryzhsk (Shpansky et al., 2008); (c, f) *M. primigenius*, specimen PM TGU, nos. 1/17 (c), 1/56 (f); Tomsk Region.

Subsequently, the wing crest is straightened. Thus, according to our data, a straightened crest on the ilium may not be unequivocally taken for a distinctive character of *M. primigenius*, although a rounded crest of the ilium has not been recorded in adult woolly mammoths. In our opinion, the presence of such a structure of pelvic bones in the specimen from Ust'-Tarka makes it closer to later members of the mammoth-like lineage.

Thus, the skull and lower jaw shape and features of pelvic bones suggest the assignment of specimen IAE, no. 18 to *M. trogontherii*.

CONCLUSIONS

Skeletons of *M. trogontherii* and their fragments are rather rare in Western Siberia. All of them are confined to the alluvial beds of the Irtysh River (Chembakchinskii Yar, Pyatiryzhsk) and its tributary, the Om River (Ust'-Tarka). The skeleton from Ust'-Tarka is one of the smallest in absolute measurements and comparable to skeletons from Novogeorgievsk and Gelsenkirchen (3.34–3.5 m high at the withers) (Shpansky et al., 2008b). It is smaller than the female skeleton from the Kagal'nitskii quarry (Azov 2) (Baigusheva and Titov, 2010). Certain anatomical features of bones (such as obliteration of epiphyseal sutures, large tusks, mental protuberance of the lower jaw, and morphology of pelvic bones) suggest that the skeleton from Ust'-Tarka belongs to a male about 55–60 years of age. Functioning teeth in its jaws are heavily worn molars of the last generation (M3/m3).

Presently known West Siberian skeletons of *M. trogontherii* are of approximately the same geological age and connected with deposits of the Tobolsk Horizon dated the beginning of the Middle Neopleistocene. The date of 550–600 ka reported for the beds enclosing the elephant skeleton from Chembakchino (Kosintsev et al., 2004) is doubtful because of morphological features and preservation of available remains. The skeletons from Europe are somewhat more ancient, come from the Early Neopleistocene beds. The steppe elephant is an intrazonal species and its remains (usually teeth) found in Western Siberia also occur in the Early Neopleistocene beds in the composition of the Vyatka Faunal Assemblage. In the Irtysh Region near Pavlodar (and in Kazakhstan as a whole), the steppe elephant is recorded in the Koshkurgan (Early Neopleistocene) and Irtysh (terminal Early Neopleistocene–basal Middle Neopleistocene: Lebyazh'e and Zhanaul formations of the Irtysh Region near Pavlodar) faunal assemblages (Shpansky et al., 2007; Shpansky, 2009).

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