Russian J. Theriol. 25 (1): 94–103

First 3D digital osteological archive of the woolly mammoth *Mammuthus primigenius* from the Zoological Institute of the Russian Academy of Sciences

Diana D. Gamzik & Julia A. Prikhlenko*

ABSTRACT. This paper presents the first 3D digital archive of the limb long bones of *Mammuthus primigenius* from the paleontological collection of the Zoological Institute of the Russian Academy of Sciences (ZIN; Saint Petersburg, Russia). A total of 189 isolated bones from 14 localities and 84 bones from nine articulated *M. primigenius* skeletons were digitised. The digital collection additionally includes nine bones of *Elephas maximus* from the ZIN collection. Scanning was performed using a portable optical 3D scanner (EinScan Pro 2X), followed by processing in EXScan Pro software. For subsequent geometric morphometric analyses, a scheme of 120 three-dimensional semi-landmarks for the tibia is proposed, taking the preservation of the palaeontological material into account. Landmark placement was performed in 3D Slicer.

How to cite this article: Gamzik D.D., Prikhlenko J.A. 2026. First 3D digital osteological archive of the woolly mammoth *Mammuthus primigenius* from the Zoological Institute of the Russian Academy of Sciences // Russian J. Theriol. Vol.25. No.1. P.94–103. doi: 10.15298/rusjtheriol.25.1.10

KEY WORDS: *Mammuthus primigenius*, Elephantidae, geometric morphometrics, 3D optical scanning, shape analysis, landmarking.

Diana D. Gamzik [diana.gamzik@zin.ru], Zoological Institute of the Russian Academy of Sciences, Universitetskaya emb. 1, Saint Petersburg 199034, Russia; Julia A. Prikhlenko (Shemyakina) [julia.shemyakina@zin.ru], Zoological Institute of the Russian Academy of Sciences, Universitetskaya emb. 1, Saint Petersburg 199034, Russia.

Первый цифровой остеологический 3Д архив шерстистого мамонта *Mammuthus primigenius* из коллекции Зоологического института Российской академии наук

Д.Д. Гамзик, Ю.А. Прихленко*

РЕЗЮМЕ. В работе представлен первый 3D-цифровой архив длинных костей конечностей *Mammuthus primigenius* из палеонтологической коллекции Зоологического института РАН (ЗИН РАН; Санкт-Петербург, Россия). Оцифрованы 189 изолированных костей из 14 местонахождений и 84 кости от девяти сочлененных скелетов *M. primigenius*. В цифровую коллекцию дополнительно включены девять костей *Elephas maximus* из коллекции ЗИН РАН. Сканирование выполнено портативным оптическим 3D-сканером EinScan Pro 2X с последующей обработкой в EXScan Pro software. Для последующего геометрического морфометрического анализа предложена схема из 120 3Д полуметок (semi-landmarks) для описания формы большой берцовой кости, учитывающая сохранность палеонтологического материала. Расстановка ландмарок выполнена в программе 3D Slicer.

КЛЮЧЕВЫЕ СЛОВА: *Mammuthus primigenius*, Elephantidae, геометрическая морфометрия, оптическое 3Д сканирование, анализ формы, установка ландмарок.

Introduction

The evolution of the genus *Mammuthus* (Elephantidae) is considered the most fully documented among extinct Pleistocene mammals due to the vast number of discoveries and the wealth of publications addressing various aspects of its palaeobiology, palaeoecology, palaeogenetics, morphological variation, and taxonomy (Wei *et al*., 2010; Baygusheva *et al*., 2012; Virág & Gasparik, 2012; Lister, 2017, 2022; Haynes *et al*., 2018). Over the last decade, the application of modern technologies has yielded amazing results in the analysis of palaeomolecular, genomic (Enk *et al*., 2016; Pečnerová *et al*., 2017; Dehasque *et al*., 2021; Van der Valk *et al*., 2021; Díez del Molino *et al*., 2023) and palaeoendocrine (Cherney *et al*., 2023) data. Nevertheless, the most accessible morphological data on proboscideans are analysed based on traditional linear measure-

* Corresponding author

ments (see Herridge, 2010; Larramendi, 2016), and only a few studies have applied novel 3D geometric morphometric techniques to investigate the morphological diversity of proboscideans (Bader *et al*., 2023, 2024). Thus, the successful application of multivariate statistical analyses to 3D models of proboscidean limb long bones by Camille Bader, and the unique results obtained, highlight the important methodological issue of the large-scale application of 3D geometric morphometrics for the analysis of isolated and mostly damaged *Mammuthus* remains — primarily those of *Mammuthus primigenius* (Blumenbach, 1799) — within the extensive Russian paleontological collections.

The paleontological collection of the Zoological Institute of the Russian Academy of Sciences (ZIN; Saint Petersburg, Russia) houses unique osteological materials, including the associated skeletons of the Lena (Adams), Berezovka, Taymyr, Kamskoe Ust'e, Khatanga, Mokhov (Kutomanov), Sanga-Yuryakh, and Gusinsky mammoths (Zalenskiy, 1903; Garutt, 1992; Averianov, 1992, 1994; Pugachev *et al*., 2008; Petrova *et al*., 2015, 2017; Slepkova & Bublichenko, 2019), as well as collections from Late Pleistocene bone accumulations, such as Berelekh (Verestshagin, 1977; Baryshnikov *et al*., 1977; Pitulko *et al*., 2024) and Kostenki 14(1) (Petrova *et al*., 2023). In 2025 the digitisation of limb long bones from the aforementioned collections and associated skeletons was conducted. The aim of this publication is to provide a quantitative and qualitative description of the resulting digital collection, as well as a description of the equipment, technical, and methodological solutions, including methods for describing the shape of isolated bones (using the tibia as an example).

Material and methods

The material described in this article comprises 189 fore- and hindlimb long bones of *M. primigenius* from 14 localities: Berelekh River, Berezovka River, Eliseevichi-1, Eliseevichi-2, Gusinaya River, Gyda River, Kamtchatka River, Kostenki 14 (Layer 1), Lena River, Mamontovaya River, Mokhovaya River, Ob' River, Ojagossky Yar, and Wrangel Island (Table 1). Furthermore, nine bones of *Elephas maximus* Linnaeus, 1758 are included. Epiphyseal fusion states were assessed by Ekaterina A. Petrova.

Isolated limb bones were digitised using a portable optical 3D scanner (EinScan Pro 2X, Shining 3D Tech Co.). EXScan Pro software (version 4.0.1.0, Shining 3D Tech Co.) was used for the scanning and subsequent

Table 1. Summary of localities for the *M. primigenius* material analysed.

nn	Locality	Geological Age	Calibrated Age	Reference
1	Berelekh River, North East of Yakutia, Russia	–	13 700–11 800	Baryshnikov *et al*., 1977; Pitulko *et al*., 2024
2	Berezovka River, Yakutia, Russia	31 750±2500, 44 000±3500 (T-299)	52 950–31 350	Zalenskiy, 1903; Averianov, 1994; Lister, 1999
3	Gusinaya River, Taymyr Peninsula, Russia	10 900±130 (LU-9796)	13 100–12 690	in press
4	Gyda River, Tazovskaya Bay, Russia	–	–	–
5	Kamtchatka River, Kamtchatka Peninsula, Far East, Russia	–	–	–
6	Lena River, Yakutia, Russia	35 800±1200 (T-171), 31 500±2000 (T-170/3)	42 600–32 220	Averianov, 1994
7	Mokhovaya River, Taymyr Peninsula, Russia	35 000–33 000	–	Averianov, 1994
8	Mamontovaya River (basin of Nizhnaya Taymyra River), Taymyr Peninsula, Russia	11 450±250 (T-297)	13 800–12 830	Garutt, 1992; Averianov, 1994
9	Ob River, Russia	–	–	–
10	Ojagossky Yar, Yakutia, Russia	–	–	–
11	Upper Paleolithic site Eliseevichi-1, Bryansk Region, Russia	–	17 000–15 000–12 000	Khlopachev *et al*., 2017
12	Upper Paleolithic site Eliseevichi-2, Bryansk Region, Russia	–	–	–
13	Upper Paleolithic site Kostenki 14 (Markina Gora), layer I, Voronezh Region, Russia	–	27 000–28 000	Petrova *et al*., 2023
14	Wrangel Island, Russia	–	–	–

processing of the 3D models. All models were saved in the Stanford PLY format.

The mounted skeletons of the Lena (Adams), Berezovka, and Taymyr mammoths are on display at the Zoological Museum of the ZIN. These skeletons were partially dismantled, and the limb bones were digitised directly in the museum exhibition halls (Fig. 1).

One of the objectives of the present study is to develop a landmark wireframe scheme for the description of isolated mammoth bones. Landmark placement was performed using 3D Slicer software (Fedorov *et al*., 2012). The final landmark scheme is presented in the Results section.

Anatomical nomenclature follows Evans (1993) and Bader *et al*. (2023).

Data availability statement. At the time of publication, the 3D models are available upon direct request to the curator of the digital collection, Dr. Ekaterina A. Petrova, via e-mail: ekaterina.petrova@zin.ru Once the digitisation of the collection is complete, the materials will be made freely accessible on the ZIN portal (www.zin.ru).

Results

Limb bones of associated skeletons. In total, limb bones from nine *M. primigenius* skeletons and two *E. maximus* skeletons were digitised, yielding 84 bones. These comprise twelve scapulae (four right, eight left), 17 humeri (nine right, eight left), 13 radii (seven right, six left), 15 ulnae (eight right, seven left), 14 femora (seven right, seven left), and 13 tibiae (six right, seven left) (Table 2). In addition, fibulae were scanned together with the associated tibiae for three skeletons: the right and left fibulae of the Taymyr mammoth (ZIN 2710), the right fibula of the Berezovka mammoth (ZIN 5315), and the right and left fibulae of the Lena mammoth (ZIN 7911).

During the scanning of mounted skeletons on display at the Zoological Museum of the ZIN (Lena, Berezovka, and Taymyr mammoths), we encountered a limitation related to the fact that the bones of each limb are rigidly fixed by a metal armature. This restricts the possibility of fully scanning the articular surfaces of the elbow and knee

Table 2. List of digitized skeletons of the *Mammuthus primigenius* (1–9) and *Elephas maximus* (10–11). Key: **Fe**, femur; **H**, humerus; **L**, left; **R**, right; **Ra**, radius; **S**, scapula; **T**, tibia; **U**, ulna.

nn	Name	Museum ID	Locality	S	H	Ra	U	Fe	T	Total:
1	Taymyr	ZIN 2710	Mamontovaya River (basin of Nizhnaya Taymyra River), Taymyr Peninsula, Russia	RL	RL	RL	RL	RL	RL	12 (R6/L6)
2	Lena	ZIN 7911	Lena River, Yakutia, Russia	RL	R	R	R	RL	RL	9 (6/3)
3	Sanga-Yuryakh	ZIN 31738	Sanga-Yuryakh, Yakutia, Russia		R	R	R	R	–	4 (4/0)
4	Berezovka	ZIN 5315	Berezovka River, Yakutia, Russia	RL	RL	RL	RL	RL	R	11 (6/5)
5	Gusinsky	ZIN 39241	Gusinaya River, Taymyr Peninsula, Russia	RL	RL	R	RL	RL	RL	11 (6/5)
6	Mokhov	ZIN 31736	Mokhovaya River, Taymyr Peninsula, Russia	L	RL	RL	RL	R	RL	10 (5/5)
7	Khatanga	ZIN 31829	Bolshaya Rassokha River(basin of Khatanga River), Taymyr Peninsula, Russia	L	L	L	L	L	–	5 (0/5)
8	Tazovsky	ZIN 13263, 13269, 13315, 13362, 13371	Gyda River, Tazovskaya Bay, Russia	–	RL	R	R	–	L	5 (3/2)
9	Kamskoe Ust'e	ZIN 30873	Kamskoe Ust'e, Tatarstan, Russia	L	RL	L	RL	L	L	8 (2/6)
10	*Elephas maximus*	ZIN 30872	The skeleton was transferred from the Military Medical Academy, Saint Petersburg	L	L	L	L	R	R	6 (4/2)
11	*Elephas maximus*	ZIN 30871	Vietnam	–	R	–	–	L	L	3 (1/2)
			Total: **84**	12 (R4/L8)	17 (9/8)	13 (7/6)	15 (8/7)	14 (7/7)	13 (6/7)	

Fig. 1. Dismantling and 3D scanning of the limb bones of mounted *Mammuthus primigenius* skeletons on display at the Zoological Museum of the ZIN. A — taxidermists Andrey A. Grigoriev and Dmitry V. Dedov with the dismantled hindlimb of the Berezovka mammoth; B — dismantled limb bones of the Lena mammoth prior to the scanning process; C — mammoth specialist Ekaterina A. Petrova during the digitization of a bone in the museum exhibition.

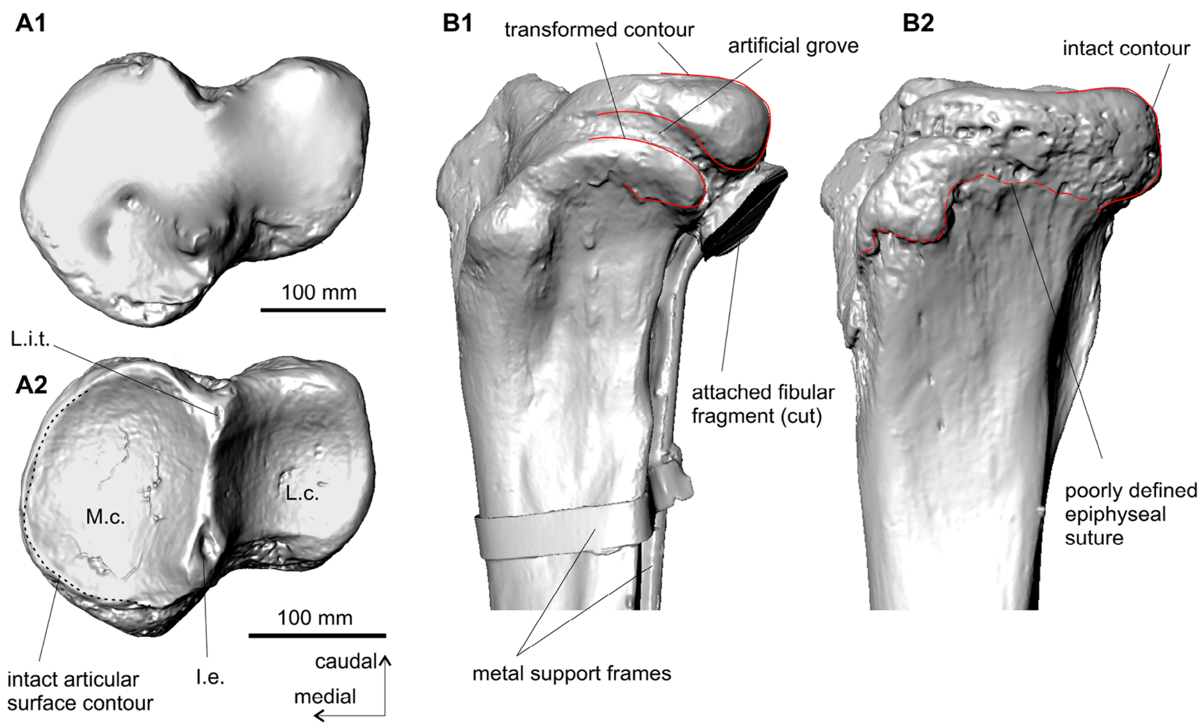

Fig. 2. Illustration of artefacts related to unseparated joints (A) and to bone restoration (B). A1 — articular surface of the proximal end of the tibia of the Berezovka mammoth (ZIN 5315), showing missing surface detail because most of the articular area was inaccessible to the scanner due to rigid articulation with the femur. A2 — articular surface of an isolated tibia of the Tazovsky mammoth (ZIN 13371). B1 — lateral aspect of the proximal part of the tibia of the Lena mammoth (ZIN 7911), showing artificial structures and metal armature. B2 — same view of the tibia of the Tazovsky mammoth (ZIN 13371), showing intact surfaces of the proximal epiphysis. Key: I.e., intercondylar eminence; L.c., lateral condyle; L.i.t., lateral intercondylar tubercle; M.c., medial condyle (terminology following Bader *et al*., 2023).

joints. When reconstructing such bones in EXScan Pro, this constraint results in artefacts in the joint surface areas (Fig. 2, A1). Moreover, these mounted skeletons have undergone repeated restoration in the joint regions, which has produced artificial features that obscure the original joint surfaces and epiphyseal sutures (Fig. 2, B1).

Table 3. List of digitized scapula of the *Mammuthus primigenius*. Key: 0, unfused apophysis; f, fused apophysis; L, left; R, right.

nn	Museum ID	Locality	Side	Apophysis
1	ZIN 30957/24	Berelekh River, Abyysky District, Yakutia, Russia	R	f
2	ZIN 30957/23		L	0
3	ZIN 30957/24		L	0
4	ZIN 30957/22		L	0
5	ZIN 30957/21		L	f
6	ZIN 30957/10		R	0
7	ZIN 30957/18		L	–
8	ZIN 30957/17		L	0
9	ZIN 30957/16		L	0
10	ZIN 30957/11		R	0
11	ZIN 30957/19		R	0
12	ZIN 30957/14		L	–
13	ZIN 5323	Yenisei River, Russia	R	–
14	ZIN 38218/1006	Upper Paleolithic site Kostenki 14, layer I, Voronezh Region, Russia	R	–
15	ZIN 38218/1001		R	–
16	ZIN 38218/1000		R	–
17	ZIN 38218/998		R	0
18	ZIN 38218/870		L	–
19	ZIN 38218/999		L	0
20	ZIN 38218/1010		L	–
21	ZIN 38218/609		R	–
22	ZIN 38218/380		R	–
23	ZIN 38218/1011		L	–
24	ZIN 38218/1009		L	–

Table 4. List of digitized humerus of the *Mammuthus primigenius*. Key: 0, unfused epiphysis; (f), fusing or recently fused epiphysis; f, fused epiphysis; L, left; R, right.

nn	Museum ID	Locality	Side	Proximal epiphysis	Distal epiphysis
1	ZIN 30957/10	Berelekh River, Abyysky District, Yakutia, Russia	R	(f)	f
2	ZIN 30957/5		L	f	f
3	ZIN 30957/7		R	f	f
4	ZIN 30957/48		L	(f)	f
5	ZIN 30957/3		L	f	f
6	ZIN 30957/9		R	f	0
7	ZIN 30957/6		L	f	f
8	ZIN 30957/8		L	f	f
9	ZIN 30957/11		R	(f)	f
10	ZIN 30957/1		L	(f)	f
11	ZIN 30957/2		L	0	f
12	ZIN 38218/1015	Upper Paleolithic site Kostenki 14, layer I, Voronezh Region, Russia	L	f	0
13	ZIN 38218/1024		R	(f)	f
14	ZIN 38218/1023		L	0	f
15	ZIN 38218/1019		L	–	f
16	ZIN 38218/1021		R	0	0
17	ZIN 38218/1014		R	–	f

Isolated limb bones. The scapula is represented in the digital collection by 24 specimens from the bone accumulations of Berelekh (n = 12) and Kostenki 14 (Layer 1) (n = 11); the sample also includes a single scapula from Friedrich Schmidt's collections (ZIN 5323). The collection comprises 11 right and 13 left scapulae. Depending on preservation, the state of apophyseal fusion was recorded as: 0 — unfused apophysis (n = 10); f — fused apophysis (n = 2) (Table 3).

The sample of isolated humeri includes 17 specimens from the bone accumulations of Berelekh (n = 11) and Kostenki 14 (Layer 1) (n = 6). The collection comprises seven right and 10 left humeri. Depending on preservation, the state of fusion of the proximal and distal epiphyses was recorded as: 0 — unfused epiphysis; (f) — fusing or recently fused epiphysis; f — fused epiphysis (Table 4).

The ulna is represented in the digital collection by 19 specimens from the bone accumulations of Berelekh (n = 10) and Kostenki 14 (Layer 1) (n = 9). The collection comprises eleven right and eight left ulnae. Information on the state of fusion of the proximal and distal epiphyses is provided in Table 5.

The femur is represented in the digital collection by 13 specimens from the bone accumulations of Berelekh

Table 5. List of digitized ulna of the *Mammuthus primigenius*. Key: see Table 4.

nn	Museum ID	Locality	Side	Proximal epiphysis	Distal epiphysis
1	ZIN 30957/6	Berelekh River, Abyysky District, Yakutia, Russia	R	f	f
2	ZIN 30957/9		L	0	0
3	ZIN 30957/5		R	f	(f)
4	ZIN 39411		R	f	f
5	ZIN 30957/7		L	0	0
6	ZIN 30957/2		R	f	0
7	ZIN 30957/4		L	f	f
8	ZIN 30957/1		R	f	0
9	ZIN 30957/3		R	f	(f)/f
10	ZIN 30957/12		R	0	0
11	ZIN 38218/1086	Upper Paleolithic site Kostenki 14, layer I, Voronezh Region, Russia	L	f	(f)
12	ZIN 38218/1079		R	f	0
13	ZIN 38218/1078		R	0	0
14	ZIN 38218/1085		R	–	–
15	ZIN 38218/1081		L	0	0
16	ZIN 38218/1113		L	f	–
17	ZIN 38218/968		L	–	0
18	ZIN 38218/1083		R	f	f
19	ZIN 38218/121		L	f	–

Table 6. List of digitized femur of the *Mammuthus primigenius*. Key: see Table 4.

nn	Museum ID	Locality	Side	Proximal epiphysis	Distal epiphysis
1	ZIN 30957/1	Berelekh River, Abyysky District, Yakutia, Russia	R	(f)	f
2	ZIN 30957/2		L	(f)	f
3	ZIN 30957/7		R	f	f
4	ZIN 30957/12		R	f	f
5	ZIN 30957/11		L	(f)	f
6	ZIN 30957/3		L	f	f
7	ZIN 30957/14		L	f	f
8	ZIN 30957/6		L	f	f
9	ZIN 30957/4		R	f	f
10	ZIN 30957/5		L	f	f
11	ZIN 38218/953	Upper Paleolithic site Kostenki 14, layer I, Voronezh Region, Russia	R	f	f
12	ZIN 38218/957		L	f	f
13	ZIN 38218/962		R	0	0

Table 7. List of digitized tibia of the *Mammuthus primigenius*. Key: see Table 4.

nn	Museum ID	Locality	Side	Proximal epiphysis	Distal epiphysis
1	ZIN 30957/41	Berelekh River, Abyysky District, Yakutia, Russia	R	f	f
2	ZIN 30957/11		L	f	f
3	ZIN 30957/39		R	(f)	(f)
4	ZIN 30957/40		L	f	f
5	ZIN 30957/33		R	f	f
6	ZIN 30957/36		L	f	f
7	ZIN 30957/4		R	(f)	(f)
8	ZIN 30957/35		L	f	f
9	ZIN 30957/141		R	f	f
10	ZIN 30957/3		L	f	f
11	ZIN 30957/1		R	f	f
12	ZIN 30957/2		L	f	f
13	ZIN 30957/34		L	f	f
14	ZIN 30957/12		L	f	f
15	ZIN 30957/38		R	f	f
16	ZIN 30957/7		L	f	f
17	ZIN 30957/8		L	f	f
18	ZIN 30957/6		L	f	f
19	ZIN ZIN 30957/37		L	(f)/f	(f)
20	ZIN 30957/5		R	f	f
21	ZIN 35430/40	Oyagossky Yar, Yakutia, Russia	R	0	(f)
22	ZIN 38218/1002	Upper Paleolithic site Kostenki 14, layer I, Voronezh Region, Russia	L	f	f
23	ZIN 38218/1003		L	f	f
24	ZIN 38218/974		L	f	(f)
25	ZIN 38218/984		R	f	f
26	ZIN 38218/979		R	f	0
27	ZIN 38218/1004		R	f	f
28	ZIN 38218/985		R	–	f
29	ZIN 38218/976		L	0	0
30	ZIN 8218/978		L	0	0
31	ZIN 38218/977		R	0	0
32	ZIN 38218/987		L	0	0
33	ZIN 38218/983		R	0	0
34	ZIN 38218/972		L	0	0
35	ZIN 38218/973		L	0	0
36	ZIN 35560	Wrangel Island, Russia	R	f	f
37	ZIN 39412	Kamtchatka River, Kamtchatka Peninsula, Russia	R	f	f
38	ZIN 39413	Upper Paleolithic site Eliseevichi-1, Bryansk Region, Russia	L	f	f
39	ZIN 39414	Upper Paleolithic site Eliseevichi-2, Bryansk Region, Russia	R	0	0
40	ZIN 35599	Wrangel Island, Russia	L	f	f
41	ZIN 39415	Ob River, Russia	L	f	f

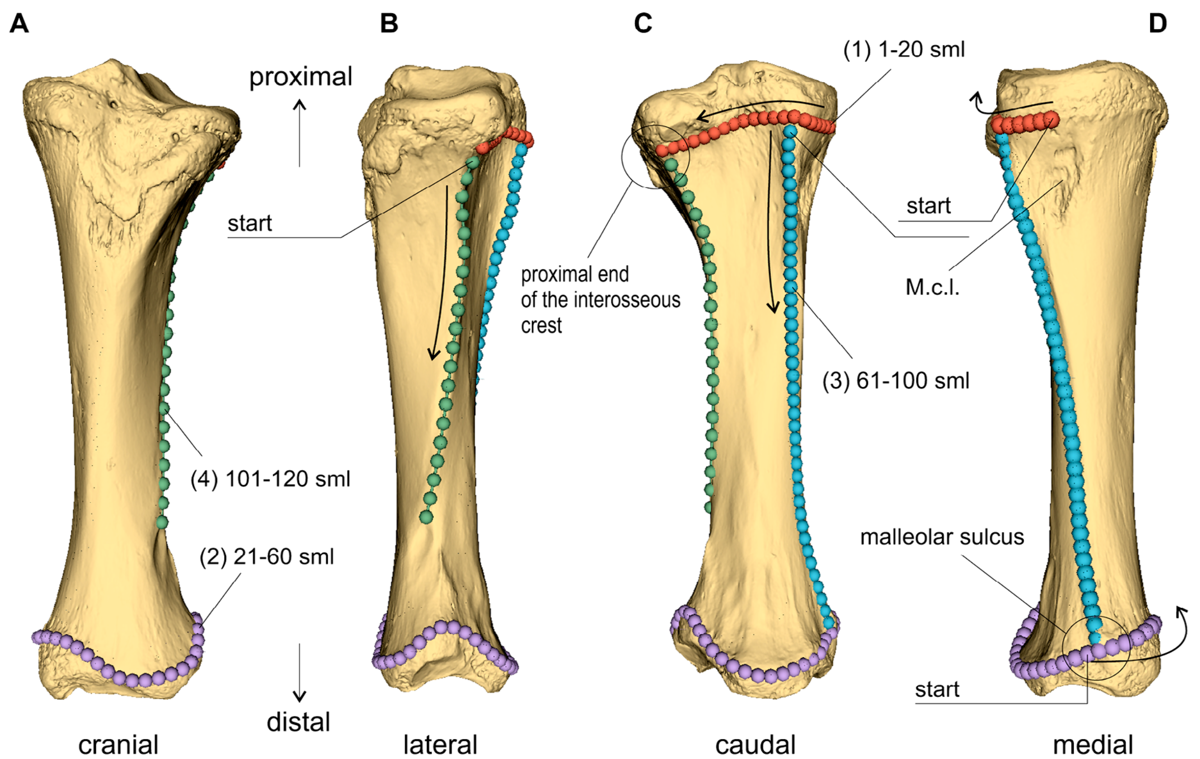

Fig. 3. Landmark wireframe placed on a 3D model of the tibia. The bone is shown in cranial (A), lateral (B), caudal (C), and medial (D) views. Key: 1–4, semi-landmark curves (see text for details); arrow, direction of semi-landmark numbering; M.c.l., medial collateral ligament groove; start, start point of a curve.

(*n* = 10) and Kostenki 14 (Layer 1) (*n* = 3). The sample comprises six right and seven left femora. Information on the state of fusion of the proximal and distal epiphyses is provided in Table 6.

The most representative sample is that of the tibia, comprising 41 specimens from the bone accumulations of Berelekh (*n* = 20) and Kostenki 14 (Layer 1) (*n* = 14), as well as isolated finds from Oyagossky Yar, the Kamtchatka River, Eliseevichi-1 and Eliseevichi-2, and the Ob' River, together with two specimens from Wrangel Island. The collection comprises 18 right and 23 left tibiae. Information on the state of fusion of the proximal and distal epiphyses is provided in Table 7.

Shape of the tibia: landmark wireframe. One of the objectives of our study was to develop a landmark scheme for subsequent geometric morphometric analyses, following the approach of Bader *et al.* (2023, 2024). The tibia was selected as the most abundant element in our digital collection. Given the extent of damage, we propose a landmark scheme consisting of four semi-landmark curves. (1) Curve 1–20 follows the epiphyseal suture from the level of the medial collateral ligament groove to the proximal end of the interosseous crest. (2) Curve 21–60 outlines the distal epiphyseal suture, with both endpoints located in the region of the malleolar sulcus. (3) Curve 61–100 links curves 1 and 2, starting at the proximal end of the popliteus muscle attachment crest, following this crest, continuing onto a weakly expressed crest along the course of the tendon of the tibialis caudal muscle, and meeting curve 2 within the malleolar sulcus. (4) Curve 101–120 extends from the proximal to the distal end of the interosseous crest (Fig. 3).

Discussion

The portable optical 3D scanner allowed us to obtain high-resolution 3D models of 189 limb long bones. Because the primary intended use of this digital collection is the analysis of shape variation using geometric morphometrics, it was necessary to develop a landmark-based description of bone shape, comparable in principle to that used by Bader *et al.* (2023, 2024). However, the preservation of the fossil material, as well as specific aspects of the mounted skeletons (Fig. 2), did not allow us to replicate Bader's tibial landmark scheme. Tibiae in our collection, particularly those from Kostenki 14 (Layer 1), often show substantial damage to the articular surfaces. In addition, cranial structures of the bone are frequently affected by marked rounding, which prevented us from including the entire proximal end in the landmark scheme; instead, we restricted the scheme to its caudal surface (Fig. 3). Another difference of our scheme is the absence of fixed landmarks. We used semi-landmarks only, and employed as the start and end points of curves those points that correspond to anatomical structures identified by fixed landmarks in Bader *et al*. (2023): Bader's fixed landmarks 9 and 12 correspond to semi-landmarks 101 and 120 of our curve 4, whereas Bader's fixed landmarks 10 and 11 approximately correspond to semi-landmarks 61 and 100 of our curve 3. No other clear landmark correspondences between the two schemes are present. Nevertheless, we consider that this enforced reduction of the tibial landmark scheme relative to that of Bader should not affect the accuracy of the analysis or the quality of describing shape transformations in relation to the structure of the data (factors presence such as, age, sex, geography, geology, etc.); this assumption remains to be evaluated.

ACKNOWLEDGMENTS. This study was funded by Russian Scientific Foundation, project no. 25-24-00418. It was partly used mammoth's collection materials from the Zoological Institute of the Russian Academy of Sciences. The authors are grateful to Ekaterina A. Petrova for her comprehensive assistance with 3D scanning, data analysis, discussions, and manuscript preparation. We are also grateful to the museum staff, Andrey A. Grigoriev and Dmitry V. Dedov, for their technical support of our study.

References

Averianov A.O. 1992. [Description of the mammoth remains from Kamskoe Ust'e] // Muraviev I.S. & Solodukho M.G. (eds.). [Volga Fauna of Pleistocene Mammals in Geological and Mineralogical Museum of Kazan University]. Kazan: Kazan University Press. P.56–65 [in Russian].

Averianov A.O. 1994. [Kutomanov mammoth] // Proceedings of the Zoological Institute of the Russian Academy of Sciences. Vol.256. P.111–135 [in Russian, with English summary].

Bader C., Delapré A. & Houssaye A. 2023. Shape variation in the limb long bones of modern elephants reveals adaptations to body mass and habitat // Journal of Anatomy. Vol.242. P.806–830. DOI: 10.1111/joa.13827

Bader C., Delapré A., Göhlich U.B. & Houssaye A. 2024. Diversity of limb long bone morphology among proboscideans: how to be the biggest one in the family // Papers in Palaeontology. Vol.10. Art.e1597. DOI: 10.1002/spp2.1597

Baryshnikov G.F., Kuzmina I.E. & Hrabrii V.M. 1977. [Results of measurements of tubular bones of mammoths from the Berelekh "Burial-ground"] // Proceedings of the Zoological Institute of the Academy of Sciences of the USSR. Vol.72. P.58–66 [in Russian].

Baygusheva V.S., Titov V.V. & Timonina G.I. 2012. Two skeletons of *Mammuthus trogontherii* from the Sea of Azov Region // Quaternary International. Vol.276–277. P.242–252. DOI: 10.1016/j.quaint.2011.05.045

Cherney M.D., Fisher D.C., Auchus R.J., Rountrey A.N., Selcer P., Shirley E.A., Beld S.G., Buigues B., Mol D., Boeskorov G.G., Vartanyan S.L. & Tikhonov A.N. 2023. Testosterone histories from tusks reveal woolly mammoth musth episodes // Nature. Vol.617. P.533–539. DOI: 10.1038/s41586-023-06242-x

Dehasque M., Pečnerová P., Muller H., Tikhonov A., Nikolskiy P., Tsigankova V.I., Danilov G.K., Díez del Molino D., Vartanyan S., Dalén L. & Lister A.M. 2021. Combining Bayesian age models and genetics to investigate population dynamics and extinction of the last mammoths in northern Siberia // Quaternary Science Reviews. Vol.259. Art.106913. DOI: 10.1016/j.quascirev.2021.106913

Díez del Molino D., Dehasque M., Chacón-Duque J.C., Pečnerová P., Tikhonov A., Protopopov A., Plotnikov V., Kanellidou F., Nikolskiy P., Mortensen P., Danilov G.K., Vartanyan S., Gilbert M.T.P., Lister A.M., Heintzman P.D., van der Valk T. & Dalén L. 2023. Genomics of adaptive evolution in the woolly mammoth // Current Biology. Vol.33. P.1–12. DOI: 10.1016/j.cub.2023.03.084

Enk J., Devault A., Widga C., Saunders J., Szpak P., Southon J., Rouillard J.-M., Shapiro B., Golding G.B., Zazula G., Froese D., Fisher D.C., MacPhee R.D.E. & Poinar H. 2016. *Mammuthus* population dynamics in Late Pleistocene North America: divergence, phylogeography, and introgression // Frontiers in Ecology and Evolution. Vol.4. Art.e42. DOI: 10.3389/fevo.2016.00042

Evans H.E. 1993. Miller's Anatomy of the Dog. Philadelphia: W.B. Saunders. 1113 p.

Fedorov A., Beichel R., Kalpathy-Cramer J., Finet J., Fillion-Robin J.-C., Pujol S., Bauer C., Jennings D., Fennessy F.M., Sonka M., Buatti J., Aylward S.R., Miller J.V., Pieper S. & Kikinis R. 2012. 3D Slicer as an image computing platform for the quantitative imaging network // Magnetic Resonance Imaging. Vol.30. P.1323–1341. DOI: 10.1016/j.mri.2012.05.001

Garutt V.E. 1992. [The skeleton of mammoth *Mammuthus primigenius* (Blumenbach, 1799) from the neighbourhood of Kozlovo village of Chermezsk area Perm Region] // Muraviev I.S. & Solodukho M.G. (eds.). [Volga Fauna of Pleistocene Mammals in Geological and Mineralogical Museum of Kazan University]. Kazan: Kazan University Press. P.31–54 [in Russian].

Haynes G., Klimowicz J. & Wojtal P. 2018. A comparative study of woolly mammoths from the Gravettian site Kraków Spadzista (Poland), based on estimated shoulder heights, demography, and life conditions // Quaternary Research. Vol.90. P.483–502. DOI: 10.1017/qua.2018.60

Herridge V.L. 2010. Dwarf elephants on Mediterranean islands: A natural experiment in parallel evolution. Ph.D. thesis. London: University College London. 480 p.

Khlopachev G.A., Gribchenko Yu.N., Kulkova M.A. & Sapelko T.V. 2017. [New data on the age and longevity of the Late Palaeolithic site of Eliseevitchi 1] // Stratum Plus. No.1. P.41–57 [in Russian, with English summary].

Larramendi A. 2016. Shoulder height, body mass, and shape of proboscideans // Acta Palaeontologica Polonica. Vol.61. P.537–574. DOI: 10.4202/app.00136.2014

Lister A.M. 2017. On the type material and evolution of North American mammoths // Quaternary International. Vol.443A. P.14–31. DOI: 10.1016/j.quaint.2017.02.027

Lister A.M. 2022. Mammoth evolution in the late Middle Pleistocene: the *Mammuthus trogontherii-primigenius* transition in Europe // Quaternary Science Reviews. Vol.294. Art. e107693. DOI: 10.1016/j.quascirev.2022.107693

Pečnerová P., Palkopoulou E., Wheat C.W., Skoglund P., Vartanyan S., Tikhonov A., Nikolskiy P., van der Plicht J., Díez-del-Molino D. & Dalén L. 2017. Mitogenome evolution in the last surviving woolly mammoth population reveals neutral and functional consequences of small population size // Evolution Letters. Vol.1. No.6. P.292–303. DOI: 10.1002/evl3.33

Petrova E.A., Burova N.D. & Sinitsyn A.A. 2015. [The skeleton of mammoth (*Mammuthus primigenius*) from the upper Palaeolithic site Kostenki 14 (Markina gora), European Russia] // Proceedings of the Zoological Institute of the Russian Academy of Sciences. Vol.319. No.3. P.378–400 [in Russian, with English summary]. DOI: 10.31610/trudyzin/2015.319.3.378

Petrova E.A., Masutin V.V. & Zhuykova I.A. 2017. Two incomplete skeletons of woolly mammoth (*Mammuthus primigenius*) from the late Pleistocene in the Kirov Region, European Russia // Russian Journal of Theriology. Vol.16. No.2. P.157–175. DOI: 10.15298/rusjtheriol.16.2.05

Petrova E.A., Voyta L.L., Bessudnov A.A. & Sinitsyn A.A. 2023. An integrative paleobiological study of woolly mammoths from the Upper Paleolithic site Kostenki 14 (European Russia) // Quaternary Science Reviews. Vol.302. Art.e107948. DOI: 10.1016/j.quascirev.2022.107948

Pitulko V.V., Pavlova E.Y., Dorozhkina M.V., Nikolskiy P.A. & Basilyan A.E. 2024. From the Berelekh 'mammoth graveyard' to Berelekh geo-archaeological complex: Paleoenvironment, site formation processes, and human-mammoth relationships // Quaternary Science Reviews. Vol.334. Art.108692. DOI: 10.1016/j.quascirev.2024.108692

Pugachev O.N., Slepkova N.V. & Tikhonov A.N. 2008. [The Academy of Sciences' long-term efforts to study mammoth fauna. The role of academic expeditions of the XVIII–XIX Centuries] // Kolchinskii E.I. (ed.). [Science and technology: historical and theoretical issues. Proceedings of the 29th international conference of the St. Petersburg branch of the national committee for the history and philosophy of science and technology of the Russian Academy of Sciences]. Is.24. St. Petersburg: St. Petersburg Branch of the Institute of Natural History and Technology of the Russian Academy of Science. P.34–40 [in Russian].

Slepkova N.V. & Bublichenko A.G. 2019. [Zoological Museum of the Zoological Institute of the Russian Academy of Sciences – the treasure of St. Petersburg] // [Environment of St. Petersburg]. Vol.4. No.14. P.28–37 [in Russian].

Van der Valk T., Pečnerová P., Díez-del-Molino D., Bergström A., Oppenheimer J., Hartmann S., Xenikoudakis G., Thomas J.A., Dehasque M., Sağlıcan E., Fidan F.R., Barnes I., Liu S., Somel M., Heintzman P.D., Nikolskiy P., Shapiro B., Skoglund P., Hofreiter M., Lister A.M., Götherström A. & Dalén L. 2021. Million-year-old DNA unravels the genomic history of mammoths // Nature. Vol.591. P.265–269. DOI: 10.1038/s41586-021-03224-9.

Verestshagin N.K. 1977. [Berelekh "cemetery" of mammothe]s // Proceedings of the Zoological Institute of the Academy of Sciences of the USSR. Vol.72. P.5–49 [in Russian].

Virág A. & Gasparik M. 2012. Relative chronology of late Pliocene and early Pleistocene mammoth-bearing localities in Hungary // Hantkeniana. Vol.7. P.27–36.

Wei G., Taruno H., Jin C. & Xie F. 2003. The earliest specimens of the steppe mammoth, *Mammuthus trogontherii* from the Early Pleistocene Nihewan Formation, North China // Earth. Vol.57. P.289–298.

Zalenskiy V.V. 1903. [Osteological and odontographic studies on the mammoth (*Elephas primigenius* Blum.) and elephants (*El. indicus* L. and *El. africanus* Blum.)] // Dubrovin N. (ed.). [Scientific results of the expedition sent by the Imperial Academy of Science for the excavation of mammoth found on Berezovka River in 1901]. Vol.1. P.1–124 [in Russian].