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The second complete skeleton of *Archidiskodon meridionalis* (Elephantidae, Proboscidea) from the Stavropol Region, Russia

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ABSTRACT

The skeleton of *Archidiskodon meridionalis* (Nesti, 1825) from the Rodionovo locality (Stavropol Administrative Region, Russia) is described in detail. It represents the second discovery of an almost complete skeleton of a fossil elephant in the Northern Caucasus. The age of the fossil is estimated as Early Pleistocene (upper Apsheronian, late Middle Villafranchian). Attribution of the skeleton to this species, widely distributed in Eurasia during the Late Pliocene-Early Pleistocene, is based on the tooth characters (M3/m3 enamel thickness and lamellar frequency). Validity of the genus *Archidiskodon* Pohlig, 1888 is discussed.

1. Introduction

Quarry excavations at the Rodionovo homestead in the Novoaleksandrovskii Administrative District of the Stavropol Region, Russia on August 27, 2007 exposed a fossil elephant skeleton (Fig. 1). The salvage operations were organized in September–October in the same year by the team from the Stavropol Museum of Natural History (Prozritelev and Prave State Stavropol Historical, Cultural, Natural and Landscapes Museum-Preserve) and led by Dr. A.K. Shvyreva. Reconstruction and study of the bones found in the quarry confirmed that the find represented the almost complete skeleton of an elephant belonging to the genus *Archidiskodon* (Pohlig, 1888).

Finds of complete fossil elephant skeletons are very rare. The discovery of two complete skeletons from the same region, the Stavropol Region, is a unique circumstance for the territory of Russia. The first skeleton of *Archidiskodon meridionalis* (Nesti, 1825) was found in the Georgievsk (Early Pleistocene, Psekups fauna) sand pit in 1960 (Garutt and Safronov, 1965). The locality of the second skeleton was at 45°15′ 44" N, 41° 27′ 8" E.

The authors recognize the genus *Archidiskodon*, separate from the genus *Mammuthus*, within the family Elephantidae Gray, 1821. Elephants of the genus *Archidiskodon* are characterized by M3/m3 molars composed of very broad, widely spaced lamellae, the interlamellar distance reaching up to 35.0–40.0 mm (Osborn, 1942; Garutt, 1998a). *Archidiskodon* was a relatively large-bodied genus of the Elephantidae, widely distributed in Eurasia (Garutt and Tikhonov, 2001). *A. meridionalis* was widely distributed in Eurasia, including the northern Caucasus where is represented by at least two local forms (subspecies), *A. m. meridionalis* and *A. m. tamanensis*. In the Early Pleistocene the genus *Archidiskodon* gave rise to the genus *Mammuthus* Brookes, 1828, which became the most common proboscidean taxon in the Holarctic. The evolutionary changes in elephants of the mammoth lineage are particularly evident in tooth morphology, including a gradual increase in the lamellar number and hypsodonty of the cheek teeth (Dubrovo, 1964).

The discovery of postcranial skeletal material of this genus is particularly significant in developing a better understanding of the evolution of proboscidean lineages (Maschenko and Kalmykov, 2008).

Abbreviations: SM, Stavropol Museum of Natural History (Prozritelev and Prave State Stavropol Historical, Cultural, Natural and Landscapes Museum-Preserve); BX, specimens belonging to the skeleton of the *A. meridionalis* from the Rodionovo locality; PIN RAN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZIN RAN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

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Fig. 1. Locations of *Archidiskodon meridionalis* (Nesti, 1825) remains in the Stavropol Region, Novoaleksandrovskii Administrative District, Russia. 1. The Rodionovo locality (the Tverdova gully); 2. The Georgievskii sand pit.

2. Geological setting

The Rodionovo locality is located on the left bank of the Tverdova gully. This is a large quarry that opens into the Egorlyk River valley and contains a series of deposits (Fig. 2C). The lithostratigraphy from the top down is as follows: 1) recent soil (0.5 m thick); 2) yellow-brown non-layered, carbonized light clay (0.7–1.0 m thick); 3) yellow-brown horizontally layered carbonized light clay with flat pebbles up to 1 cm in diameter (2.3–2.5 m thick); 4) red-brown lumpy carbonized clay with large pebbles and gypsum crystal clusters up to 2.5–3.0 cm in diameter (2.5–2.7 m thick; upper boundary of this unit poorly defined); 5) clayey pebbles: upper portion composed of large, smooth-surfaced pebbles; lower portion composed of small pebbles mixed with coarse sand (0.8–0.9 m thick). The elephant carcass was deposited in the alluvial deposits of the upper part of the lowest unit (layer 5), 7 m below the surface. The bones were included in a sandy-clay lens filled with small-sized pebbles; the lens was resting on large pebbles cemented by coarse sand (Shvyreva, 2007).

The depth of the alluvial deposits at the fossil site, in relation to their depth at the river bed, demonstrates a high rate of accumulation resulting from increased and irregular drainage, increased sediment load, and decreased volume of drifting material in the stream. All these processes are indicative of fluvial erosion of floodplain terraces. The predominance of floodplain alluvium is characteristic of open ground environments (savanna, steppe, etc.). The predominance of fluvial erosion at the fossil site was bound to low-energy stream flow of the ancient Egorlyk River forming alluvial lenses and layers that covered the elephant's carcass. The lithological features of the 4th stratigraphic layer (lumpy texture, multicolored layers with predominance of yellow-brown colors, presence of gypsum crystal clusters) indicate subaerial formation,

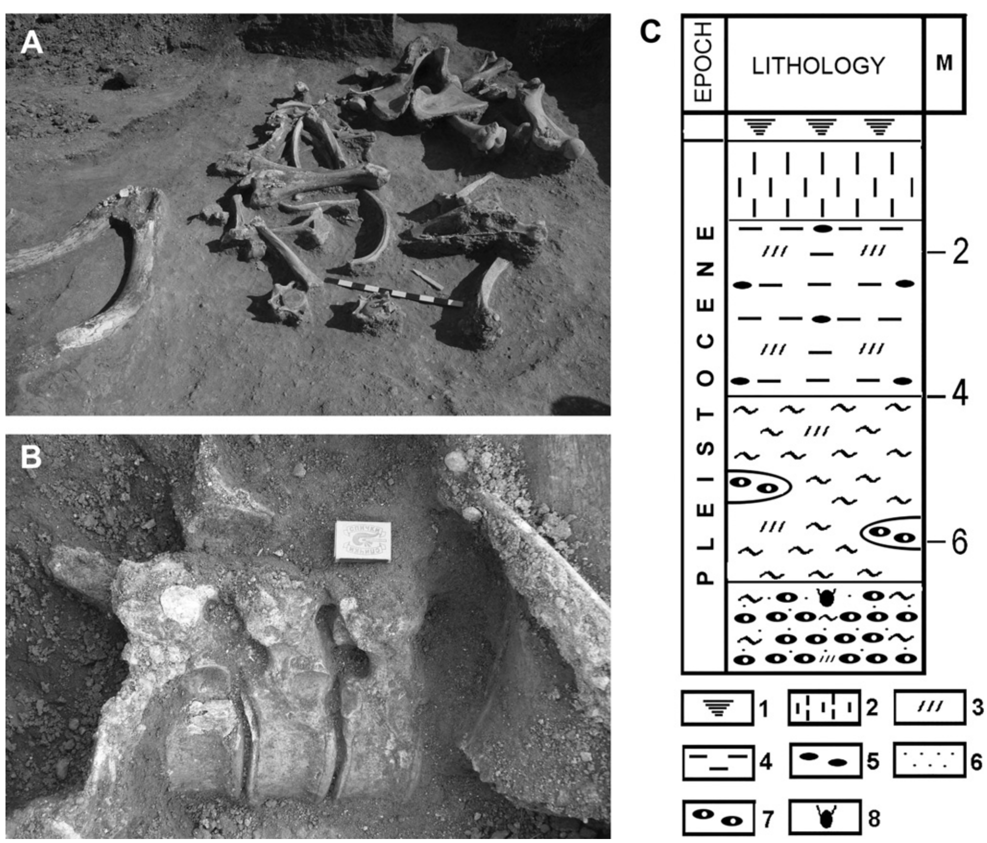

Fig. 2. Excavations at the Rodionovo locality, Stavropol Region, Novoaleksandrovskii Administrative District, Russia. A. Position of the bones of the *A. meridionalis* skeleton *in situ*. B. Anatomical position of the 17th–19th thoracic vertebrae *in situ*. C. The excavation pit section of the Rodionovo locality (in cm). 1. Modern soil; 2. Yellow-brown unstratified loam; 3. Multilayered yellow-brown loam deposits with carbonated nodules; 4. Red-brown lumpy clay with druses of gypsum and ferrous manganese dendrites; 5. Lens of clays and sands with small-sized gravel; 6. Large gravel cemented by carbonates; 7. Crossbedded sands; 8. Position of the elephant skeleton.

and the presence of red colored clays and gypsum concretions ("roses") indicates relatively warm climate and well-drained conditions.

The skeleton was resting on its right side with most of its bones disarticulated. The bones covered an area of about 35 m^2 (Fig. 2A) (Shvyreva, 2007). According to the location of the cranial bones that were broken during excavation, the skull originally rested on its molars. The mandible, also damaged during excavation, was located *in situ*, in front of the premaxillae. Some of the bones, including vertebrae and a few ribs, were also found *in situ* in anatomical position (Fig. 2B). This incomplete set of articulated bones indicates that the carcass was moved at most only a short distance from the place of death, and was gradually buried under alluvial deposits. Presumably most parts of the distal limbs were lost during burial.

The Tverdova gully deposits belong to the Burunduksk Formation which has yielded fossils indicative of the Psekups Fauna (Lebedeva, 1978). The age of this late Middle Villafranchian fauna is estimated as earliest Pleistocene (Garutt and Safronov, 1965; Kahlke et al., 2011).

3. Systematic description

Order Proboscidea Illiger, 1811
Family Elephantidae Gray, 1821
Genus *Archidiskodon* Pohlig, 1885

Selected synonyms

Elephas: Nesti 1825, p. 195–216, pl. 1, fig. 1–3;
Mammuthus Brooks 1828, p. 73, 74;
Parelephas: Osborn 1928, p. 672, figs. 1–2;

Diagnosis (emended from Pohlig, 1888; Osborn, 1942; Garutt, 1954 and Garutt, 1998a): M3/m3 crown is short and broad; number of plates (excluding talons) is 7–15 (9–17 including talons); the average length of plate is 26.5–17.5 mm; lamellar (plate) frequency is 4–6.5; enamel thickness is 2.9–4.3 mm. Cement on the molars is very thick. The skull is low; the length/height ratio of the skull ranges from 78.9 to 86.1%. The occipital bones are concave and occipital condyles project above the occipital surface. The lower rim of the nasal opening is situated higher than the upper rims of the orbits. The mandible is low, with low ascending rami. The submental process is long and massive. The cervical vertebrae are relatively short.

Remarks

The genus *Archidiskodon*, with type species *Elephas meridionalis* Nesti, 1825, was established by Pohlig (1888). The present authors also include the species *Archidiskodon subplanifrons* Osborn, 1928 and *Archidiskodon garutti* Maschenko, 2010 in the genus *Archidiskodon*.

The nominal taxon *A. meridionalis* was subsequently recognized as composite, and one of the syntype skulls, "skull C", was selected as the lectotype (Depéret and Mayet, 1923). *E. meridionalis* has been fixed as the type species of the genus *Mammuthus* Brooks, 1828 by monotypy (see Garutt et al., 1990 for details). This would imply that *Archidiskodon* should be considered a junior synonym of *Mammuthus*.

Garutt et al. (1990), however, indicate that the generic name *Archidiskodon* Pohlig, 1888 is available for the purposes of nomenclature, with type species *E. meridionalis* Nesti, 1825. In our opinion, the distinction between the two genera, *Archidiskodon* and *Mammuthus*, differing in important characters, should be maintained. The former genus shows a lower number of dental plates, thicker enamel, a lower hypsodonty index, more concave occipital bones, and has its nasal opening located higher in relation to the upper border of the orbits.

The incorporation of all proboscideans of the mammoth lineage into the genus *Mammuthus* was proposed by Aguirre (1969) who considered that lamellar density, hypsodonty and other characters of the molars and the skull pattern are diagnostic for this genus. This viewpoint was supported by Maglio (1973) and Lister (1996). On the other hand, Garutt (1998a), Garutt and Tikhonov (2001), and the present authors regard the above characters as criteria of generic differentiation between the *Archidiskodon* and *Mammuthus* lineages.

A. meridionalis (Nesti, 1825)
E. meridionalis Nesti 1825, p. 195–216, pl. 1, fig 1–3;
Elephas antiquus: Falconer et Cautley 1845–1849 (partium), pl. 14 B, fig. 17–18; pl. 42, fig 19;
Elephas planifrons: Falconer et Cautley 1846, p. 38. pl. 2, fig. 5a, 5b;
Elephas lyrodon: Weithofer 1890, p. 173–181, tabl. 3, fig. 2, tabl. 4, fig 2, tabl. 5, fig. 1;
A. meridionalis: Osborn 1942, p. 969, fig. 858–864, fig. 866–868; Garutt 1954, p. 81, fig. 6;
Archidiskodon tokunagai: Teilhard de Chardin et Trassaert 1937, pl. 9, fig. 1a, 1b, 2; pl. 10, fig. 1a, b, fig. 2;
Archidiskodon planifrons: Garutt 1954, p. 6;
Archidiskodon gromovi: Alexeeva et Garutt 1965, p. 162, fig. 1;
Mammuthus meridionalis Maglio 1973, p. 53, pl. 17, fig. 1–5
Palaeoloxodon pingliangengensis: Zhang et al. 1983, p. 65–67, pl.1.

Diagnosis (emended from Garutt, 1998a; Garutt and Tikhonov, 2001): M3/m3 complete number of plates 9–15/9–15 excluding talons (11–17/11–17 including talons); enamel thickness: 2.6–4/2.5–3.9 mm; lamellar frequency: 4–6.5/4–6.5; hypsodonty index: 1.25–1.6/1.1–1.4; crown height: 101.0–160.0/90.0–140.0 mm.

Remarks

Concerning *A. meridionalis*, Osborn (1942, p. 974) cited the M3/m3 plate formula, excluding talons, as 13–14/11–14, based on specimens from Central Italy (Upper Valdarno) and elsewhere. This corresponds approximately to a formula of 15–16/13–16 including talons. In contrast to this, data from the youngest representatives from the Northern Caucasus (*A. m. tamanensis*), indicate an extension of the maximum plate formula to 15/15 plates (17/17 including talons). A single m3 reported by Palombo and Ferretti (2005) from Mugello (Central Italy, Late Villafranchian) seems to show a similar maximum value of 15 talons (17 including talons). At the low end of the range, Dubrovo (1989) indicated *A. m. meridionalis* to include M3/m3 with as few as 8 plates (10 including talons) (Table 19), although Eurasian molars with 8–10 plates (10–12 including talons) have been referred by other authors (e.g. Lister & van Essen, 2003) to the species *Mammuthus rumanus*. The authors of the present paper do not support *M. rumanus* as a taxon within the genus *Archidiskodon* (see Obada, 2010 for details).

4. Material and methods

This paper is the first detailed description of the fossil bones of the specimen from the Rodionovo homestead site. The following *A. meridionalis* skeletons were used for comparisons: specimen ZIN N 24239 from the Nogaisk locality (Zaporozhye Region, Ukraine) (Garutt, 1954) and the specimen from the Georgievsk sand pit (Stavropol' Region, North Caucasus) (Garutt and Safronov, 1965; Garutt, 1998b).

Most of the bones of the *Archidiskodon* skeleton from Rodionovo, including all but one of the long bones, were recovered. The skull

Table 1
Metrics of M3/m3 molars of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965; Garutt, 1998b) and Nogaisk (Garutt, 1954) sites. Measurements are taken according to the methods described by Garutt and Foronova (1976). Measurements for M3 and m3 are separated by a horizontal line.

Measurements, mm	Rodionovo locality M3/m3 (sin) BX 2120/55	Georgievsk locality M3 (dex)/m3 (sin) SN 14120	Nogaisk locality Collection ZIN 24239 Date for M3 dex and m3 dex
Length/width of crown	$\frac{-/98.9}{-/89.5}$	$-\frac{267.0/104.0}{252.0/98.0}$	$-\frac{302.0/122.0}{>280.0/119.0}$
Complete number of lamellae (in brackets, number of preserved lamellae), excluding talons	$\frac{-}{\sim 12-13/(10)11?-12?}$	$\frac{-/12}{-/11}$	$\frac{(14)?}{14}$
Complete number of lamellae (in brackets, number of preserved lamellae), including talons	$\frac{-}{\sim 14-15/(12)13?-14?}$	$\frac{-/14}{-/13}$	$\frac{(16)?}{16}$
Lamellar (plate) frequency (in 10 cm)	$\frac{4.7}{4.5}$	$\frac{4.5-5}{4.5(\text{at occlusal surface})}$	$\frac{4.5-5}{5}$
Enamel thickness	$\frac{-}{3.5}$	$-\frac{3.0-3.8}{3.2-4.0}$	$\frac{3.3-3.7}{2.5-3.0}$
Length/width of plate	$\frac{-}{9-10.5/82.0-87.0}$	$\frac{19.0/-}{19.0/-}$	$\frac{1.1-1.7}{1.1-2.4}$
Inter-lamellae distance	$\frac{-}{3.0-4.0}$	$\frac{0.3-0.35}{0.3-0.35}$	–
Number of plates in wear/length of grinding surface	$\frac{-}{7-8?/-}$	–	$\frac{13}{14}$
Height of unworn plates	$\frac{-}{\sim 140.0}$	–	$\frac{192.0}{128.0}$

and lower jaw were completely destroyed in the process of quarrying; only a few small fragments of the brain case, alveoli, upper tooth and mandible ramus were rescued. The M3 were not preserved, but data on the upper tooth fragments, allowing estimation of crown width and lamellar frequency, were obtained directly during excavations. The distal fragment of m2 and a fragment of m3 (from plate 5 to plate 8) were collected. However, photos of some elements that were destroyed were taken by the quarry operator, and kindly shared with the authors. All the bones removed from the pit were preserved and restored. The skeleton is currently stored in the Stavropol Museum of Natural History (Prozritelev and Prave State Stavropol Historical, Cultural, Natural and Landscapes Museum-Preserve). The specimen number is BX 2120.

The following parts and fragments of the skull and lower jaw were discovered: fragment of m3 sin (BX 2120/55), fragment of m2 sin (BX 2120/56), fragments of the tusks (BX 2120/57 sin, BX 2120/58 dex), fragment of the right mandibular ramus (BX 2120/60).

The postcranial skeleton of the *Archidiskodon* from the Rodionovo locality is represented by long bones, one scapula and the complete pelvis: humeri (BX 2120/5 sin, BX 2120/6 dex); ulna (BX 2120/7 dex); radii (BX 2120/8 sin, BX 2120/9 dex); femora (BX 2120/14 sin, BX 2120/15 dex); tibiae (BX 2120/10 dex, BX 2120/11 sin); fibulae (BX 2120/12 sin, BX 2120/13 dex); scapulae (BX 2120/16 sin, BX 2120/17 dex); complete pelvis (BX 2120/59).

Vertebrae are preserved as follows: Cervical vertebrae: 2nd (epistropheus) (BX 2120/4), 3rd (BX 2120/1), 4th (BX 2120/2), 6th (BX 2120/5/1), and 7th (BX 2120/3). Thoracic vertebrae: 1st (BX 2120/26), 2nd (BX 2120/25), 3rd (BX 2120/27), 4th (BX 2120/28), 5th (BX 2120/29), 6th (BX 2120/30), 17th (BX 2120/31), 18th (BX 2120/32), 19th (BX 2120/33), and 20th (BX 2120/34). Lumbar vertebrae: 2nd (BX 2120/18/1) and 4th (BX 2120/18/2, fused to sacrum). Sacrum (BX 2120/18). First caudal vertebra (BX 2120/18/3, fused to the sacrum).

Ribs are preserved as follows: Left ribs: 1st (BX 2120/35), 3rd (BX 2120/36), 4th (BX 2120/37), 5th (BX 2120/38), 7th (BX 2120/39), distal fragment of 15–18th rib (BX 2120/40). Right ribs: 2nd (BX 2120/41), 3rd (BX 2120/42, fragment), 5th (BX 2120/43), 6th (BX 2120/44), 7th (BX 2120/45), 8th (BX 2120/46), 9th (BX 2120/47), 10th (BX 2120/48), 11th (BX 2120/49), 14th (BX 2120/50), 15th (BX 2120/51), 16th (BX 2120/52), 17th (BX 2120/53), and heads of the 12th or 13th ribs (BX 2120/54).

Foot bones preserved are: calcaneum (BX 2120/19 dex), astragalus (BX 2120/20 dex), central cuneiform (BX 2120/21 dex), lateral cuneiform (BX 2120/23 dex), and capitatum (BX 2120/24), metatarsal V (BX 2120/22 dex).

Measurements are given in millimeters and were taken with calipers and tape measure. The measurements follow Garutt (1954) with some modifications (Maschenko, 2002). The bone nomenclature follows Garutt (1954). Bones that could not be precisely measured had their lengths estimated to within 1.5 cm. The abbreviations M3 and m3 indicate the upper and lower molars, respectively. The size of the M3 was estimated from highly damaged tooth fragments to within 5 mm. Measurement of teeth

Table 2
Tusk measurements (in mm) of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965) and Nogaisk (Garutt, 1954) sites.

Locality, side (sin/dex), and catalogue number	Length: Lateral curvilinear/chord (straight line from tip to base on medial side)	Maximum transversal (mediolateral) and dorsoventral diameters	Length of alveolar part of tusk	Transverse diameters at the alveolar edge
Rodionovo locality. BX 2120/57, sin.	2050/1700	216.0/184.0	~290.0	210.0/240.0
Georgievsk locality. SM 14120, sin	3200/–	300.0/238.0	–	–
Nogaisk locality ZIN 24239, dex	>1940/–	207.0/138.0	–	198.8/177.0

Table 3
Humerus measurements of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965; Garutt, 1998b) and Nogaisk sites (Garutt, 1954).

Measurements, mm	Rodionovo locality Humerus BX 2120/5, dex	Georgievsk locality Humerus SM 14120/1, sin	Nogaisk locality Humerus ZIN 24239
Greatest length	1260.0	1225.0	1292.0
Length (medial side) from top of *caput humeri* to distal end	–	–	1270.0
Mediolateral/anteroposterior diameters of distal end of diaphysis	353.0/238.0	334.0/250.0	312.0/232.0
Mediolateral/anteroposterior diameters of proximal end of diaphysis	–/257.0	335.0/380.0 (estimation)	–
Smallest mediolateral/anteroposterior diameters of diaphysis	133.0/128.0	165.0/147.0	135.0/-
Width of *trochlea humeri*	287.0	290.0	–
Anteroposterior diameter of lateral/medial edge of *trochlea humeri*	183.0/218.0	205.0/240.0	–
Width/transversal diameter/height of *caput humeri*	235.0/–/143.0 (estimation)	–	302.0/–/–
Height/width of diaphysis at the level of upper edge of the *crista epicondylus lateralis*	435.0/225.0	415.0/–	–

was made by the method of Garutt and Foronova (1976). This differs from the scheme of Maglio (1973) in regarding talons as complete lamellae and including them in the plate count. Measurements of the teeth, long bones, scapula, pelvis, vertebrae and ribs are given in Tables 1–18. Determination of the body/skeletal height follows the method suggested by Garutt (1954) and the formula developed for recent elephants (Lang, 1980).

5. Description of the skeleton

5.1. Dentition

Fragments of m3 sin (BX 2120/55) and m2 sin (BX 2120/56) (Fig. 3a and b) were recovered. A photograph of the mandible *in situ*, showing that the lower molar m3 had more than 12 lamellae (including talons), was taken by the tractor operator. The first lamella was possibly worn away, and the mandibular alveolus possibly covered a posterior lamella. The total number of lamellae present on the third molars (including talons) may have been 13 or 14 (11 or 12 excluding talons).

Data obtained from the studied fragments of M3/m3 are presented in Table 1. These include the following estimated values: crown width 98.9/89.5 mm; number of plates : ~14–15/13–14 including talons (equivalent to ~12–13/11–12 excluding talons); enamel thickness: -/3.5 mm; plate height: ca -/140.0 mm (m3).; lamellar (plate) frequency: 4.7/4.5. The quoted m3 plate height is the height of a weakly worn isolated plate (number 6–8), with worn cement in the apical part, and two separated ovals formed by wear. The m3 of the *Archidiskodon* from Georgievsk have similar values (Table 1).

5.2. Tusks

Proximal fragments of the left (BX 2120/57) and right (BX 2120/58) tusks (Fig. 3C) were recovered. Maximum length of each tusk fragment is about 1000 mm. Length of the right tusk, estimated during excavation of the *in situ* specimen, is 2050.0 mm (Table 2). Maximum transversal diameter of the tusk is 216.0 mm. Maximum transversal diameter of the distal end of the premaxillae is 650.0 mm. Distance between medial surfaces of the left and right tusks in life position, at the distal ends of the premaxillae, is estimated to have been 176.0 mm.

The length of the tusk of the Rodionovo specimen is significantly smaller than tusks from the Georgievsk specimen (transversal diameter 300 mm, length along major curvature 3200 mm). Based on available data, the Georgievsk specimen has the largest tusk sizes among currently known specimens from the Northern Caucasus and Italy. The maximum transverse diameter of the Rodionovo specimen falls within the range of variation for *A. meridionalis* specimens. For *A. m. meridionalis,* Azzaroli (1977) reports the transversal diameter of tusks as 190–240 mm. For the tusks of female *A. m. tamanensis* the corresponding value is reported as 90–100 mm (Dubrovo, 1964). Such a difference is evidence of substantial sexual dimorphism in this character in *A. meridionalis*.

5.3. Limb bones

The long bones of *Archidiskodon*, *Mammuthus* and recent elephants are characterized by a relatively poor development of surface relief for the main muscle attachments (Garutt, 1954). In comparison with *Mammuthus primigenius*, *A. meridionalis* has larger surfaces for the main muscle attachments, due to its larger body size.

5.3.1. Scapula

The Rodionovo shoulder blade is very tall and relatively narrow in comparison with the specimens from Georgievsk and Nogaisk, and also in comparison with *M. primigenius*. Estimated full length with unfused proximal epiphysis is 1103.0 mm. Unfused proximal epiphysis of right scapula (BX 2120/17) has maximum height of 133.0 mm; its maximum transverse diameter is 105.0 mm (Table 6). The specimens from Rodionovo and Georgievsk differ from the Nogaisk specimen by their broad, more robust glenoid facet. These differences obviously reflect individual variation between the specimens and the rather larger size of the Nogaisk skeleton.

Table 4
Ulna measurements of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965; Garutt, 1998b) and Nogaisk sites (Garutt, 1954).

Measurements, mm	Rodionovo locality Ulna BX 2120/7, dex	Georgievsk locality Ulna SM 14120/2 dex	Nogaisk locality Ulna ZIN 24239
Greatest length	1075.0	1100.0	–
Length from proximal articulation surface to distal edge of diaphysis	910.0	885.0	1100.0
Length/mediolateral diameter of diaphysis at the level of articular surface	290.0/345.0	290.0/305.0	312.0/–
Mediolateral/anteroposterior diameters of distal end of diaphysis	225.0/200.0	~215.0.0/225.0	220.0/270.0
Smallest mediolateral/anteroposterior diameters of diaphysis	138.0/134.0	130.0	145.0/–
Width/diameter of *olecranon* (from anterior edge of articulation facet to *olecranon* apex)	293.0/260.0	244.0/247.0	–

Table 5
Radius measurements of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965; Garutt, 1998b) and Nogaisk sites (Garutt, 1954).

Measurements, mm	Rodionovo locality Radius BX 2120/8, sin	Georgievsk locality Radius SM 14120/3	Nogaisk locality Radius ZIN 24239
Greatest length	945.0;815.0 (diaphysis length)	956.0	1040.0
Mediolateral/anteroposterior diameters of distal end of diaphysis	144.0/84.0	210.0/188.0	164.0/–
Mediolateral/anteroposterior diameters of proximal end of diaphysis	173.0/165.0	–/127.0	213.0/–
Smallest transversal diameters of diaphysis	72.0/43.0	43.0/71.0	–/68.0

Table 6
Scapula measurements of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965; Garutt, 1998b) and Nogaisk sites (Garutt, 1954).

Measurements, mm	Rodionovo locality Scapula BX 2120/16, sin	Georgievsk locality Scapula SM 14120/4, sin	Nogaisk locality Scapula ZIN 24239, sin
Length from middle point of *glenoid fossa* to top of proximal epiphysis/greatest width	970.0 (without proximal epiphysis)/675.0 (estimation)	~1040.0/–	1155.0
Length of *margo frontalis*	~770.0	740.0	–
Length of *margo superior*	760.0	~735.0	980.0
Length of *margo posterior*	540.0	530.0 (estimation)	705.0
Transversal diameter of *collum scapulae*	292.0	328.0	330.0
Width/length of *glenoid fossa*	135.0/235.0	140.0/270.0	169.0/270.0
Length of *spinae scapulae*	880.0	820.0	–

5.3.2. Humerus

BX 2120/5 sin, BX 2120/6 dex (Fig. 4a and b; Table 3). Distal and proximal epiphyses are completely fused, suture lines obliterated. The specimen from Rodionovo has a relatively low *caput humeri*. The transversal diameter of the proximal end of the humerus shaft is equal to the width of the shaft at the level of the upper edge of *epicondylus lateralis*. The position of *epicondylus lateralis* is almost at the level of the median line of the diaphysis. *Crista deltoidea* is high and laterally curved. The diaphysis length and transversal diameters of the proximal and distal ends of the humerus appear to be similar in the elephants from all three localities: Rodionovo, Nogaisk, and Georgievsk.

5.3.3. Ulna

BX 2120/7 sin (Fig. 4c and d; Table 4). The distal epiphysis is fused, with the epiphysis suture visible. The epiphysis of the *tuber olecrani* is completely fused and its epiphysis suture is obliterated. The diaphysis is slightly curved. The proximal end of the ulna is more massive than the ulna of the Georgievsk specimen, but smaller than the ulna from the Nogaisk locality. These differences in ulna proportions demonstrate the variation of size in males of *A. meridionalis* from the Northern Caucasus and Ukraine populations. The ratio of length of the humerus to that of the ulna, in specimens from the Rodionovo and Georgievsk sites, are 1.17 and 1.12 respectively, which is characteristic of male specimens of elephant and mammoth (Maschenko, 2006).

5.3.4. Radius

Radius. BX 2120/8 sin, BX 2120/9 dex (Fig. 4e and f; Table 5). The proximal end of the left radius is damaged. All measurements of the proximal radius end were therefore taken from the right radius. The distal epiphyses are completely ossified, but unfused. Transverse sections of the proximal end are significantly enlarged in the lateral–medial plane and rounded. The shaft of the radius bends anteriorly and is twisted to fit the shape of the ulna. In this character the specimen from Rodionovo differs from the *Archidiskodon* from Georgievsk. The radius is articulated with the ulna by the medial facet on its distal end (Fig. 4e). Vertical crests developed on the proximal end of the radius (Fig. 4f) indicate the presence of strong ligaments between its proximal end and the ulna.

5.3.5. Femur

BX 2120/14 sin, BX 2120/15 dex (Fig. 5a and b; Table 7). All the epiphyses of the Rodionovo femur, including the epiphyses of the *trochanter major*, are completely fused, and the suture lines are obliterated. A well-developed crest for attachment of *musculus biceps femoris* on the distolateral part of the diaphysis is present. The relief and crest for the attachment of *musculus vastus* are moderate. The individuals from the Rodionovo, Georgievsk, and Nogaisk localities all have similar proportions of the femur. The specimen from Rodionovo differs in a lower position of the *trochanter major* and in having a relatively gracile diaphysis of the femur, in comparison with the *A. meridionalis* from the Georgievsk locality.

Table 7
Femur measurements of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965; Garutt, 1998b) and Nogaisk sites (Garutt, 1954).

Measurements, mm	Rodionovo locality Femur BX 2120/14, sin	Georgievsk locality Femur SM 14120/5	Nogaisk locality Femur ZIN 24239
Greatest length	1440.0	1430.0	1460.0
Length to *trochanter major*	1335.0	1310.0	–
Smallest anteroposterior/mediolateral diameters of distal end of diaphysis	112.0/200.0	185.0/212.0	133.0/207.0
Mediolateral/anteroposterior diameters of distal end of diaphysis	288.0/303.0	288.0/280.0	320.0/295.0
Anteroposterior diameters of medial/lateral condyles on distal end	308.0/231.0	127.0/308.0 (estimation)	–
Width of patellar facet	134.0	119.0	–
Mediolateral/anteroposterior diameter of proximal part of diaphysis under the *caput femoris*	405.0	420.0/180.0	–
Diameter of *collum femoris*	193.0	195.0	182.0
Caput femoris transversal/longitudinal diameters	203.0/196.0	226.0/–	210.0/–

Table 8
Tibia measurements of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk and Nogaisk (Garutt and Safronov, 1965; Garutt, 1998b) sites (Garutt, 1954).

Measurements, mm	Rodionovo locality Tibia BX 2120/11, sin	Georgievsk locality Tibia SM 14120/11 sin	Nogaisk locality Tibia ZIN 24239
Length at lateral side/greatest length of diaphysis	800.0/850.0	820.0/-	980.0 (estimation)
Mediolateral/anteroposterior diameter of proximal end of diaphysis	283.0/236.0	–	340.0/228.0
Mediolateral/anteroposterior diameter of distal end of diaphysis	238.0/191.0	130.0/–	198.0/210.0
Smallest transversal/anteroposterior diameters of diaphysis	122.0/104.0	–	135.0/127.0
Max height/width of *tuberositas* on tibia	230.0/150.0	–	–

Table 9
Fibula measurements of *Archidiskodon meridionalis* from the Rodionovo, Georgievsk (Garutt and Safronov, 1965; Garutt, 1998b) and Nogaisk sites (Garutt, 1954).

Measurements, mm	Rodionovo locality Fibula BX 2120/12, dex	Georgievsk locality Fibula SM 14120/11, dex	Nogaisk locality Fibula ZIN 24239
Greatest length	823.0	810.0	901.0 (estimation)
Mediolateral/anteroposterior diameters of proximal end of diaphysis	68.0/48.0	–	–
Mediolateral/anteroposterior diameters of distal end of diaphysis	135.0/72.0	138.0/–	154.0/–
Smallest mediolateral/anteroposteriors diameter of diaphyses	47.0/23.0	–	–

5.3.6. Tibiae

BX 2120/10 dex, BX 2120/11 sin (Fig. 5c, d and j; Table 8). The proximal and distal epiphyses are completely fused on both bones. The suture lines of the proximal epiphyses are obliterated, while the suture lines of the distal epiphyses are visible. The length of the tibiae from Rodionovo and Georgievsk is smaller than in the Nogaisk specimen. Interestingly, the specimens from Rodionovo and Georgievsk have a more massive proximal part of tibia than the *A. meridionalis* from Nogaisk, which otherwise has very massive bones. Two *foramina nutritia*, 10.5 mm and 9.5 mm in diameter, are located in a cavity 22.0–61.0 mm in size in the middle part of the diaphysis on its anterior-lateral surface, 380 mm from the proximal end of left tibia (Fig. 5j). The tibiae from the Georgievsk have the similar enlarged *foramina nutritia* (Fig. 5k).

5.3.7. Fibulae

BX 2120/12 dex, BX 2120/13 sin (Fig. 5e, f and g; Table 9). The proximal and distal epiphyses are fused. The suture lines of the distal epiphyses are completely obliterated, while the suture lines of the proximal epiphyses are visible in some places. The distal end of the fibula BX 2120/13 sin (Fig. 5g) indicates life damage or abnormal bone development; the medial surface of the lower part of the diaphysis has an oval-shaped cavity 68 mm wide and 90 mm long that reduces the thickness of the shaft to 10–15 mm.

Table 10
Pelvis measurements of *Archidiskodon meridionalis* from the Rodionovo and Georgievsk sites.

Measurements, mm	Rodionovo locality Pelvis BX 2120/59	Georgievsk locality Pelvis SM 14210/15
Length of symphysis	580.0	520.0
Vertical/horizontal diameters of acetabulum	228.0/222.0	198.0/182.0
Vertical/horizontal diameters of *foramen obturatum* (pelvic aperture)	267.0/133.0	263.0/125.0
Length of ilium	990.0	1050.0
Smallest diameter of ischium	240.0	227.0
Greatest length from middle point of lateral edge of ilium to middle point of pubis edge	1370.0	1145.0
Distance between the right and left *tuber coxae*	1620.0	1680.0
Smallest width of ilium	610.0	525.0
Length of pubis (along posterior side)	–	363.0

5.3.8. Pelvis

BX 2120/59 (Fig. 6; Table 10). The innominate bones were found in articulated condition. The iliar bones are relatively short and broad with rounded *tuber coxae*, fused apophyses and pronounced suture lines. The acetabulum diameter is 225.0 mm and is similar in size to the Nogaisk specimen (Table 10), and only minimally different in size from the *A. meridionalis* from Georgievsk. The elephants from Rodionovo and Georgievsk show the same distance between the right and left *tuber coxae* of the pelvis.

5.4. Columna vertebralis

The degree of epiphysis formation, fusion of epiphyses to *corpus vertebrae*, and ossification and fusion of the *processus transversus* and *processus spinosus* apophyses, are valuable features indicating animal gender and maturity of both sexes (Maschenko, 2006). Significant features in the Rodionovo specimen include the stage of formation of the vertebral body in the cervicals, the degree of ossification of the *foramen transversarium*, and the shape and ossification of the pleuropophyses. Other features, including

Table 11
Epistropheus (Axis) measurements of *Archidiskodon meridionalis* from the Rodionovo and Nogaisk (Garutt, 1954) sites.

Measurements, mm	Rodionovo locality Epistropheus BX 2120/4	Nogaisk locality Epistropheus ZIN 24239
Greatest height	–	350.0
Greatest width/anteroposterior diameter	–/147.0	–
Height/width of anterior articulation facets	261.0/110.0	259.0/–
Height/width of posterior articulation facets	154.0/185.0	–
Height/width of foramen vertebrae	–/78.0	77.0/67.0
Mediocaudal/anteroposterior diameters of spinal process	–	–/146.0
Height of *corpus vertebrae*/neural arch	–	–
Anteroposterior/mediolateral diameter of *pedunculus arcus ventralis*	–	–
Vertical/horizontal diameter of *foramen transversarium*	48.0/–	–
Anteroposterior diameter of the *pleuropophysis*	340.0	–

Table 12
Cervical vertebrae (3rd – 7th) measurements of the skeleton of *Archidiskodon meridionalis* from the Rodionovo locality.

Measurements, mm	Diameter between pleuropophyses /max height of vertebra	*Corpus vertebra* Length/height/ width	Length of *processus spinosus* (from foramen vertebra)/greatest height of vertebra	Width/anteroposterior diameter of neural arch (at prezygapophysis)	Height of neural arch (from base of *processus spinosus* to upper surface of corpus vertebra)/width of neural arch (at lateral surfaces of *pedunculus arcus ventralis*)	Height/ width of vertebral foramen	Vertical/ horizontal diameter of *foramen transversarium*
3rd, BX 2120/1	375.0/245.0	50.0/161.0/198.0	123.0/245.0	210.0/91.0	74.0/210.0	64.0/102.0	54.0/41.0
4th, BX 2120/2	348.0/– (lacking apophysis transversal processes)	50.0/171.0/193.0	–	210.0/91.0	84.0/	82.0/108.0	56.0/45.0
7th, BX 2120/3	–/273.0	50.0/171.0/192.0	–/273.0	238.0/99.0	105.0/213.0	89.0/112.0	–/46.0

Table 13
Thoracic vertebra measurements of the skeleton of *Archidiskodon meridionalis* from the Rodionovo locality.

Measurements, mm	1st, BX 2120/ 26	2nd, BX 2120/25	3rd, BX 2120/ 26	4th, BX 2120/28	5th, BX 2120/29	6th, BX 2120/30	17th, BX 2120/31	18th, BX 2120/32	19th, BX 2120/33
Length/height/ width of *corpus vertebrae*	163.0/150.0/ 79.0	146.25/162.0/ 79.0	161.0/137.0/ 81.0	143.0 (estimation) /135.0/82.0	158.0/129.0/ 78.0	147.0/116.0/ 75.0	131.0/133.0/ 93. 0	–/137.0/93.0	153.0/117.0/ 86.0
Maximal width (at lateral edges of transversal processes)	364.0 (estimation)	400.0	350.0	338.0	330.0	316.0 (estimation)	243.0	235.0	–
Greatest height of vertebra	–	700.0	675.0 (without apophysis of spinal process)	655.0 (without apophysis of spinal process)	–	–	–	–	–
Height/width of *foramen vertebrae*	73.0/82.0	87.0/89.0	58.0/76.0	44.0/84.0	–/72.0 (estimation)	54.0/75.0	54.0/53.0	–	~38.0/71.0
Length/width of base of spinal process	–/150.0	484.0/185.0	513.0/127.0 (without apophysis of spinal process)	525.0/134.0 (without apophysis of spinal process)	470.0/103.0 (estimation)	-/87.0	-/102.0	–	–/107.0 (estimation)
Lateromedial diameter of neural arch (between lateral surfaces of *pedunculus arcus ventralis*)	~184.0	~198.0	~178.0	~168.0	~161.0	202.0	175.0	165.0	158.0
Length/anteroposterior diameter of transverse processes (measured at lateral wall of *canalis vertebrae*)	152.0/74.0	147.0/77.0	140.0/70.0	127.0/67.0	125.0/70. 0	133.0/72.0	124.0/89.0	–/93.0	–/90.0
Anteroposterior diameter of *pedunculus arcus ventralis*	47.0	47.0	77.0	57.0	65.0	64.5	93.0	74.0	–

development of ridges and tuberosities on the neural arch, and the great length of the *processus spinosus*, are characteristics of individual variation within the species. Only the third cervical vertebra of the specimen has completely ossified pleuropophyses and completely fused apophyses. The walls of the *foramen transversarium* are completely ossified in the second and third cervical vertebrae; the walls of the fourth and seventh cervical vertebrae are not ossified.

Similarly to other elephantid species, *A. meridionalis* is characterized by an increase of the vertical, transverse, and cranial-caudal diameters of *corpus vertebrae* from the third to the seventh cervical vertebrae. From the first to last thoracic vertebrae the height of the *corpus vertebrae* increases while the transverse diameter decreases.

5.4.1. Axis (Epistropheus) C2

BX 2120/4 (Fig. 7a; Table 11). *Corpus vertebrae* relatively long with a massive ventral edge. Caudal epiphysis of *corpus vertebrae*

Table 14
Lumbar vertebra measurements of the skeleton of *Archidiskodon meridionalis* from the Rodionovo locality.

Measurements, mm	4th Lumbar BX 2120/18/1
Length/height/width of centrum (*corpus vertebra)*	135.0/185.0/91.0
Greatest width (between lateral edges of transverse processes)	281.0
Greatest height of vertebra	216.0
Height/width of vertebral foramen	53.0/94.0
Length/width of base of spinal process	108.0/–
Lateromedial diameter of neural arch (on lateral surface of *pedunculus arcus ventralis*)	–
Length/anteroposterior diameter of transverse process (from lateral wall of vertebral foramen)	–
Anteroposterior diameter of *pedunculus arcus nevralis*	~64.0

Table 15
Sacrum measurements of the skeleton of *Archidiskodon meridionalis* from the Rodionovo locality.

Measurements, mm	BX 2120/18
Greatest length (fused 1st–4th sacral vertebrae)	410.0
Greatest height/width of 1st sacral vertebra	197.0/270.0
Greatest height/width of 4th sacral vertebra	137.0/170.0 (estimation)
Greatest length/height of sacrum	192.0/247.0
Total length of fused 4th lumbar, sacrum, and 1st caudal vertebra	600.0

Table 16
Rib measurements of the skeleton of *Archidiskodon meridionalis* from the Rodionovo locality.

Collection number, rib number, side	Length: Lateral curvilinear/ chord (straight line)	Longitudinal/ transverse diameters of rib head	Longitudinal/transverse diameters of *collum costae*	Longitudinal/transvere diameters of *corpus costae* in middle part	Longitudinal/transverse diameters of distal end
BX 2120/35, 1st, sin	800.0/61.5 (estimation)	81.0/81.0	65.0/42.0	86.0/36.0	161.0/63.0
BX 2120/36, 3rd, sin	1010.0/810.0 (estimation)	83.0/77.0	80.0/62.0	75.0/25.0	–
BX 2120/37, 4th, sin	1190.0/997.0	81.0/84.0	81.0/54.0	76.0/36.0	70.0/43.0
BX 2120/38, 5th, sin	1290.0/985.0 (estimation)	–	87.0/34.0 (estimation)	76.0/35.0	–
BX 2120/39, 8th, sin	1405.0/1115.0 (estimation)	–	85.5/29.5	76.5/23.0	-/31.0
BX 2120/40, 15th–(?)18th, sin	–	–	–	49.0/23.0	–
BX 2120/41, second, dex	837.0/800.0	–	85.5/29.5	76.5/23.5	–/31.0
BX 2120/42, 3rd, dex	–	–	–	–	–
BX 2120/43, 5th, dex	1290.0/993.0	–	78.0/46.0	78.0/27.0	74.0/40.0
BX 2120/44, 6th, dex	1370.0/1080.0	71.0/78.0	62.0/43.0	68.0/31.0	72.0/33.0
BX 2120/45, 7th, dex (fragment)	–/1070.0 (length of preserved part of rib	–	–	57.0/37.0	70.0/29.0
BX 2120/46, 8th, dex	1390.0/1050.0	64.0/67.0	41.0/47.0	52.0/40.0	58.0/34.0
BX 2120/47, 9-th, dex	1345.0/1015.0	–	41.0/41.0	47.0/39.0	62.0/26.0
BX 2120/48, 10th, dex	1325.0/943.0	65.0/57.0	47.0/36.0	44.0/42.0	61.0/22.0 (estimation)
BX 2120/49, 11th, dex	–	–	35.0/42.0	40.0/38.0	68.0/31.0
BX 2120/54, 12–(?)13th (head of rib only preserved)	–	77.0/72.0	–	–	–
BX 2120/50, 14th, dex	1085.0/885.0	–	41.0/35.0	35.0/45.0	68.0/27.0
BX 2120/51, 15th, dex	900.0/810.0	–	43.0/31.0	48.0/30.0	–/18.0
BX 2120/52, 16th, dex	910.0/760.0 (estimation)	–	50.0/30.0	46.0/28.0	45.0/27.0
BX 2120/53, 17th, dex	740.0/680.0	–	41.0/28.0	47.0/18.0	32.0/14.5

completely fused, suture obliterated. Ventral wall of vertebral foramen asymmetrical and significantly narrowed on the right side, reducing the area of the spinal cord to 2/3 of its normal volume. Ventral side of the *corpus vertebrae* shows bony projection.

5.4.2. *Cervical vertebrae C3–C7*

(C3-BX 2120/14; C4- BX 2120/2; C7- BX 2120/3) (Fig. 7b, c and d; Table 12). All the recovered cervical vertebrae have *corpus vertebrae* with completely fused cranial epiphysis and unfused (and missing) caudal epiphysis. Height of the neural arch and size of the vertebral canal increase from third to seventh vertebrae. Size of transverse canal increases slightly from second to seventh cervical vertebrae. Pleuropophysis apophyses completely fused in C3 and not fused in C4 and C7. In C7, pleuropophysis ossification less advanced than on C3 and C4. Walls of transverse canal completely ossified in C3 and not ossified in C4 and C7.

5.4.3. *Thoracic vertebrae*

T1–T6, T17-T20 (T1 - BX 2120/26, T2 - BX 2120/25, T3 - BX 2120/27, T4 - BX 2120/28, T5 - BX 2120/29, T6 - BX 2120/30, T17 - BX 2120/31, T18 - BX 2120/32, T19 - BX 2120/33, T20 - BX 2120/33). (Fig. 7g and j; Table 13). The estimated number of thoracic vertebrae in the skeleton from Rodionovo is 20. According to Garutt (1954), the specimen of *A. meridionalis* from the Nogaisk locality has 19 thoracic vertebrae. Ten thoracic vertebrae are preserved in the skeleton from Georgievsk (Garutt, 1998b). For the material from the Upper Valdarno Azzaroli (1977) reports 19 thoracic vertebrae in two female skeletons and one male.

The first to fourth thoracic vertebrae at Rodionovo have long and large spinal processes with particularly robust apophyses. The length of the spinal process increases from first to third thoracic vertebra and gradually decreases towards the last thoracic vertebra.

The apophyses are completely fused to the top of the *processus spinosus*, with pronounced suture lines. The first and second vertebrae have cranial and caudal epiphysis of *corpus vertebrae* completely fused, with suture lines obliterated. Other vertebrae show suture lines, some with vertebral epiphyses separated from *corpus vertebrae*. The apophyses of *processus transversus* are completely fused, with sutures lines obliterated. The first to seventeenth thoracic vertebrae preserve two costal facets laterally on both sides of the *corpus vertebra*. The eighteenth to twentieth vertebrae show only one costal facet.

Table 17
Calcaneus measurements of the skeleton of *Archidiskodon meridionalis* from the Rodionovo locality.

Measurements, mm	BX 2120/19, dex
Greatest length	276.0
Greatest width/height	185.0/166.0
Width/height of calcaneus process	119.0/175.0
Length of the calcaneus process	145.0
Length/width of lateral facet	137.0/188.0
Length/width of medial facet	118.0/59.0

Table 18
Astragalus measurements (in mm) of *Archidiskodon meridionalis* from the Rodionovo locality.

Catalogue #, side	Greatest width	Greatest length	Greatest height	Width/anteroposteior diameter of *trochlea humeri*	Length/width of medial facet	Length/width of lateral facet
BX 2120/20, dex	199.0	164.0	119.0	162.0/146.0	111.0/54.0	126.0/89.0

5.4.4. Sacrum

BX 2120/18 (Fig. 7e and f; Table 15) is composed of six fused vertebrae: four sacral vertebrae and two additionally fused vertebrae. One unique feature of this specimen of *Archidiskodon* is the complete fusion of the fourth lumbar vertebra (BX N 2120/18/1) and first caudal vertebrae (BX N 2120/18/2) to the sacrum. Suture lines are obliterated on the dorsal surface of the sacral vertebrae, but are visible on ventral surface of sacrum. *Processus trasversus* of the 4th lumbar and 1st caudal vertebrae is completely fused to sacrum. The cranial vertebral plate of the 4th lumbar vertebra is fused to the centrum, with suture line present.

According to Garutt (1954), the sacrum of *Archidiskodon* from the Nogaisk locality consists of five vertebrae. Its length is 498.0 mm and the maximum transversal diameter (across the first sacral vertebra) is 324.0 mm. The length and width of the first sacral vertebra of *Archidiskodon* from the Nogaisk locality are 129.0 and 216.0 mm respectively. Differences in size and morphology of the sacra from Rodionovo (Table 15) and Nogaisk are insignificant. The total number of sacral vertebrae in the skeleton from Georgievsk is not known (Garutt, 1998b). According to Azzaroli (1977), the sacrum of the male *A. meridionalis* from Scoppito includes five vertebrae; the same number is reported for the two female skeletons from the Upper Valdarno. The male skeleton from the Upper Valdarno has four sacral vertebrae.

Caudal vertebra, Ca1, BX 2120/18/2. Height of centrum cranial surface 59.0 mm, height of caudal surface 56.0 mm, maximum transversal diameter of centrum at its cranial surface 93.0 mm, maximum width of vertebra 180.0 mm.

5.5. Ribs

(Fig. 8; Table 16) The total number of ribs in *Archidiskodon* is relatively stable and typically numbers 19–20 (Garutt, 1954, 1998b; Azzaroli, 1977). In the genus *Mammuthus* (*M. primigenius*), the number of rib pairs sometimes reaches 22 (Maschenko, 2002). In the skeleton from Rodionovo, only an incomplete set of ribs was recovered: six left and 14 right ribs. The morphology of the thoracic vertebrae gives good evidence that the animal had 20 pairs of ribs.

The stage of development of the *incisura costales* of the sternum bones of the *Archidiskodon* from the Nogaisk locality indicates that the first three rib pairs were fused directly to the sternum and did not have any traces of cartilage inserts. The latter were possibly present within the fourth to 14th/15th pairs of ribs.

The sternum of the *Archidiskodon* from Rodionovo is missing, but the morphology of the distal parts of the first three pairs of ribs (Fig. 8a, b and c) is similar to the specimen from Nogaisk. We therefore infer that these ribs were likewise fused directly to the sternum, and that there was no significant cartilage formation in the *incisurae costales* area of the sternum.

The morphology of first pair of ribs is similar in all elephants of the mammoth lineage, including both *A. meridionalis* and *M. primigenius*. The first rib is the only one that has two heads (caput costae). All the other ribs have only one head. The second rib has an enlarged *tuberculum costa*, but other ribs have only moderately developed *tuberculum costae*. Most of the ribs from the second to the 16th have their heads (*caput costae*) subdivided into two parts, due to their connection to two costal facets in the

Table 19
Metrics of M3/m3 molars of *Archidiskodon meridionalis meridionalis* from the Upper Valdarno, Italy, and from the Northern Caucasus and Ukraine, in comparison with *A. m. tamanensis* from the Northern Caucasus. Measurements are taken according to the methods described by Garutt and Foronova (1976). Measurements for M3 and m3 are separated by a slash.

Characters	M3/m3 *A. m. meridionalis* Upper Valdarno (a) Maglio, 1973; (b) Dubrovo, 1989; (c) Palombo and Ferretti, 2005	M3/m3 *A. m. meridionalis* Northern Caucasus and Ukraine (Garutt, 1954; Garutt and Safronov, 1965)	M3/m3 *A. m. tamanensis* Dubrovo, 1964, 1989
Number of plates, excluding talons	(a) 13–14/13 (b) 8–12/10–11 (c) 11–14/12–14	11–13/12(?)–13	10–15/10–15
Number of plates, including talons	(a) 15–16/15 (b) 10–14/12–13 (c) 13–16/14–16	13–15/14(?)–15	12–17/12–17
Lamellar frequency	(a) 4.2–5.9/– (b) 4.0–5.0/4–5.5 (c) 4.0–6.0/4.5–6.0	4.5–5.0/–	4.5–6.5/4.0–6.0
Plate height (max)	(a) 92.0–126.0/– (b) 113–150/114–136 (c) 101–160/91–140	~120.0/–	122–185/115–150
Enamel thickness	(a) 2.9–3.7/– (b) 3.0–4.0/3.0–4.0 (c) 2.6–39/2.4–3.7	3.0–4.0/3.0–3.6	2.5–3.5/2.5–4
Hypsodonty index	(a) 0.9–1.3/– (b) 1.2–1.3/1.3 (c) 1.1–1.6/1.2–1.3	~1.0/–	1.48–1.6/1.23–1.4

adjacent vertebrae. The rest of the ribs (from 17th to the last) have undivided *caput costae*.

The morphology of elephants' ribs is dictated by the increasing size of the rib cage in the caudal direction. It also defines the length of rib necks (*collum costae*) and the degree of curvature, which also gradually increases caudally from the 5th/6th to 17th rib (Fig. 8 f and g). All the recovered ribs of the Rodionovo specimen have the epiphyses of the *caput costae* completely fused and the suture lines obliterated. The length of the ribs of the Rodionovo specimen increases from the first to the eighth rib, and gradually decreases from the 11th (Table 16).

The length of the first rib of the *Archidiskodon* from the Nogaisk locality is 760.0 mm, and the width of distal end is 186.0 mm (Garutt, 1954), which doesn't differ significantly from the Rodionovo specimen (Table 16).

5.6. Foot bones

Only five foot bones were recovered, including the calcaneus (dex, BX 2120/19), astragalus (dex, BX 2120/20) (Tables 17, 18) and one carpal bone. None of the bones has any pathological changes.

5.6.1. Naviculare

(dex, BX 2120/21) has an anterior-posterior diameter of 128.0 mm, maximum transversal diameter (dorsal side) of 145.0 mm, maximum height on the dorsal side of 56.0 mm, and maximum height (plantar side) of 63.0 mm.

5.6.2. Cuneiforme laterale

(dex, BX 2120/23) has maximum length/width of 86.0/55.0 mm, and maximum height on dorsal side of 42.0 mm.

5.6.3. Carpale 3 (or Capitatum)

(dex, BX 2120/24) has a maximum anterior-posterior diameter of 156.0 mm, maximum transversal diameter of 121.0 mm, and dorsal/plantar heights of 98.0/132.0 mm. Transverse diameters of proximal facets on the dorsal/plantar sides are 122.0/120.0 mm; transverse diameters of distal facets on the dorsal/plantar sides are 103.0/81.0 mm.

5.6.4. Metatarsale V

(dex, BX 2120/22). Maximum height 106.0 mm, anterior-posterior (transversal) diameter of proximal end 87.0/74.0 mm, anterior-posterior (transversal) diameter of distal end 93.0/68.0 mm, maximum transversal diameter in the middle part of shaft 85.0 mm.

6. Discussion

Because of scarcity of material, accurate criteria for the determination of the individual age of *A. meridionalis* specimens based on tooth development, wear generation, succession and wear stages, are lacking. However, these data have been collected for modern elephants (Jachmann, 1988) and successfully applied for age determinations in *M. primigenius* (Maschenko, 2002), and *Mammuthus columbi* (Agenbroad, 1994).

The lower jaw of *A. meridionalis* from the Rodionovo locality has a distal fragment of deeply worn m2 in front of m3. The number of worn plates in m3 is 7 or 8. Of the upper jaw fragments only one partial tooth plate of M3 is preserved.

It appears that *M. primigenius* is characterized by a somewhat accelerated succession of premolar (DP2 – DP4) generations and also possibly by an accelerated succession of the molar (M1 – M3) generations, in comparison with recent elephants (Maschenko, 2002). Using an ageing criteria similar to that applied to *M. primigenius,* the age of the *A. meridionalis* individual from the Rodionovo locality should be between 28 and 32 years, though this may slightly underestimate the absolute age because *A. meridionalis* was a larger (and therefore possibly longer-lived) animal than living elephants or *M. primigenius*.

Based on the diameter of the tusk cross-section (216 mm), pattern of tooth replacement, average size of long limb bones and degree of their fusion with the epiphyses, we believe that the *A. meridionalis* from Rodionovo may unambiguously be identified

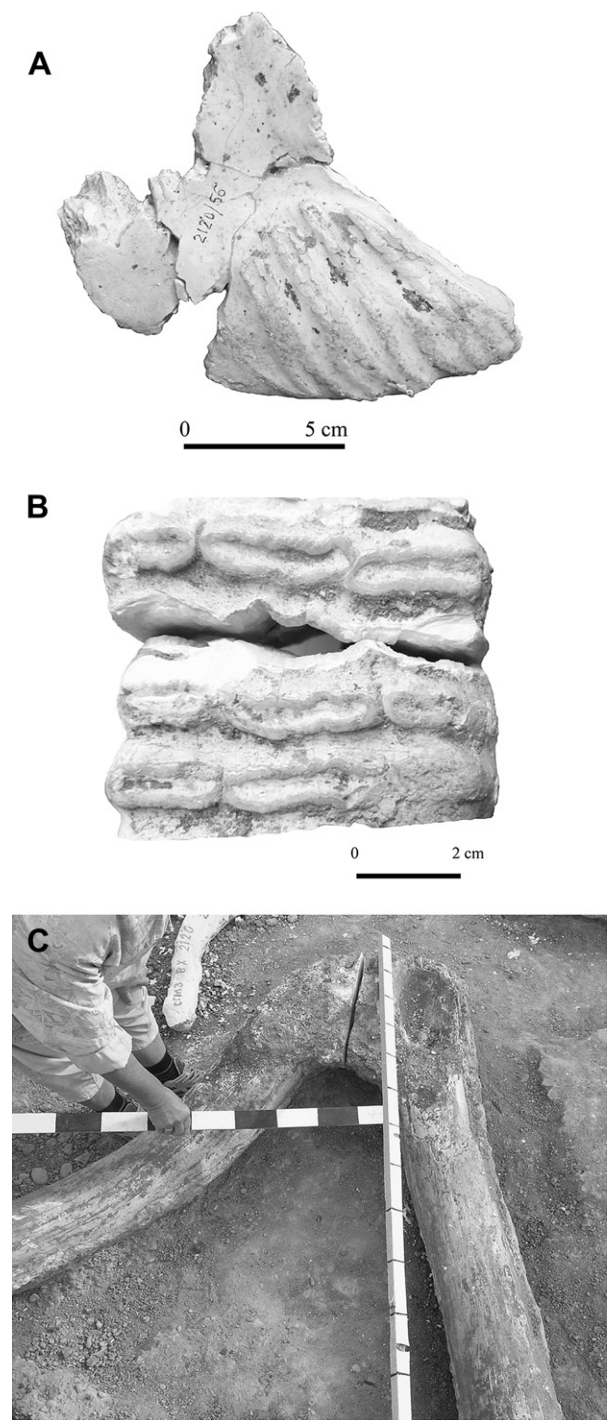

Fig. 3. Molars. A – The fragment of distal part of the m2 sin (BX 2120/56), occlusal view. B – The fragment of the m3 sin (BX 2120/55), occlusal view. C – Permanent tusks "*in situ*".

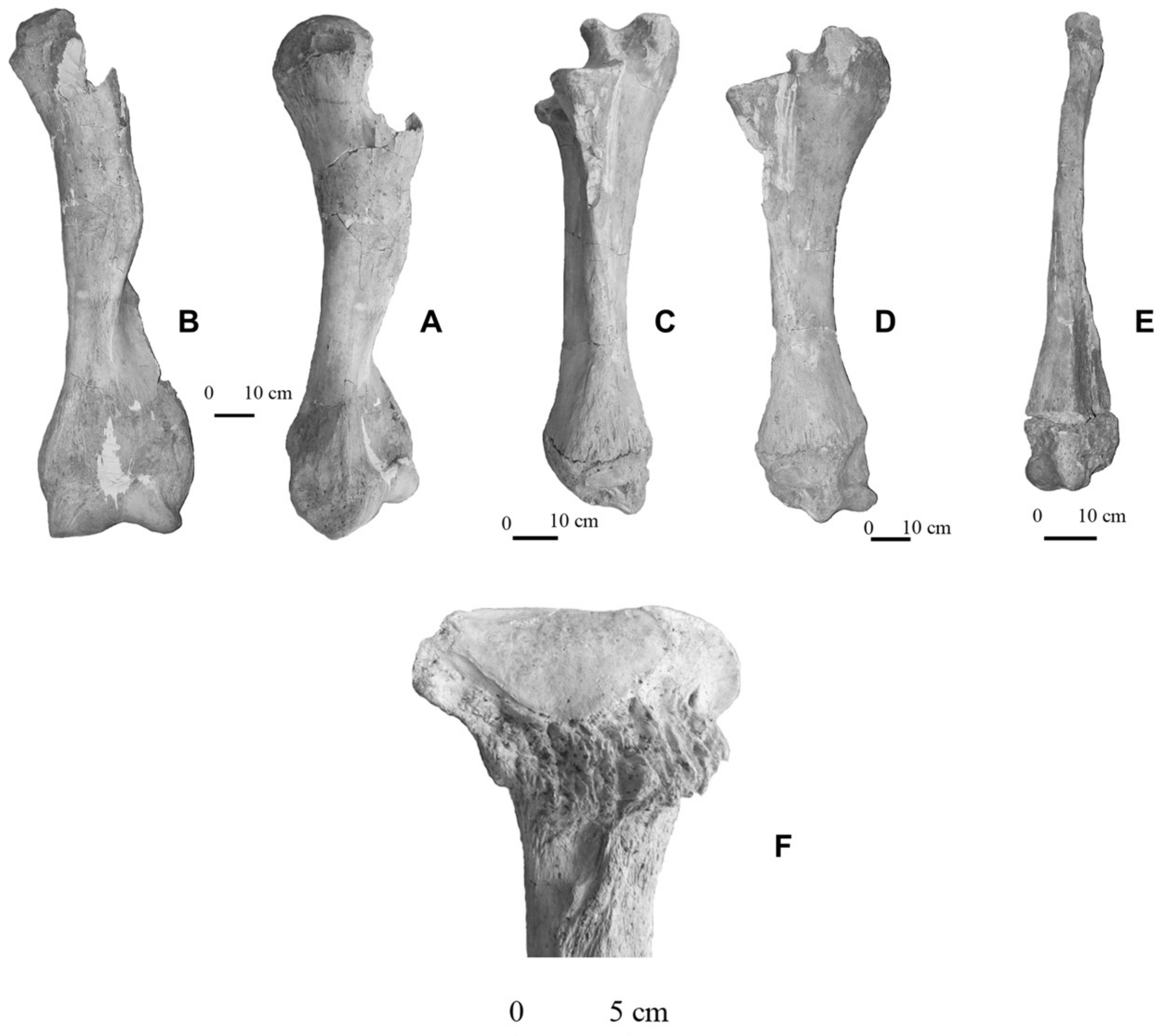

Fig. 4. The long bones of the forelimb and shoulder-blade. A – Humerus, sin BX N 2120/5, medial view. B – Humerus, sin BX N 2120/5, anterior view. C – Ulna, dex BX N 2120/7, lateral view. D – Ulna, dex BX N 2120/7, medial view. E – Radius, sin BX N2120/20, anterior view. F – Proximal end of radius, sin BX N 2120/20, medial view.

as a male. All of the sizes of long bones and tusks fall within the male size range of *A. meridionalis* (Garutt, 1954, 1998b; Garutt and Safronov, 1965; Azzaroli, 1977).

At the initial stage of wear of M3/m3, corresponding to individual age 28–32 years, both in recent elephants (Roth, 1984) and in *M. primigenius* (Maschenko, 2006), only males have distal epiphyses of long limb bones not completely fused, along with partly fused epiphyses of *corpus vertebrae*. In contrast, in the females at the stage at which M3/m3 begin to function, the epiphyses of long limb bones and *corpus vertebrae* are fused, and the epiphyseal sutures are obliterated (Maschenko, 2006).

Using the method developed by Garutt (1954), we estimate the shoulder height of the Rodionovo skeleton at 3800 mm. The skeleton from Georgievsk is about 3780 mm, and that from Nogaisk about 3900 mm high. The estimated shoulder height of the Rodionovo specimen, including spine muscles and skin volume, is 3950 mm. Based on the method suggested by Lang (1980) we estimate the live weight of the Rodionovo elephant at about 6.2–6.7 tonnes.

Individual characters of the male *A. meridionalis* from Rodionovo include fused epiphyses with obliteration of the suture lines in the proximal limb elements (humerus, femur). The distal portions of the limbs (ulna, radius, tibia, fibula) are characterized by fused epiphyses on the proximal ends, and by unfused epiphyses (or not obliterated suture lines) on the distal ends. Scapula and pelvis apophyses are also characterized by presence of the visible suture lines. The Rodionovo specimen demonstrates a pattern of long bone epiphysis fusion that gives evidence of an extended maturation process of *A. meridionalis* females. The 28- to 32-year-old elephant was not completely mature and would have continued growing. A similar progression and timing of epiphyses fusion and suture line obliteration is reported for males of recent elephants (Roth, 1984).

The Rodionovo specimen is characterized by thoracic vertebrae showing different stages of fusion of the *processus spinosus apophysis*, and vertebral plates show different stages of fusion to centra; however, no specific pattern differentiating those stages is evident. Fusion of the caudal epiphysis of *corpus vertebrae* to the vertebral body is more commonly observed than fusion of the cranial epiphysis. The cervical vertebrae are characterized by maximum ossification of the *foramen transversarium* on the second and third vertebrae, and minimum ossification of the foramen on the seventh vertebra. Possibly, the different stages of ossification in different parts of the vertebral column are characteristic of males of *A. meridionalis*, and determined by its prolonged growth and maturation.

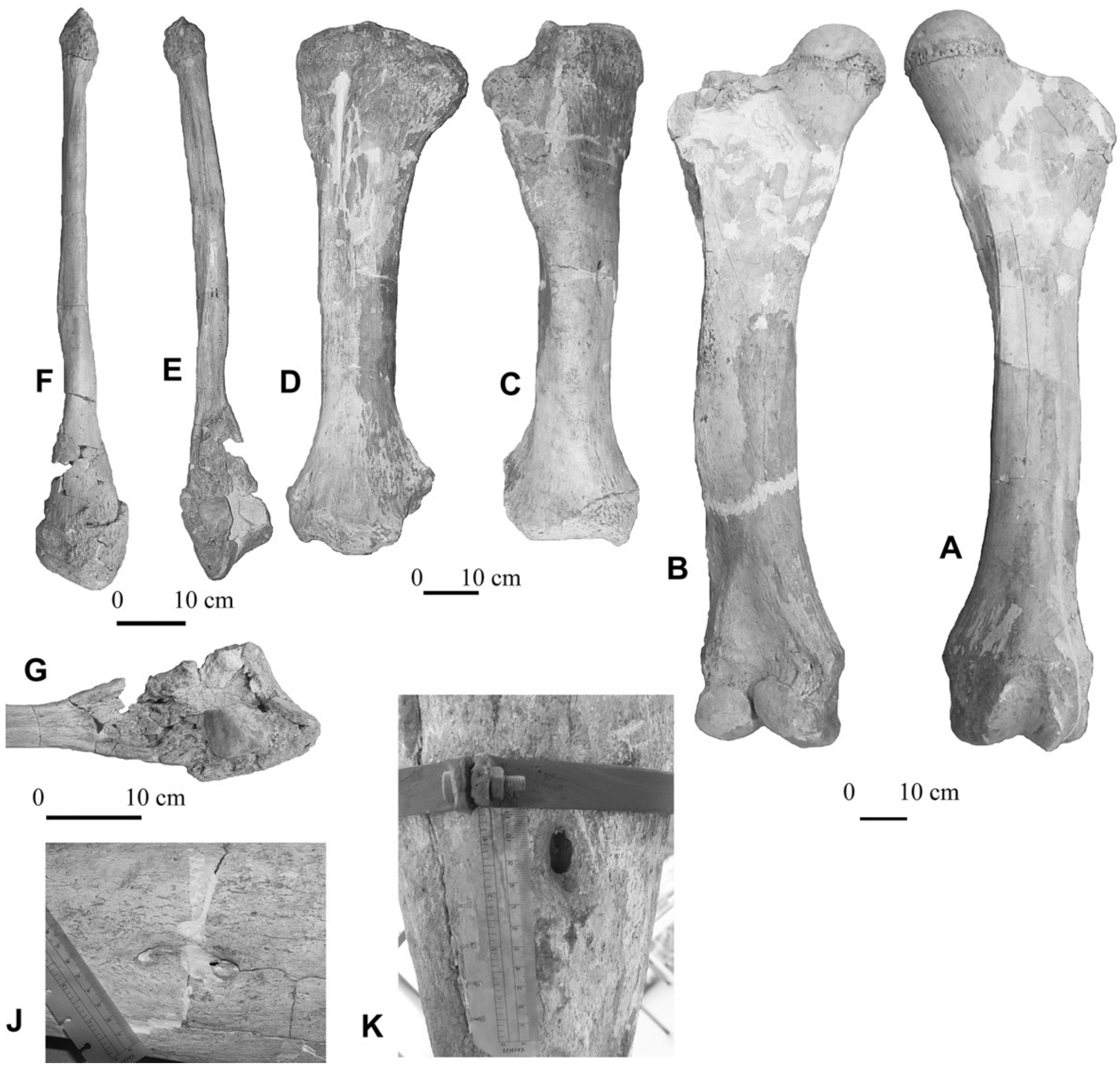

Fig. 5. The long bones of the hind limb. A – Femur, sin BX N 2120/14, anterior view. B – Femur, sin BX N 2120/14, posterior view. C – Tibia, sin BX N 2120/15, anterior view. D – Tibia, sin BX N 2120/15, posterior view. E – Fibula, sin BX N2120/13, anterior view. F – Fibula, sin BX N2120/13, lateral view. G – Distal end of fibula, sin BX N 2120/13, medial view. Abnormal compact layer (*substantia compacta*) of the bone. J – *Foramen nutritium* on tibia (sin BX N 2120/15), lateral view. K – *Foramen nutritium* on tibia sin, lateral view. Specimen SM N 14120/10; Georgievsk locality.

Good preservation of bones of the Rodionovo specimen has allowed the observation of deformation of the *substantia compacta* on the medial surface of the distal end of the fibula (dex, BX N 2120/12) (Fig. 5g). The structure of the *substantia compacta* is deformed only on a small area of the distal diaphysis, slightly affecting its shape. This type of deformation is not characteristic of osteoporosis, that normally affects a whole bone, or several bones, of the limb, but might be due to inflammation of a localized bone area caused by trauma or infection, which, however, could not have been responsible for the death of the animal.

The similarities in position and shape of the *foramina nutritia* on the tibiae of the skeletons from Rodionovo (Fig. 5j) and Georgievsk (Fig. 5k) are striking. In both individuals, the foramina are located in a similar way in the cavities on the medial surface of the tibia diaphyses. The position of *foramina nutritia* and other canals for blood vessels and nerves are hereditary and similar in close relatives. Such hereditary bone features were observed on skeletons belonging to a single family of *M. primigenius* (Maschenko, 2002). The similar overall skeletal morphology of the skeletons from the Rodionovo and Georgievsk localities, including the characteristic shape, size and location of *foramina nutritia*, could indicate close relationship of the animals at the population or even family level.

7. Taxonomy

The characteristics of the m3 of the specimen of *A. meridionalis* from Rodioinovo (Table 1) are close to those of the m3 molars of the *Archidiskodon* from the Georgievsk locality and Upper Valdarno (Garutt, 1998b; Palombo and Ferretti, 2005).

The structural pattern of M3/m3 in *A. m. meridionalis* was first described on material from Italy (Maglio, 1973; Azzaroli, 1977; Ferretti, 1999; Ferretti and Croitor, 2001). The type specimen of this taxon, along with a reference series (termed population by Ferretti, 1999 and Ferretti and Croitor, 2001), have been based on the finds from the type locality (Upper Valdarno, Tasso and Olivola Faunal Units, beginning of the Early Pleistocene) (Azzaroli, 1977; Napoleone et al., 2003.). Palombo and Ferretti (2005), when reexamining the same material, assumed that the differences displayed by the specimens of *Archidiskodon* from the Middle to Late Villafranchian of Italy all fall within the range of variability of a single species, *A. meridionalis*.

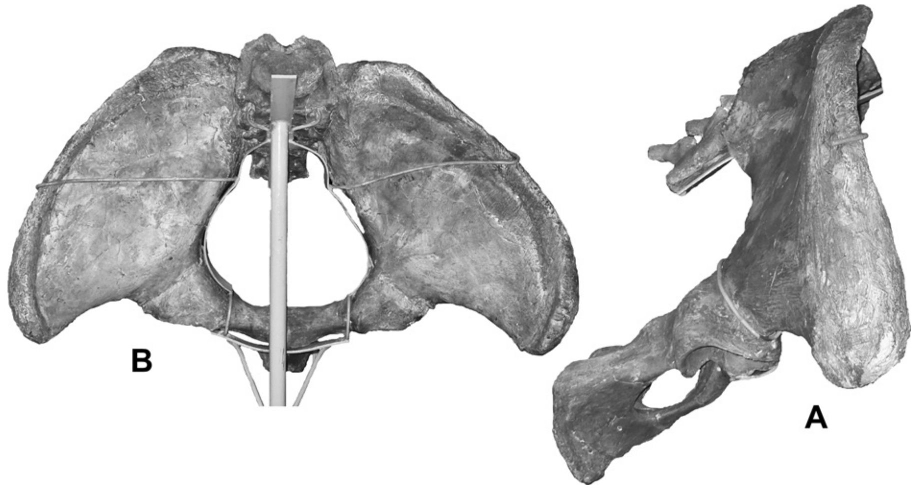

Fig. 6. Pelvis, BX N 2120/59. A – Lateral view. The distance between the right and left tuber coxae is 162.0 cm. B – Frontal view.

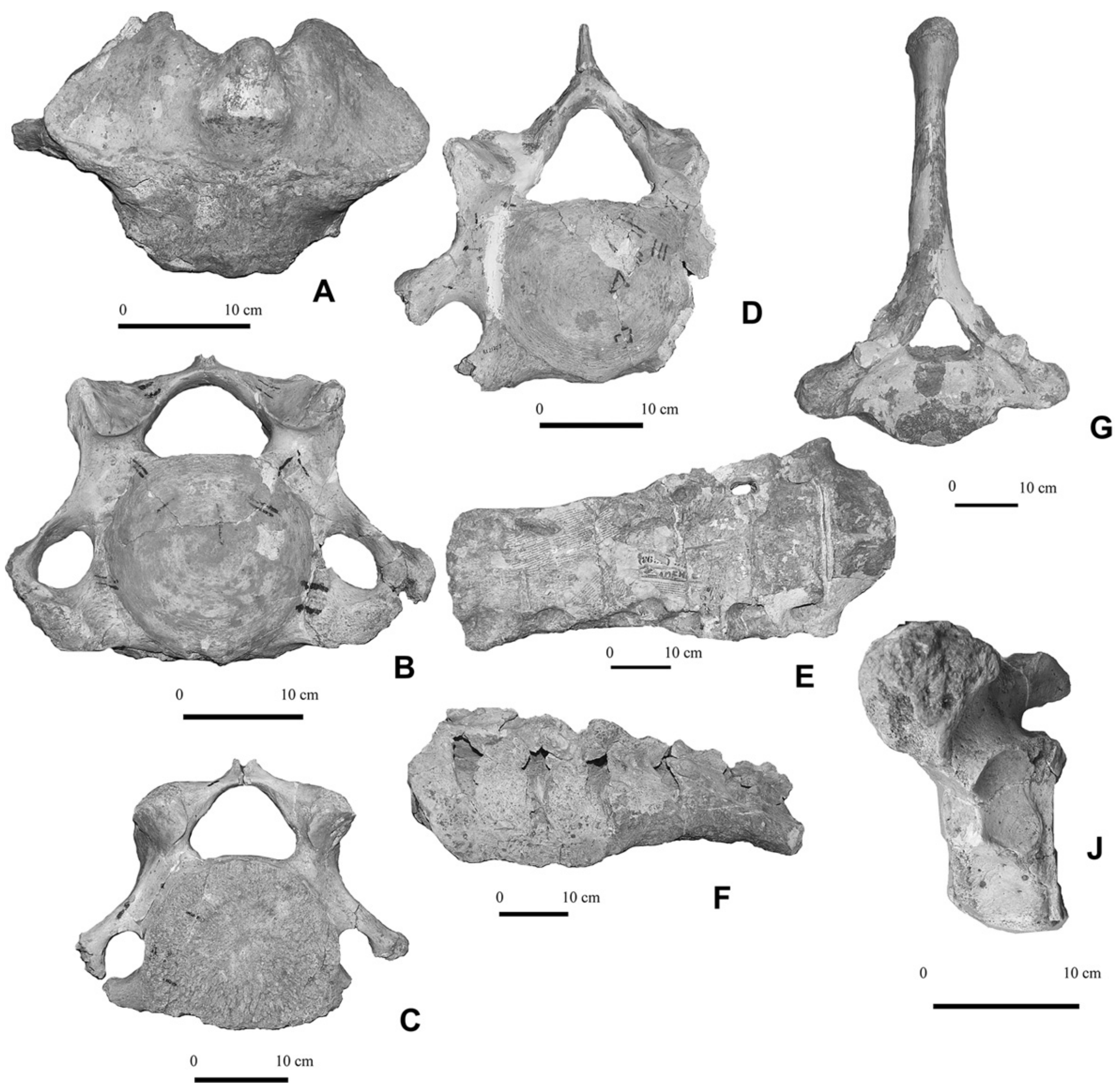

Fig. 7. Vertebrae. A – Axis (Epistropheus), BX N 2120/4, cranial view. B – Third cervical vertebra, BX N 2120/1, cranial view. C – Fourth cervical vertebra, BX N 2120/2, cranial view. D – Seventh cervical vertebra BX N 2120/3, cranial view. E – Sacrum BX N 2120/18, dorsal view. F – Sacrum BX N 2120/18, lateral view. G – Second thoracic vertebra BX N 2120/25, cranial view. J – Sixth thoracic vertebra BX N 2120/30, lateral view.

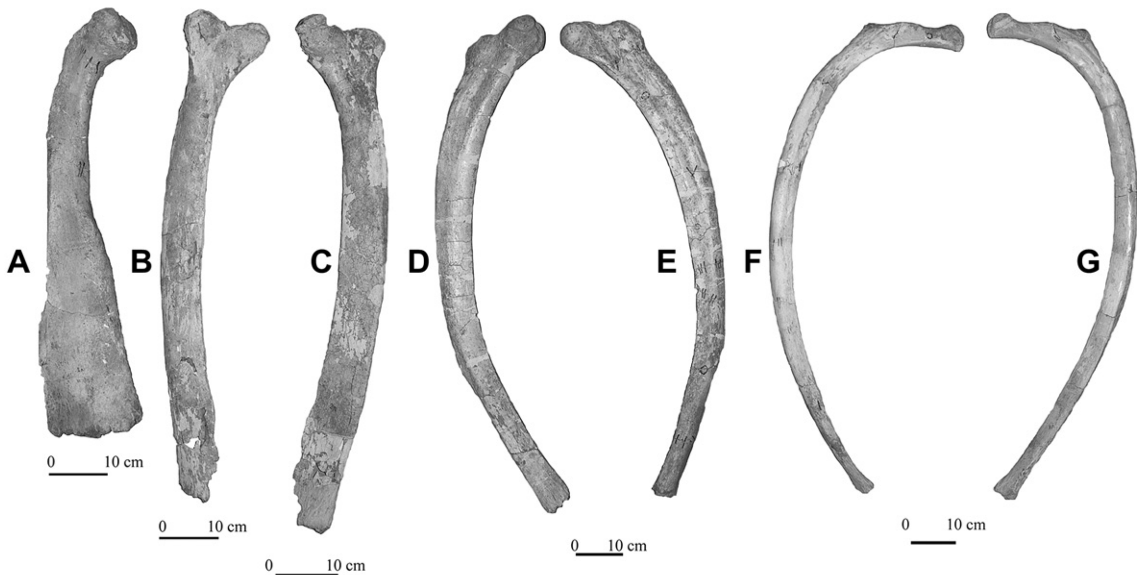

Fig. 8. Ribs. A – First rib, sin BX N 2120/35, posterior view. B – Second rib, dex BX N 2140/41, anterior view. C – Second rib, dex BX N 2140/41, posterior view. D – Third rib, sin BX N 2120/36, anterior view. E – Third rib, sin BX N 2120/36, posterior view. F – Eighth rib, dex BX N 2120/46, anterior view. G – Eighth rib, dex BX 2 N 120/46, posterior view.

In the North Caucasus, two subspecies of *A. meridionalis* have been identified (Garutt, 1954; Dubrovo, 1964). One of them, *A. m. meridionalis,* recognized in the Early Pleistocene (as a member of the Psekups fauna) was described from Georgievsk and Nogaisk (Garutt, 1954; Garutt and Safronov, 1965). The other, *A. m. tamanensis,* comes from the late Early Pleistocene of the same region (Sinyaya Balka and Port Katon localities: Dubrovo, 1964; Titov, 2001). Garutt (1981) advanced the rank of *A. m. tamanensis* to a separate species *Archidiskodon tamanensis*.

The authors of this paper support the validity of the two subspecies of *A. meridionalis* for the Northern Caucasus and Southern Ukraine. This conclusion is based on both their geochronological succession and the difference in their M3/m3 structure. The diagnostic characters of the latter are presented in Table 19. These data show different M3/m3 patterns in number of plates and hypsodonty index. The enamel thickness values show considerable overlap, with the minimum values displayed by *A. m. tamanensis*. In this paper we consider all the southern elephants of the late Early Pleistocene (Taman' fauna) as a valid subspecies, *A. m. tamanensis*. Lister and Sher, (2001) suggested that more advanced mammoths occur at the Sinyaya Balka locality as well as *A. m. tamanensis*.

The M3/m3 characteristics of the Rodionovo specimen are in the overlap zone between the two subspecies, *A. m. tamanensis* and *A. m. meridionalis* as defined by (Dubrovo, 1964), so is not possible to determine the subspecies of this specimen. However, the age of the Burundugulsk Formation (earliest Pleistocene) suggests that the specimen belongs to *A. m. meridionalis*.

8. Conclusions

The examined skeleton of *A. meridionalis* from the Rodionovo locality includes most of the major postcranial bones (except for the distal limb bones, sternum and caudal vertebrae). This is the second find of a nearly-complete skeleton of *A. meridionalis* discovered in this region, a rare event in the history of fossil elephant paleontology. The localities that yielded these finds are of the same age and belong to the Burunduksk Formation of the Early Pleistocene, (Lebedeva, 1978).

The large diameter of the tusks, the size of skeleton, and the relation between the timing of fusion of the epiphyses of the long bones, on the one hand, and the early stage of wear of M3/m3 on the other, support attribution of the Rodionovo specimen to a male *A. meridionalis.*

Comparison of the Rodionovo skeleton with those from Georgievsk (Stavropol Administrative Region) and Nogaisk (Zaporozhye Region, Ukraine), demonstrate little size variability in these skeletons of male *A. meridionalis*. However, the large tusk diameters of these *A. meridionalis* males, compared with the same character in the female individual from the Sinyaya Balka locality, demonstrates the degree of sexual dimorphism in *A. meridionalis.* Assessment of data on numbers of thoracic vertebrae and rib pairs and the diameter of the tusk cross-section, in *A. meridionalis* from the Early Pleistocene of Italy (Azzaroli, 1977), shows some minor variations in skeletal morphology in comparison with the members of the same species from the Northern Caucasus and Southern Ukraine. The linear body size and diameter of tusk cross-section in male *A. meridionalis* from Northern Caucasus is somewhat bigger than in males of the same species known from the Northern Italy.

The morphology of the M3 and m3 in the Rodionovo skeleton demonstrates that it belongs to the species *A. meridionalis* (Nesti, 1825). The values of most informative characters of m3 (crown width 98.9/89.5 mm, number of plates –/12 (13?–14?), enamel thickness –/3.5 mm, plate height –/~140.0 mm and lamellar frequency –/4.5 fall in the metrical 'overlap zone' of *A. m. meridionalis* and *A. m. tamanensis*, so on the basis of this single, incomplete dentition a subspecies determination is not possible.

Consideration of the credibility of the genus *Archidiskodon* has been undertaken by the authors for the first time in 12 years. Garutt (1998a) showed at least 28 differences in morphology of the molars, skull, lower jaw and postcranial skeleton between the genera *Archidiskodon* and *Mammuthus*. Besides, Garutt et al. (1990) demonstrated the availability of the name *Archidiskodon* in terms of the rules of zoological nomenclature. We substantiate the validity of the genus *Archidiskodon,* and propose a series of amended diagnoses both for this taxon and the species *A. meridionalis*. The morphological changes seen in the lineage *Archidiskodon* - *Mammuthus* show adaptive evolution. The distinctiveness of the molars and skeleton shown by Pliocene to Early Pleistocene members of this lineage justify generic rank (genus *Archidiskodon*). The morphology of Middle Pleistocene to Early Holocene members of the same lineage, on the other hand, defines their position within the genus *Mammuthus*. Maglio (1973), following Aguirre (1969), regards these changes as merely gradational, not leading to any marked advance in organizational level. In reality, these changes imply significant divergence of forms that deserves recognition at the generic level rather than as a species radiation within a single lineage.

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