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The evolution of Eastern European meridionaloid elephants' dental characteristics

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ABSTRACT

In Late Pliocene – Early Pleistocene of Eastern Europe there was a sequence of replaced each other subspecies of *Archidiskodon meridionalis*: *A. m. rumanus* - *A. m. gromovi* - *A. m. meridionalis* - *A. m. tamanensis*, which replaced each other. A specimen of *A. m. rumanus* from Novotroitsk site was described. Features of stratigraphically attached forms of different age meridionaloid elephants' samples from the localities of Liventsovka, Georgievsk, Psekups and Sinaya Balka were examined. Dental characteristics of "southern elephants" evolved in a direction with increases of number and lamellar frequency on M2/m2-M3/m3, and increases in length and heights of a crown on DP4/dP4-M1/m1. For large samples, average values of teeth parameters considered together are important.

1. Introduction

The Late Pliocene – Early Pleistocene history of elephants' development in the territory of Eastern Europe is well-presented. The Early Villafranchian – Early Galerian stage of Elephantidae evolution on this territory is associated mainly with elephants of the genus *Archidiskodon*. This group of animals is called "southern elephants", and includes proboscideans close to *Archidiskodon* (= *Mammuhus*) *meridionalis*. Remains of these "meridionaloid" elephants are common and well represented in Eastern Europe in different Late Pliocene – Early Pleistocene deposits (Fig. 1). In spite of the commonness of these finds and the prevalence of these elephants in the territory of Eurasia, and their stratigraphical importance, their taxonomic structure is accepted ambiguously.

There are disagreements regarding the genus affiliation and the species stuff of "meridionaloid" elephants. Some researchers do not recognize the validity of the genus *Archidiskodon* and include "southern elephants" in the genus *Mammuthus* (Maglio, 1973; Aguirre and Morales, 1990; Lister, 1993, 1996; Lister and Sher, 2001; Lister and van Essen, 2003; Palombo and Ferretti, 2005, and others). According to another point of view, the genus *Archidiskodon* is autonomous and it is regarded as a primitive stage of elephants of tribe Mammuthini Brookes (Osborn, 1942; Garutt, 1954, 1986, 1998a; Dubrovo, 1960, 1963, 1964, 1989; Baygusheva, 1971; Alexeeva, 1977; Azzaroli, 1977, and others). Some of these paleontologists rate them as "mammuthoid" elephants. The present authors hold the opinion that Late Pliocene – Early Pleistocene mammuthoid elephants should be attributed to the separate genus *Archidiskodon*, being a paraphyletic group, according to non-cladistic attitude (c.f. Lister, 1996). This point of view is based on distinct differences between Late Pliocene-Early Pleistocene and Middle-Late Pleistocene representatives of this elephants' tribe. Moreover, the phyletic transition between *Archidiskodon meridionalis* and *Mammuthus trogontherii* is not obvious, although it is supposed.

From Garutt (1998a), there are 28 distinctive cranial, dental, and postcranial skeleton characters separating *Archidiskodon* and *Mammuthus* (*M. trogontherii-M. primigenius*), such as: the different shapes of several cranial bones, and proportions of skull parts; some parameters of lower jaw (smaller height, more elongated sagittally, smaller width at the level of external edges relative to the same at the condyli, longer and more massive submental process); the form, specific features, and erasing character of teeth; the length ratio of different parts of vertebral column and limb bones; construction and composition of carpal and tarsal bones. In particular, meridionaloid elephants' characteristics are: relatively shorter and lower skull, higher position of nasal foramen, shorter supraorbital processes, weakly developed tuber of lacrimal bone,

Abbreviations:: AMZ, Azov historical, archeological and paleontological museum-reserve, Azov, Russia; FGGUB, Department of Geology and Paleontology of the University, Bucharest, Romania; GIN, Geological institute of Russian Academy of Sciences, Moscow, Russia; IGF, Museum of Geology and Paleontology of the University of Florence, Italy; PIN, Paleontological museum of Russian Academy of Sciences, Moscow, Russia; PKM, Pyatigorsk regional museum, Pyatigorsk, Russia; ROMK, Rostov-on-Don Regional museum, Rostov-on-Don, Russia; SMZ, Stavropol state museum-reserve, Stavropol, Russia; ZIN, Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia.

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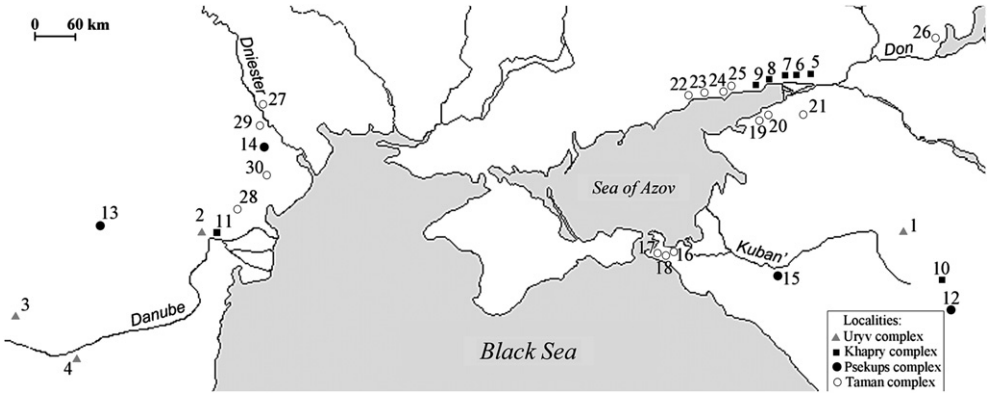

Fig. 1. The location of some Late Pliocene – Early Pleistocene localities of mammuthoid elephants, Black Sea, Sea of Azov and adjacent regions. *Early Villafranchian sites*: 1 – Novotroitsk, 2 - Tulucesti, 3 - Orodelu, 4 –Bossilkovtsi; *Middle Villafranchian sites*: 5 - Liventsovka, 6 - Khapry, 7 -Mokriy Chaltyr', 8 - Morskaya 1, 9 -Volovaya balka, 10 - Sablya, 11 - Râpa Scortsescu; *Late Villafranchian sites*: 12 - Georgievsk, 13 - Olteni, 14 - Salcia, 15 - Psekups (Saratovskaya and Bakinskaya); *Late Villafranchian – early Biharian sites*: 16 - Sinyaya Balka, 17 - Tsimbal, 18 - Ahtanizovskaya, 19 - Port-Katon, 20 – Semibalki, 21 - Samarskoe, 22 - Nogaysk (= Obytichnoe), 23 - Berdyansk, 24 - Zukalova Balka, 25 - Mariupol, 26 - Sarkel, 27 - Kalinovka, 28 - Velen'-2, 29 - Kitskany, 30 – Chishmikioy.

strongly developed mental process of a mandible, greater relative length of the cervical part of a spine, the serial arrangement of wrist bones, and relatively elongated phalanxes (Garutt, 1998a).

A diagnosis of the genus *Archidiskodon* and its systematic position were taken by the diagnosis given in the papers of Garutt (Garutt, 1954, 1998a; Garutt and Tikhonov, 2001, with authors' additions). A lectotype of *A. meridionalis* is the cranium with M3 from the Late Villafranchian locality Upper Valdarno (IGF, №1054). A nominotypical taxon of southern elephant is *A. m. meridionalis* from Late Villafranchian Western European localities and from synchronous Eastern European and Asian sites. Meridionaloid elephants include elephants, which are characterized by rather low molars, with the height of crowns reaching 120–180 mm at M3, and 104–150 mm at m3. Teeth crowns are wide, enamel plates' width is up to 126 mm at M3, and to 122 mm at m3. The total number of plates at last molars M3/m3 is from 9 to 17 (excluding talons). A lamellar frequency is 3.07–6.5/3.25–6.25 (for upper and lower teeth, respectively). The hypsodonty index (the ratio of the height to the width of unerased plate) is 0.94–1.79/1.0–1.72. The length of the crown is 216–340/244–350 mm. The incipient wear figures on the occlusal surface of trinomial plates are variable, predominantly of "meridionaloid" type. In some instances, the median sinus is present in upper and lower teeth. Usually, the posterior sinus's protuberance is developed more strongly than the anterior one. Thickness of enamel varies from 4.9 to 2.1 mm (Garutt and Tikhonov, 2001).

Meridionaloid elephants were typical for four faunal complexes of Eastern Europe: Early Villafranchian Uryv complex, Middle Villafranchian Khapry complex, Late Villafranchian Psekups complex, and late Late Villafranchian-Early Galerian Taman complex (Fig. 2; Gromov, 1948). In Eastern Europe during the Pleistocene there were two phylogenetic lines of elephants, *Archidiskodon-Mammuthus* and *Phanagoroloxodon*, which possessed similar characteristics of the dental system (Garutt, 1977). However, in the Early Pleistocene meridionaloid elephants were the most common form in the savanna-like landscapes of Eastern Europe, the index taxon of the associations.

Besides *A. meridionalis* the genus *Archidiskodon* is represented by some mainly African species: *Archidiskodon subplanifrons, Archidiskodon africanavus,* and *Archidiskodon moghrebensis* (Garutt and Tikhonov, 2001). Considering the significant variability seen in cranial, dental, and postcranial characteristics, the following subspecies of *A. meridionalis* from Eastern Europe and the Northern Caucasus are accepted as valid: *A. m. rumanus* (Early – early Middle Villafranchian), *A. m. gromovi* (Middle Villafranchian), *A. m. meridionalis* (late Middle – Late Villafranchian), and *A. m. tamanensis* (Late Villafranchian - Early Galerian). A similar range of differences between them requires the same taxonomic rank. Taking into account the environmental differences and faunistic distinctions between Eastern and Western Europe during Middle – Late Villafranchian (Titov, 2008), the presence of other age and geographical

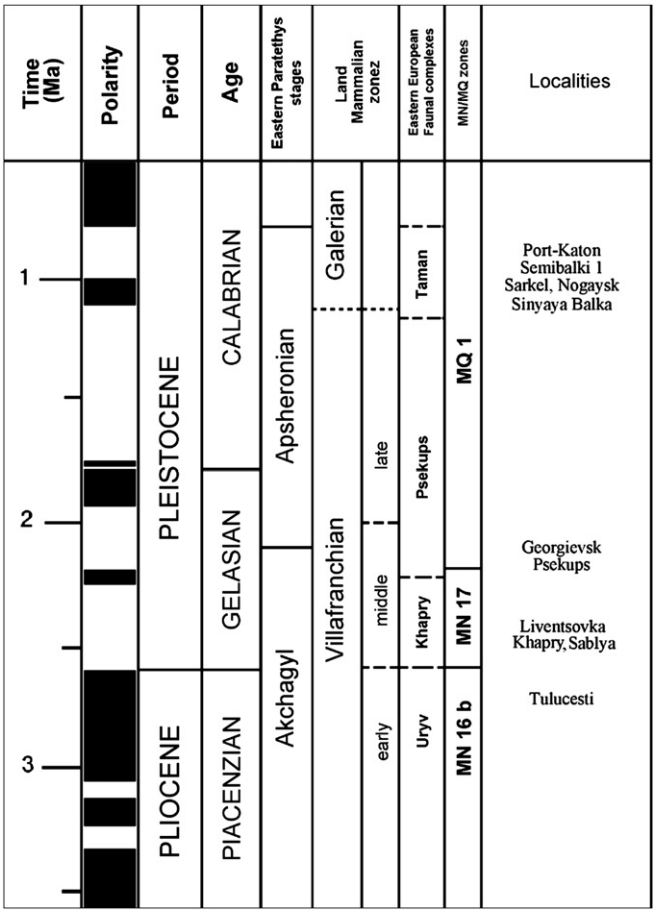

Fig. 2. Stratigraphical position of some Eastern European Late Pliocene – Early Pleistocene localities of meridionaloid elephants.

subspecies of meridionaloid elephants are not excluded: *A. m. taribanensis* Gabunia and Vekua, 1963, *A. m. vestinus* Azzaroli, 1977.

Features and measurements of teeth were accepted by Dubrovo (1960), Maglio (1973), Garutt and Foronova (1976). All diagnostic measurements: crown length, height and width of enamel plates, tooth formula (number of plates including and excluding anterior talon and posterior one (=platelet) to eliminate contradiction in counting a total amount of plates), lamellar frequency, and enamel thickness overlap between the different forms of southern elephants. Comparisons between different subspecies of *A. meridionalis* that use only minimal and maximal values are insufficient, because these parameters considerably depend on the sample size. Mean values, determined for different samples, are also necessary for the analysis. Another problem is that some researchers included plates that form talons in dental formula, while others did not.

Below is the character of changes in dental system characteristics on the basis of stratigraphically attached forms of different age meridionaloid elephants' samples.

2. Systematic paleontology

Elephantidae
Archidiskodon
Archidiskodon meridionalis (Nesti, 1825)
A. meridionalis rumanus (Stefanescu, 1924)

Selective synonymy:

Elephas antiquus rumanus: Stefanescu, 1924, p. 1418; Obada, 2010, p. 83.
Archidiskodon planifrons rumanus: Osborn, 1934, p. 6.
Mammuthus meridionalis: Lister, 1993, p. 78; Lister and Sher, 2001, p.1094.
Mammuthus rumanus: Ferretti, 2003, p. 392; Lister and van Essen, 2003, p. 47; Markov and Spassov, 2003, p. 57; Lister et al., 2005, p. 51.
Archidiskodon rumanus: Obada and David, 1997, p. 172; Garutt, 1986, p. 27; Garutt and Tikhonov, 2001, p. 48; Radulesco and Samson, 2001, p. 288.
Archidiskodon gromovi: Alexeeva, 1977, p. 91.
A. meridionalis rumanus: Titov, 2001, p. 152; 2008, p. 51.
Elephas (Palaeoloxodon) rumanus: Obada, 2010, p. 83.
Archidiskodon garutti: Maschenko, 2010, p. 202.

Holotype. FGGUB, ♂ 356, incomplete lower tooth m3.

Type locality. Tulucești (Rapa Balaii), Galati Country, Romania; Lower Villafranchian, mammal zone MN 16a.

Material. The incomplete left ramus of lower jaw with tooth m3 from the Novotroitsk locality. Collection of SMZ, OF 37797.

Geological age of locality. The geological age of fossiliferous deposits is unknown.

Description and comparison. The find was made in 1968 in a local sand pit on the left bank of the Egorlyk River near Stanitsa Novotroitskaya (Stavropol Region). It was embedded in obliquely laminated poorly sorted alluvial sands with ferruginous interbeds. Geology and stratigraphy of the locality have not been studied in detail. Related fossils were absent. Thus, it is difficult to speak precisely about the age of the location.

The tooth of last generation is of wear stage 4, consists of 9 plates, and anterior and posterior (=platelet) talonids. The length of the crown is 306 mm, width - 106 mm, lamellar frequency - 3.25, thickness of enamel - 4.35 mm, and length of a single plate - 30.1 mm. The approximate height of the crown is 142 mm (its exact determination is impossible due to the placement of the teeth in the mandible). Incipient wear figures on the occlusal surface of plate are of mixed type. Median sinuses are well expressed on the posterior side of medium wearing plates. Due to the large distance between plates, removal of cement in the interplate intervals is observed.

According to its characteristics the tooth is similar to those of Early Villafranchian elephants "*M. rumanus*" from Western and Eastern Europe. Currently, this find and the complete lower jaw from Bossilkovtsi (Bulgaria; Markov and Spassov, 2003) are the most complete specimens of this taxon. The supposition of Obada (2010) that this form of elephants is related to another genus of elephants *Elephas* (*Palaeoloxodon*) based on a relatively significant development of median sinus and incipient wear figures of a plate of mixed type, which sometimes appeared in the form of antiquoid type. However such median sinuses and mixed type of incipient wear of plates are developed in one way or another for most "southern" elephants. For example, such features are noted in the late form *A. m. tamanensis* (Dubrovo, 1963). Therefore, these features taken separately from other dental characteristics cannot be considered as decisive ones for genus determination. Especially, this is applicable in case of strongly worn teeth, as for the holotype of *A. m. rumanus*.

Discussion. The specimen from Novotroitsk has been proposed by Maschenko (2010) as a holotype of *Archidiskodon* "*garutti*". It was wrongly associated with the remains of the more progressive elephant *A. m. gromovi* from Sablya (Northern Caucasus, Stavropol Region). That site contains Middle Villafranchian fauna of large and small mammals (Lebedeva, 1978; Tesakov, 2004; Tesakov and Pismenskaya, 2005).

A. m. rumanus is one of the most primitive stages of southern elephant. It was first described from the localities of the second half of Early Villafranchian of Romania (Tulucești, Orodelu; Obada, 2010). Previously the finding from Cernățești (Romania) was attributed to the same species. However, as was shown by Obada (2010), the tooth of *A.* "*stefanescui*" Obada, 2010 has primitive characteristics, and is similar with those of African *A. subplanifrons, A. africanavus*. Recently some European findings from England (Red Crag; Lister and van Essen, 2003), Italy (Montopoli; Lister and van Essen, 2003), Bulgaria (Bossilkovtsi; Markov and Spassov, 2003) and China (Wei et al., 2006) were ascribed to *"M." rumanus*. However, some of these finds, for example, from Red Crag (Rendlesham and Pontier; Middle Villafranchian), and Montopoly (Middle Villafranchian) presumably belong to Middle Villafranchian *A. m. gromovi*, since they have a higher lamellar frequency in comparison with the Romanian elephant.

Distribution. The Black Sea and the Northern Caucasus regions, Central Asia, Early – early (?) Middle Villafranchian.

Archidiskodon meridionalis gromovi Garutt and Alexeeva, 1964.

Selective synonymy:

Elephas aff. planifrons: Pavlowa, 1910, p. 10.
Elephas cf. *planifrons*: Pavlowa, 1931, p. 67; Gromov, 1948, p. 44; Burchak-Abramovich, 1951, p. 75.
Elephas meridionalis: Bogachev, 1923, p. 108; Gromov, 1948, p. 42; Aguirre, 1969, p. 1372.
Archidiskodon planifrons: Nikiforova and Alexeeva, 1959, p. 15.
A. meridionalis: Yan'kova, 1959, p. 42; Dubrovo and Baygusheva, 1964, p. 35; Dubrovo, 1964, p. 82; 1989, p. 78; Tobien, 1970, p. 90; Gabunia and Dubrovo, 1990, p. 75; Maschenko, 2010, p. 201.
A. gromovi: Garutt and Alexeeva, 1964, p. 7; Alexeeva and Garutt, 1965, p. 161; Alexeeva, 1977, p. 13; Baygusheva, 1971, p. 14; 1984, p. 169; Garutt and Foronova, 1976, p. 35; Azzaroli, 1977, p. 149; Gromov, 1977, p. 83; Garutt et al., 1977, p. 4; Garutt and Bajgusheva, 1981, p. 7; Foronova and Zudin, 1999, p. 111; Vangengeim and Pevzner, 2000, p. 77; Baygusheva and Titov, 2001, p. 71; Garutt and Tikhonov, 2001, p. 54.

M. meridionalis: Aguirre and Morales, 1990, p. 9; Lister, 1993, p. 80; 1996, p. 205; Lister and Sher, 2001, p. 1095; Lister and van Essen, 2003, p. 50.
A. meridionalis gromovi: Titov, 2001, p. 152; 2008, p. 50.
Archidiskodon sp.: Obada, 2010, p. 87.

Holotype. ROMK, No L-113, the cranium of an adult male, collection of ROMK.

Type locality. Liventsovka, northeast Sea of Azov Region, Russia; Lower Pleistocene, Middle Villafranchian, MN 17.

Material. The material includes about 380 teeth and postcranial bones from various Khapry fauna localities (Liventsovka, Khapry, Volovaya Balka, Morskaya 1, Mokriy Chaltyr') from the north-eastern Sea of Azov Region (Rostov region, Russia), and Sablya (Stavropol Region, Russia). There are more than 150 specimens of upper and lower molars.

Geological age of locality. Early Pleistocene, Middle Villafranchian.

Description and comparison. The cranium is relatively low and elongated in the sagittal direction (the ratio of the length to the height is 0.86). The forehead is concave and exhibits notable narrowing (the ratio of the forehead's weight to the skull's weight in the occipital area is 0.29). The occiput is wide and its angle with the tooth occlusal surface is nearly 90. The top of the cranium is weakly convex. The intermaxillary bones are slightly elongated anteriorly (Alexeeva and Garutt, 1965; Garutt and Bajguševa, 1981). These features distinguish the skull of *A. m. gromovi* from other representatives of *Archidiskodon*. The cranium, ROMK No. L-113, was damaged across the top during excavation. According to Garutt, who restored this specimen, the cranium was slightly distorted: this distortion of the cranium's height was no more than 50–60 mm.

Molars are relatively low and wide (the crown width is 80–85% of its height). The *Archidiskodon* teeth from Khapry association localities have a relatively small number of enamel plates and a small lamellar frequency in comparison with other elephants of the "meridionalis" group. The restored number of enamel plates on the holotype's teeth is 12, and 14 including talons. The analysis of 13 weakly worn teeth M3/m3 of "Gromov's" elephants from Liventsovka revealed that in all cases there are two plates and a talon at the front main root of a crown. The same situation is observed in M2/m2. This is somewhat different from those data described by Sher and Garutt (1985), which indicated the presence of 3–4 plates at the main root of M3/m3 of *A. meridionalis*.

Elephants from Khapry and Sablya have a greater number of enamel plates in the teeth and on average a higher lamellar frequency than does the more archaic *A. m. rumanus* (Tables 1–3). *A. m. rumanus* has a greater length for a single plate (28.4 mm average) than does *A. m. gromovi* (15.8–25.6 mm).

Molars of *A. m. gromovi* are similar to the teeth of elephants from Red and Norwich Crag (England; Lister and van Essen, 2003), Laiatico, Montopoli, San Regolo, San Miniato, Inchiza Belobo (Italy; Azzaroli, 1977; Lister and van Essen, 2003), Aszód (Hungary; Vörös, 1985), Ferladany, Salcia sand pit, Râpa Scortsescu (Moldova; Pavlowa, 1910; Obada and David, 1997), Podpusk (Kazakhstan; Vislobokova, 1996) and Kuruksay (Tajikistan) in lamellar frequency and enamel thickness.

The primitive "southern elephants" were referred by Maglio (1973) to *A. meridionalis* "Laiatico stage". However, frequently the fragmentariness of elephant remains from these Early – Middle Villafranchian sites of Western, Central and Southern Europe does not allow comparisons to be made with the numerous collection of *A. m. gromovi*.

On average, the teeth from Liventsovka and Sablya have a smaller number of plates on M3/m3 and a smaller lamellar frequency than do teeth of typical *A. m. meridionalis* from Upper Valdarno (Italy), Seneze, Chagny (France), Georgievsk sand pit (Russia) and other Late Villafranchian localities of Europe (Garutt and Safronov, 1965; Maglio, 1973; Azzaroli, 1977; Dubrovo, 1989; Lister, 1993, 1996; Palombo and Ferretti, 2005). The comparison is compromised somewhat by the fact that tooth data for *A. m. meridionalis* often includes combined data from several sites (Maglio, 1973; Dubrovo, 1989). In general, tooth size in *Archidiskodon* from the Khapry Faunal Unit is smaller, and the unworn enamel plate height is lower, than in *A. m. meridionalis*. The proportion of the teeth (the ratio of crown width to its length) is similar in both taxa.

Comparison of *A. m. gromovi* M3/m3 with those of Early Pleistocene *A. m. tamanensis* from Sinyaya Balka (Taman peninsula,

Table 1
Tooth measurements of some upper teeth M3 of *Archidiskodon meridionalis gromovi* from Middle Villafranchian localities Liventsovka (North-Eastern Sea of Azov Region, Russia), and Sablya sand pit (Northern Caucasus, Russia). Collection of AMZ (OP), ROMK (L), GIN (GIN), and SMZ (SMZ).

M3	Length (mm)	Width (mm)	Height (mm)	Dental formula (number of plates and talons)	Enamel thickness (mm)	Lamellar frequency (mm)	Hypsodonty index (H/W)	Wear stage
Liventsovka								
L-113 dex holotype	242.8	100.0	–	t12t[a]	3.30	4.75	–	5
OP-1441	>232	88.0	129.0	t12t	3.30	5.13	1.47	1
OP-1317	253.00	87.8	97.0	t11t	3.00	4.50	1.10	2
L-489	270.0	95.0	118.0	t13t	2.60	4.75	1.24	2
OP-1322	292.0	101.0	105.0	t13t	3.35	4.50	1.04	3
OP -1454	283.00	118.8	123.0	t14t[a]	3.30	4.75	1.00	3
L-20	>262	–	135.0	t11t[a]	3.25	4.50	–	3
L-268	295.0	93.0	128.0	t13t	3.10	4.50	1.38	3
L-901	257.0	110.0	134.0	t12t	2.90	4.50	1.22	3
L-1529	216.0	96.0	92.0	t11t	3.70	5.00	0.96	3
L-360	>240	95.0	–	t12t[a]	3.10	4.50	–	4
L-580	>240	95.0	–	t11t[a]	3.10	4.50	–	4
L-928	253.0	108.0	–	t11t	3.50	4.50	–	4
OP-1320	238.0	>88	–	t10t	3.40	4.75	–	4
OP-1457	>235	95.6	–	t12t[a]	3.20	4.75	–	4
GIN 270/1	297.00	107.00	129.00	t12t[a]	3.20	4.50	1.21	4
Sablya								
SMZ 31306/12	>242	105.2		t11t[a]	3.23	4.00	–	5
SMZ 19977	>221	101.3		t11t[a]	3.23	4.5	–	5

[a] restored number of plates; t – talon.

Table 2
Tooth measurements of some lower teeth m3 of *Archidiskodon meridionalis gromovi* from Liventsovka sand pit (Middle Villafranchian, North-Eastern Sea of Azov Region, Russia), and Sablya sand pit (Northern Caucasus, Russia). Collection of AMZ (OP), ROMK (L), ZIN (ZIN), GIN (GIN) and SMZ (SMZ).

m3	Length (mm)	Width (mm)	Height (mm)	Dental formula (number of plates and talonids)	Enamel thickness (mm)	Lamellar frequency (mm)	Hypsodonty index (H/W)	Wear stage
Liventsovka								
OP-1125	290.0	89.8	105.0	t13t[a]	3.0	4.0	1.17	2
L-239	305.0	103.0	123.0	t13t	2.55	5.0	1.19	2
L-1367	266.0	90.0	–	t11t	3.1	4.0	–	2
GIN-270/10	>271	96.00	114	t12t[a]	2.80	4.25	1.19	2
ZIN no	310	95.00	127	t12t	3.25	4.00	1.34	2
OP-1125	292.0	91.0	105.0	t13t[a]	3.0	4.0	1.38	2
OP-1456	268.0	94.0	–	t12t[a]	3.2	4.5	–	3
L-358	301.0	87.0	101.4	t13t	3.3	4.5	1.17	3
L-615	257.0	79.0	108.0	t13t	3.0	5.0	1.37	3
L-1095	285.0	88.0	113.0	t11t	3.65	4.25	1.28	3
L-2044	303.0	101.0	–	t13t[a]	3.35	4.5	–	3
GIN-302/7	302	96.00	121		2.80	4.25	1.26	3
OP-1173	299.8	96.7	108.0	t11t[a]	3.2	3.75	1.12	4
OP-1326	272.0	92.0	–	t11t[a]	3.5	4.25	–	4
OP-1452	290.0	91.0	95.0	t12t	3.2	4.0	1.04	4
OP-1458	>256	90.4	95.0	t10t[a]	3.2	4.0	1.05	4
OP-1459	340.0	105.8	121.0	t13t	3.4	4.25	1.14	4
L-119	320.0	103.0	–	t12t[a]	3.5	3.9	–	4
L-125	328.0	108.0	–	t12t[a]	3.6	4.0	–	4
L-591	288.0	106.0	–	t11t	3.1	4.13	–	4
L-1426	287.0	99.0	>127	t12t[a]	3.3	4.5	–	4
L-1497	266.0	104.0	–	t12t[a]	3.5	4.75	–	4
L-1702	258.0	90.0	–	t12t[a]	3.7	4.25	–	4
ZIN, no	287.0	92.0	–	t13t[a]	3.0	4.5	–	4
Sablya								
SMZ 20701/1	236.0	95.60	115.0	t11t[a]	2.50	4.50	1.20	4
GIN 4358-306\70	341.0	112.0	129.0	t12t	3	4.7	1.15	3
GIN 4358-10-308/70b	308.0	96.6	–	t11t[a]	–	4.0	–	4

[a] restored number of plates; t – talonid.

Russia) and other sites showed that in such parameters as length of the crown and lamellar frequency, these forms partly overlap. Elephants from Liventsovka have a lower number of plates, and on average, a smaller lamellar frequency (Baygusheva and Titov, 2001).

Postcranial bones of *A. m. gromovi* have similar dimensions and proportions to other *A. meridionalis* subspecies but are somewhat smaller. The reconstructed height at the withers in a skeleton is nearly 3.2–3.5 m "Gromov's" elephant has measurements similar to those of *Mammuthus primigenius*, but differs from them by more slender limb bones and elongated humeri (Titov, 2008).

Discussion. *A. m. gromovi* was common in Middle Villafranchian associations of Eastern Europe, and they account about 23% of fossil remains in the collections from Khapry fauna's locations of that geological time. They coexisted with another form of elephant Elephantinae gen., *Pliocrocuta perrieri*, *Homotherium crenatidens*, late *Anancus arvernensis alexeevae*, large and slender *Equus (Allohippus) livenzovensis, Elasmotherium chaprovicum,* small *Paracamelus alutensis, Eucladoceros dicranios* ssp., *Arvernoceros* cf. *verestchagini*, and *Cervus (Rusa) philisi* (Gromov, 1948; Baygusheva, 1971; Titov, 2008). The major part of large animal's bones as the holotype of *A. m. gromovi* occurs from the bottom of alluvial cross sections of Khapry and Liventsovka sand pits. This layer with megafauna is accompanied by a rich small mammal association, including *Mimomys praepliocaenicus, Borsodia praehungaricus cotlovinensis*, *Mimomys* ex gr. *reidi*, correlated with Late Villanyian and zone MN 17 (Tesakov, 2004).

Due to several differences from typical *A. meridionalis*, the Khapry association elephant is considered a separate subspecies. The larger range of variability at *A. m. gromovi* in comparison with other subspecies of the southern elephant can be explained by the larger size of the sample, by the diversity of habitats in Eastern Europe, and by a relatively large period of accumulation of fossiliferous layers in Khapry alluvium (2.6–2.2 Ma; Titov, 2008). The presence of a primitive "southern elephant" in Europe was noted by

Table 3
Tooth measurements of upper and lower teeth M3/m3 of *Archidiskodon meridionalis gromovi* from localities from Khapry alluvial layers: Liventsovka, Khapry, Mokriy Chaltyr', Morskaya 1 (Middle Villafranchian, North-Eastern Sea of Azov Region, Russia).

Measurements	M3				m3			
	n	min	M	max	*n*	min	M	max
Length (mm)	16	216.0	258.43	297.0	26	235.0	287.52	340.0
Width (mm)	31	87.8	102.05	121.0	41	79.0	96.58	111.4
Height (mm)	20	92.0	122.80	140.0	21	95.0	115.92	137.0
Number of plates (excluding talons)	18	10	11.94	14	26	10	12.0	13
Number of plates (including talons)	17	12	13.94	16	13	12	14.0	15
Enamel thickness (mm)	31	2.60	3.23	4.0	40	2.55	3.23	3.9
Lamellar frequency (mm)	33	3.50	4.55	5.13	43	3.25	4.25	5.0
Hypsodonty index (H/W)	19	0.94	1.20	1.47	20	1.03	1.21	1.4

several investigators (Ramaccioni, 1936; Maglio, 1973; Azzaroli, 1977; Lister, 1993, 1996; Palombo and Ferretti, 2005). However, its taxonomic status is controversial. Dental characteristics of early and late meridionaloid elephants show directional conversion from Early to Late Villafranchian types (Figs. 3 and 4).

According to Alexeeva and Garutt (1965), one of the diagnostic species characters of "*A. gromovi*" is the unvarying presence of the last permanent upper left and right premolars, which are considered a primitive feature. These teeth are presented, but reduced, on the skull from Khapry (specimen GIN, ♀ 300/122) and consist of variable numbers of plates-tubercles (it is impossible to determine their real number). The presence of simultaneously functioning "P4" and M1 caused Gromov (1977) and Garutt et al. (1977) to propose vertical replacement of the first generation of teeth. This feature is typical for more primitive proboscideans and unknown for *A. m. meridionalis*. There is information that such a peculiarity is apparent on the skull from Olteni in the museum of Kraiova (Romania; Garutt, pers. com, 1998). Other researchers consider this feature as an individual atavism (Dubrovo, 1989), rudiment (Titov, 2001), or abnormal development of dp^2 (Maschenko, 2002).

Distribution. Eurasia, Middle Villafranchian.

A. meridionalis meridionalis (Nesti, 1825).

Selective synonymy:

E. meridionalis: Nesti, 1825, p. 195.
Elephas antiquus: Falconer and Cautley, 1846, p. 17.
Elephas planifrons: Deperet et al., 1923, p. 101.
Archidiskodon meridionalis: Osborn, 1942, p. 969.
M. meridionalis: Maglio, 1973, p. 53; Lister, 1993, p. 78; 1996, p. 204; Lister and Sher, 2001, p.1094, Lister et al., 2005, p. 54; Ferretti, 2003, p. 392; Palombo and Ferretti, 2005, p. 111.

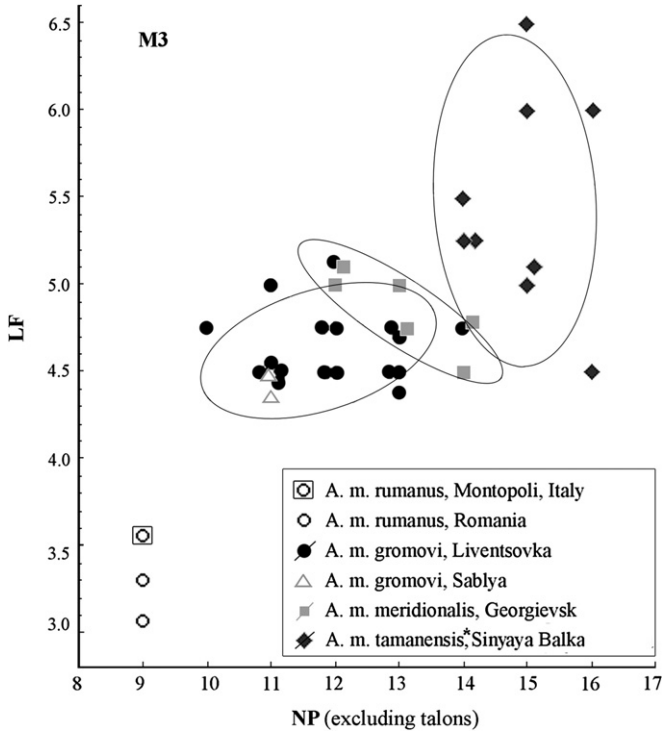

Fig. 3. Ratio of lamellar frequency and number of plates of upper teeth M3 of different age subspecies of *Archidiskodon meridionalis* from Eastern Europe and adjacent territories. *A. m. tamanensis from Sinyaya Balka specimens, which may be refer to another taxon, were excluded. Crossed symbols show the correspondence between the samples and the ellipses of assumption of normal distribution of the variables (coefficient 0.6).

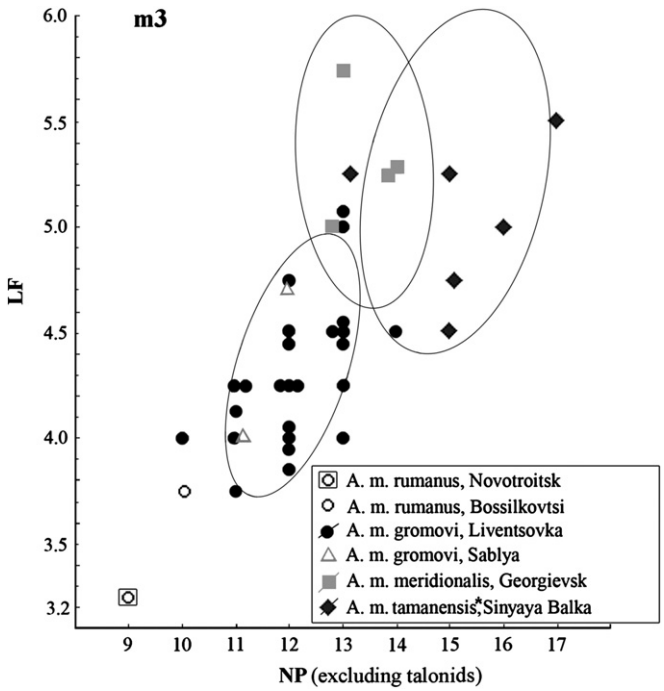

Fig. 4. Ratio of lamellar frequency and number of plates of lower teeth m3 of different age subspecies of *Archidiskodon meridionalis* from Europe. * *A. m. tamanensis* from Sinyaya Balka specimens, which may be refer to another taxon, were excluded. Crossed symbols show the correspondence between the samples and the ellipses of assumption of normal distribution of the variables (coefficient 0.6).

A. meridionalis meridionalis: Obada and David, 1997, p. 174; Titov, 2001, p. 152; 2008, p. 51.

Holotype. IGF 1054, the skull with M3.

Type locality. Upper Valdarno, Italy; Early Pleistocene, Late Villafranchian.

Material. Upper and lower teeth of the M3/m3 from Psekups fauna localities of the Northern Caucasus: Georgievsk (collections of SMZ, and PKM), and Psekups (a collection of GIN RAS). The material includes 11 upper and lower molars.

Geological age. Early Pleistocene, early Late Villafranchian.

Description and discussion. Finds of the southern elephant in Eastern Europe are not as numerous as in Western Europe. There is a series of specimens from Lower Pleistocene alluvium from Georgievsk sand pits (Georgievsk town, Stavropol Region), including a skeleton, skull, and a series of isolated teeth (Garutt and Safronov, 1965; Garutt, 1998b). From other localities at Ciscaucasus (sites Saratovskaya and Bakinskaya), isolated teeth and bones of elephants occur from the basis of the Psekups River sections (tributary of Kuban River).

The number of plates at nominative subspecies *A. m. meridionalis* of this age from the territory of Eastern Europe varies from 12 to 14, and the lamellar frequency from 4.25 to 5.0 for the upper and from 5.0 to 5.75 for the lower teeth (Table 4, Fig. 5). Teeth of *A. m. meridionalis* are somewhat larger and, on average, more advanced compared with those for *A. m. gromovi* (Figs. 3 and 4), and correspond with those from the typical meridionaloid elephants from the Upper Valdarno (Matassino and Tasso Faunal Units) and other Late Villafranchian locations of Western Europe (Palombo and Ferretti, 2005).

A. m. meridionalis was typical for the Psekups (Odessa) Faunistic Complex, which can be considered as a later stage development of the Khapry. It coexisted with *Phanagoroloxodon mammontoides*, *Stephanorhinus* cf. *etruscus*, *Equus (Allohippus)* cf. *major*,

Table 4
Tooth measurements of upper and lower teeth M3/m3 of *Archidiskodon meridionalis meridionalis* from localities Georgievsk and Psekups (Late Villafranchian, Northern Caucasus, Russia).

Measurements	M3				m3			
	n	min	M	max	*n*	min	M	max
Length (mm)	5	253.0	284.40	327.0	3	258.0	299.67	322.0
Width (mm)	6	104.0	114.17	121.0	5	90.0	101.56	110.8
Height (mm)	2	125.0	148.5	172.0	3	102.0	127.33	147.0
Number of plates (excluding talons)	6	12	12.67	14.0	5	12	13.2	14
Number of plates (including talons)	4	14	14.0	14	4	14	15.0	16
Enamel thickness (mm)	6	2.7	3.08	3.6	4	3.15	3.28	3.5
Lamellar frequency (mm)	6	4.25	4.79	5.0	4	5.0	5.31	5.75
Hypsodonty index (H/W)	2	1.19	1.32	1.46	3	1.0	1.21	1.44

Eucladoceros orientalis ssp., and *Pseudodama nestii*. Over this period, *Anancus* and *Paracamelus alutensis* continued to exist, but became less numerous. For the first time *Bison* appeared. Deposits with Psekups fauna belong to the early part of the Matuyama, and small mammal fauna occur to the end of Villanyian, and early Late Villafranchian, to the end of zone MN 17 (Tesakov, 2004).

Distribution: Eurasia, late Middle – Late Villafranchian.

A. meridionalis tamanensis Dubrovo, 1964.

Selective synonymy:

A. meridionalis tamanensis: Dubrovo, 1964, p. 86; Titov, 2001, 2008, p. 152, p. 50.
Archidiskodon tamanensis: Garutt and Tikhonov, 2001, p. 54.
M. meridionalis: Maglio, 1973, p. 53; Lister, 1993, p. 78; 1996, p. 204; Lister and Sher, 2001, p.1094, Lister et al., 2005, p. 54; Palombo and Ferretti, 2005, p. 111.

Holotype. PIN, No. 1358-57, the cranium of female with M2 and M3.

Type locality. Sinyaya Balka, Taman Peninsula, southern Sea of Azov Region, Russia; Late Villafranchian-early Galerian.

Material. The material includes about 60 upper and lower teeth of the last generations and 40 DP4/dp4 and M1/m1 from Taman fauna stratotype locality Sinyaya Balka (a collection of PIN).

Geological age. Early Pleistocene, late Late Villafranchian - early Galerian.

Description and comparison. "Taman" elephant is known from a number of Eastern European locations of the Sea of Azov and Lower Don Region (Port-Katon, Semibalki, Samarskoe, Berdyansk, Nogaysk (= Obytichnoe) Zukalova Balka, Mariupol (= Zhdanov), Sarkel), Taman Peninsula (Sinyaya Balka, Tsimbal, Ahtanizovskaya, Iskra), and North-Western Black Sea Region (Kalinovka, Velen'-2, Kitskany, Chishmikioy; Moldova). However, the most numerous finds are from the stratotype locality of Taman complex - Sinyaya Balka (Obada and David, 1997; Baygusheva and Titov, 2008). Due to the recent discovery of Early Paleolithic stone tools, the site was awarded the second name of Bogatyri (Shchelinsky et al., 2010).

This later form of archidiskodont elephant from the Sea of Azov Region by its characteristics (number of plates excluding talons on M3/m3 is 13–17, in average 15; lamellar frequency = 5.25; Table 5) is more progressive than the ancient subspecies of the southern elephant, and is closer to those of *A. m. vestinus* from Italy, and is similar to the meridionaloid elephant from Farneta Faunal complex of Italy (Palombo and Ferretti, 2005).

Discussion. *A. m. tamanensis* was typical representative of late Late Villafranchian-early Galerian Taman Faunistic Complex and coexisted with another form of Proboscidea Elephantidae gen., *Canis tamanensis, Canis (Xenocyon) lycaonoides, Ursus* sp., *Lutra simplicidens tamanensis, Pachycrocuta brevirostris, Panthera* sp., *Homotherium latidens, Stephanorhinus* cf. *etruscus, Elasmotherium caucasicum, Equus* (*Allohippus*) *major, Sus* cf. *strozzii, E. orientalis* ssp., *Bison tamanensis, Pontoceros ambiguus, Tragelaphus* sp., and *Gazella* sp. (Verestchagin, 1957; Baygusheva, 2000; Sotnikova and Titov, 2009). Microtheriofauna from these sites refers to Early Biharian (Tesakov, 2004).

There are different views about the specific structure of elephants from Sinyaya Balka. Belyaeva (1925) allocated 2 forms: "*Elephas*" *meridionalis* and *"E." trogontherii*. Verestchagin (1957) also pointed out several species: *"E." meridionalis*, *"E." trogontherii*, and *"E." antiquus*. Dubrovo (1963) described the new subspecies *A. meridionalis tamanensis* on the basis of numerous materials from the locality and brought all morphological differences to the individual variability of a single form. Garutt ascribed one tooth from the collection to *Phanogoroloxodon mammonthoides*. Lister et al. (2005) assumed a presence of remains of progressive *"M." meridionalis* and early *M. trogontherii* at the collection, reflected in the bimodal characteristics of the teeth. The authors' research of last and penultimate molar generations of 2–4 stages of wear confirmed the bimodal distribution of M3/m3 and m2 features (the number of plates, the lamellar frequency, and index of hypsodonty). In the Sinyaya Balka sample there are morphologically similar teeth, which can be divided into 2 groups. The first is characterized by a smaller plate number and lamellar frequency, and thicker

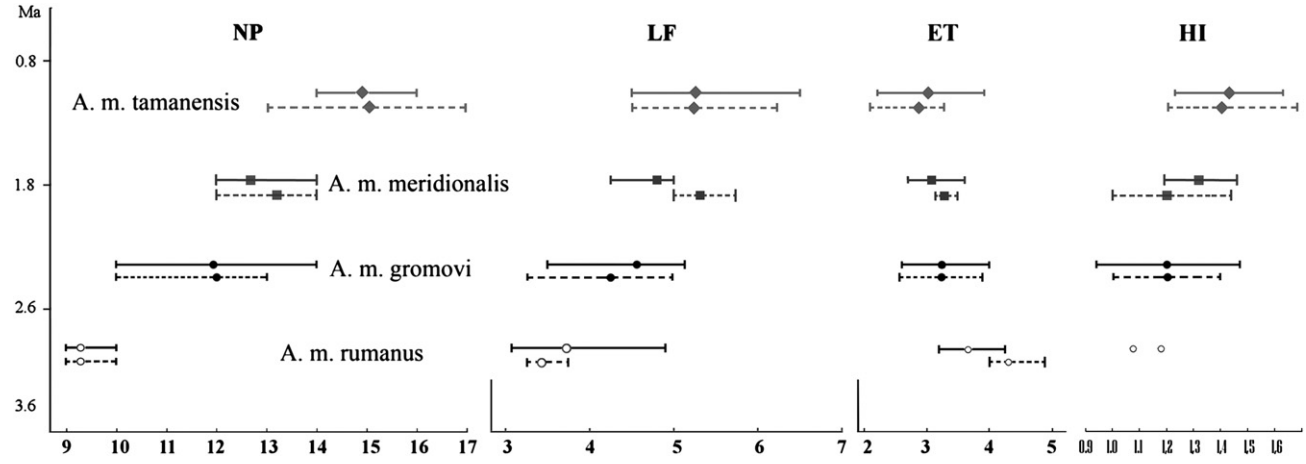

Fig. 5. Changes in number of plates, lamellar frequency, enamel thickness, and hypsodonty index of last molars generations M3/m3 of different age subspecies of *Archidiskodon meridionalis* from Eastern Europe. A firm line for upper M3 and dotted line for lower m3.

Table 5
Some M3/m3 parameters of Early Pleistocene elephants from Late Villafranchian-Early Galerian Sinaya Balka/Bogatyri locality (data in brackets are mean). Collection of PIN.

Measurements	*Archidiskodon meridionalis tamanensis*, $n = 9/7$	Elephantidae form 2, $n = 2/3$
	min-(med)-max	min-(med)-max
Number of plates (including talon)	15 – (16.25) – 17 / 15 – (16.0) – 17	16 – (17.2) – 18 / 17 – (17.3) – 18
Lamellar frequency	4.4 – (5.25) – 5.5 / 5.0 – (5.25) – 5.5	5.5 – (5.9) – 6.5 / 6.0 – (6.1) – 6.25
Enamel thickness, mm	2.5 – (3.0) – 3.4 / 2.6 – (2.9) – 3.3	2.1 – (2.4) – 2.6 / 2.1 – (2.4) – 2.6

enamel on the M3/m3. The second one has, on average, a larger number of plates and lamellar frequency, smaller thickness of enamel (Table 5). A hypsodonty index in the sample varies within the limits of 1.2–1.8; no difference by this characteristic is found between two groups. The first group is reliably correlated with *A. m. tamanensis*. The taxonomic status of the second form requires further study. By teeth features, it refers to the lower limits of variability of Middle Pleistocene *M. trogontherii*. However, the same parameters can be attributed to the upper limits of *A. m. tamanensis* sample. The absence of distinct morphological differences does not prove or disprove the existence of trogontherii mammoth remains in the sample.

The presence of the partial bimodal distribution of some parameters in the Sinyaya Balka locality sample can be explained in various ways:

1. The recent studies have shown that remains of elephants in the site occur from 2 layers formed with some difference in time, and associated with different facies. The composition of animal remains from these layers allows combining them into a single faunal complex. In this case, the mixture of two populations with slightly different characteristics can occur.
2. The collections of the first half of the 20th century were often sampled from the surface. This could cause a contamination of remains of *M. trogontherii*, also known from the neighboring sites close to Sinyaya Balka in the collection.

The presence of two forms of elephants ("southern" elephant, and a more progressive form) at Sinyaya Balka corresponds to some Early Pleistocene localities of Europe: Dorn-Dürkheim 3 (Germany), Ubeidiya (Israel), Psekups (Russia) and others (Garutt, 1992; Lister *et al.*, 2005). However, the majority of these indications is based on small series, and dental features overlap over a wide range. The archaic forms of elephants, well differentiated by craniological characteristics, have a similar teeth structure. This is due to convergence or homeomorphic teeth development (Gabunia and Vekua, 1963). In the late Early Pleistocene of Europe, the southern elephants lived together with other proboscideans – "*Phanogoroloxodon mammonthoides*" and *Elephas (Palaeoloxodon) "ausonius*" with similar teeth morphology (Garutt, 1986). It is possible that the teeth samples from the Sinyaya Balka may contain remains of one of these non-trogontherii elephants. Taking into account the possible presence of another form of elephant in the Taman sample, divergent specimens can be excluded from consideration.

According to Lister et al. (2005), the appearance of the first trogontherii mammoths occurred about 2.0–1.5 million years ago in the northeastern regions of Asia and probably in very specific circumstances. These elephants branched from the main stem of "meridionaloid" elephants. After this, during some time they coexisted with "*M. meridionalis*" in some regions of Eurasia. According to this model of Lister et al., there was genetic mixing between them in some places. However, considering the Sinyaya Balka site, it is difficult to imagine that the two taxa of elephants, which have a number of morphological differences, and diverged several tens thousands years ago, retained the ability for efficient hybridization. Taken into consideration the simultaneous findings of *A. meridionalis* and *M. trogontherii* in the Early Pleistocene in China, Eastern and Central Europe, and the Near East (Lister et al., 2005) a possibility of such large hybrid zone availability seems doubtful.

Distribution. Eastern Europe, ?Western Europe, Late Villafranchian - Early Galerian.

3. Discussion

Meridionaloid elephants evolved from Early Villafranchian up to Late Villafranchian and early Biharian for more than 2 million years, and survived several appreciable climatic reorganizations. During this time, several faunal assemblages changed. The degree of

Table 6
Tooth measurements of DP4/dP4 - M1/m1 from Early Pleistocene elephants of Eastern Europe (data in brackets are mean).

Measurements	*Archidiskodon m. gromovi*, Liventsovka, Khapry				*Archidiskodon m. tamanensis*, Sinaya Balka/Bogatyri			
	$dP^4/_4$		$M^1/_1$		$dP^4/_4$		$M^1/_1$	
	n	min–(med)–max	*n*	min–(med)–max	*n*	min–(med)–max	n	min-(med)-max
Length, mm	5/8	89.8 – (99.1) – 120.6 / 105.6 – (121.5) – 141.2	8/8	138.0 – (149.7) – 164.0 / 132.0 – (142.6) – 150.0	6/1	113.0 – (129.5) – 145.0 / 117.0	6/4	140.0 – (149.2) – 174.0 / 148.0 – (157.0) – 169.0
Width, mm	5/10	46.8 – (56.9) – 64.2 / 41.0 – (58.1) – 60.6	11/14	60.0 – (69.4) – 77.0 / 57.2 – (60.5) – 66.8	14/6	50.4 – (59.8) – 74.2 / 55.0 – (61.4) – 66.0	9/12	66.0 – (74.5) – 82.2 / 60.0 – (69.1) – 79.0
Height, mm	2/5	61.2; 66.2 / 42.0 – (52.2) – 60.0	5/8	82.3 – (88.1) – 94.8 / 70.0 – (76.6) – 87.5	11/4	63.2 – (73.7) – 98.0 / 57.0 – (82.8) – 105.8	5/8	95.0 – (103.8) – 82.2 / 77.0 – (91.8) – 110.0
Number of plates (excluding talon)	3/8	7 – (7.33) – 8 / 8 – (8.5) – 9	2/7	7; 8 / 8 – (8.43) – 9	5/2	8 – (8.8) – 10 / 9; 9	5/4	8 – (9.2) – 10 / 8 – (8.75) – 10
Lamellar frequency	5/8	7.0 – (7.5) – 8.0 / 6.0 – (7.2) – 8.0	10/14	4.5 – (5.7) – 6.5 / 5.5 – (6.05) – 7.0	14/7	5.8 – (7.2) – 9.0 / 5.2 – (7.2) – 9.6	9/12	5.5 – (6.6) – 7.8 / 5.0 – (5.7) – 6.8
Length of single plate, mm	5/12	11.8 – (13.8) – 15.0 / 11.0 – (12.4) – 15.6	10/11	17.1 – (18.8) – 20.0 / 15.5 – (16.7) – 18.2	14/6	11.2 – (13.9) – 14.5 / 12.4 – (15.5) – 17.2	9/12	12.8 – (14.6) – 19.0 / 15.8 – (17.7) – 19.7
Enamel thickness, mm	5/8	1.6 – (1.7) – 2.1 / 1.2 – (1.7) – 2.2	9/14	1.7 – (2.3) – 3.0 / 1.8 – (1.9) – 2.3	14/5	1.3 – (1.9) – 2.5 / 1.8 – (2.0) – 2.7	9/12	1.4 – (2.3) – 2.7 / 1.7 – (2.3) – 2.9
Hypsodonty index (HI=H/W)	2/1	1.08; 1.20 / 1.08	6/5	1.16 – (1.23) – 1.31 / 1.19 – (1.37) – 1.49	11/4	1.08 – (1.26) – 1.57 / 0.95 – (1.31) – 1.65	5/10	1.3 – (1.46) – 1.62 / 0.96 – (1.32) – 1.69

differences between different aged taxa of meridionaloid elephants can be interpreted at subspecies level. Average values of plate number and lamellar frequency and other measurements considered together show the tendency in changes from early to late representatives of meridionaloid elephants. They are supported by modification of skeletal size, and shape of the skull. The patterns of changes in the most diagnostic dentitions M2/m2-M3/m3 from early to late forms of *A. meridionalis* are known. For the M3/m3 of elephants from Eastern Europe, in the lineage *A. m. rumanus - A. m. gromovi - A. m. meridionalis - A. m. tamanensis,* an increase in the number of plates and the lamellar frequency is revealed (Figs. 3 and 4). Taking into consideration more numerous samples of teeth from Khapry and Liventsovka, the data does not agree completely with the data presented by Lister (Lister, 1993; Lister et al., 2005).

The patterns are confirmed by statistical analysis. Due to the fact that the considered parameters do not have a normal distribution and the size of some groups is very small, the study used the tools of nonparametric statistics – Kruskal–Wallis one-way analysis of variance to compare the groups. According to this analysis, *A. m. gromovi*, *A. m. meridionalis* and *A. m. tamanensis* significantly ($p < 0{,}05$) vary by number and frequency of the plates on M3/m3. In particular, significant differences for the lamellar frequency are observed between *A. m. gromovi* and *A. m. meridionalis* for upper M3 ($p = 0.003$) and lower m3 ($p = 0.013$); and between *A. m. gromovi* and *A. m. tamanensis* for upper M3 ($p = 0.005$) and lower m3 ($p = 0.019$), respectively. For the number of plates, significant differences were observed between *A. m. gromovi* and *A. m. tamanensis* for M3 ($p = 0.002$) and m3 ($p = 0.007$). Upper teeth of *A. m. gromovi* and *A. m. tamanensis* differ in crown height ($p = 0.036$). Lower m3 at earlier and later forms meridionaloid elephants differ in the thickness of the enamel. So, m3 of *A. m. rumanus* differs from the same of *A. m. gromovi* ($p = 0.011$). This analysis used the following samples: *A. m. gromovi* from Liventsovka and Khapry ($n = 21$–42), *A. m. meridionalis* from Psekups and Georgievsk ($n = 5$), and *A. m. tamanensis* from Sinyaya Balka ($n = 5$). Findings from Tulucești, Orodelu, Bossilkovtsi, and Novotroitsk were assigned to the group of *A. m. rumanus*.

Teeth of previous dentition are considered less informative, and for some taxa these deciduous teeth are unknown. Material of DP4/dp4 and M1/m1 of early and late representatives of southern elephants was accumulated from typical localities of the Khapry and Taman Faunal complexes. Finds of *A. m. meridionalis* are single, because deposits with large mammal fauna of early Late Villafranchian in Eastern Europe are rare. The data analysis also confirms the general trend of changes in dental characteristics observed in the latest teeth generations. For DP4/dp4 - M1/m1, the following changes from early to the late form of meridionaloid elephants are observed: the length and height of the crown appreciably increase. Such parameters as the width of the crown, lamellar frequency, length of a single plate, and number of plates show an insignificant increase. The thickness of enamel does not change essentially (Fig. 5, Table 6). The tendency of main tooth characteristic change for the teeth of the last permanent generations is also traced on the teeth of deciduous generations.

Recently, a new kind of elephant *A. garutti* (Maschenko, 2010) from Sablya (Stavropol Region, Southern European Russia) was described. It might establish an intermediate species between *A. "rumanus"* and *A. m. meridionalis* to substitute for taxon "*A. gromovi*", which is invalid according to this author. However, the author made several inaccuracies and incorrect assumptions, for example: 1) misinterpretation of age of the "stratotype" Sablya site ("more ancient than Middle-Late Akchagylian" instead of "Middle Akchagylian" (Lebedeva, 1978; Tesakov, 2004) or early Late Akchagylian (Tesakov and Pismenskaya, 2005); 2) misinterpretation of age of fossiliferous layers with remains of large animals of the Khapry Faunal complex stratotype locality with *A. m. gromovi* ("Middle-Late Villafranchian" instead of "Middle Villafranchian" fauna (Tesakov, 2004; Titov, 2008); 3) the specimen with more primitive features from another locality with unclear geological age (*A. m. rumanus* from Novotroitsk site, Stavropol Region) was proposed as the holotype of *A. garutti*; 4) the number of plates in holotypes of "*A. garutti*" and "*A. gromovi*" were not correctly restored. This makes it possible to consider that the specific taxon "*A. garutti*" can be regarded as a form of doubtful taxonomic position, and it is inconsistent.

4. Conclusion

The analysis of the data of meridionaloid elephant teeth of various generations from the territory of Eastern Europe shows a distinct tendency of transformation of the basic characteristics from Early Villafranchian to Late Villafranchian - early Galerian forms. Taking into account a number of distinct differences in cranial and postcranial skeletons, the authors hold the opinion that these "mammuthoid" elephants must be placed in the separate genus *Archidiskodon*. Four different chronosubspecies of southern elephants are recognized in Eastern Europe: *A. m. rumanus - A. m. gromovi - A. m. meridionalis - A. m. tamanensis.* Directed time-dependent evolutionary changes affected several dental characters. Evolutionary changes of several diagnostic features are observable in M2/m2-M3/m3 teeth (number of plates, lamellar frequency, hypsodonty index), as well as in dP4/dp4-M1/m1 (length and height of a crown). Findings of teeth dP2 and dP3 are very rare, and therefore comparison is impossible at the moment. For large samples, the most significant average values of plate number and lamellar frequency and other measurements considered together are important. The minimal and maximal values of teeth parameters considerably depend on the sample size.

The climatic and paleogeographical changes on the territory of Eurasia during Late Pliocene – Early Pleistocene suggest different environmental conditions and the types of food, which caused evolutionary adaptations. These factors could cause the presence of age and possible geographical diversity of meridionaloid elephants which were widely distributed on the territory of the continent.

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