The evolution of Eastern European meridionaloid elephants’ dental characteristics

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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 (= Mammutus) 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 Mammutthus (Maglio, 1973;

Abbreviations:: AMZ, Azov historical, archeological and paleontological museum-reserve, Azov, Russia; FGGUR, 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.

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.

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strongly developed mental process of a mandible, greater relative
dependent 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 posi-
tion 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, N
/C14 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 *N*3/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 Vill-
afranchian 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 *Phanagrolaelapodon*, 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 planifrons*,
*Archidiskodon africanus*, 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. mer-
idionalis* (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 Villa-
franchian (Titov, 2008), the presence of other age and geographical
developments.
subspecies of meridionaloid elephants are not excluded: *A. m. tar-

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:


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

Type locality. Tulucești (Rapa Balaii), Galati Country, Romania; Lower Villafranchian, mammoth 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 lami-
nated 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 fromBossilkovtsi (Bulgaria; Markov and Spassov, 2003) are the most complete specimen 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 Sabha (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 Cernatești (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 Montopoli (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.


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.


*Archidiskodon planifrons*: Nikiforova and Alexeeva, 1959, p. 15.


**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 I, Mokry Chaltyr) from the northeastern 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 elongation in the sagittal direction (the ratio of the length to the upper and lower molars. (Stavropol Region, Russia). There are more than 150 specimens of upper and lower molars.

**Comparison 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. rumans* 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; Vorós, 1985), Ferladany, Salcia sand pit, Rápa Scortsescu (Moldova; Pavliowa, 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. m. 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, 1988; 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. gromovi* M3/m3 with those of Early Pleistocene *A. m. tamanensis* from Sinyaya Balka (Taman peninsula, Russia), and Sablya sand pit (Northern Caucasus, Russia), Collection of AMZ (OP), ROMK (L), GIN (GIN), and SMZ (SMZ).

**Table 1**

<table>
<thead>
<tr>
<th>Material</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Height (mm)</th>
<th>Dental formula (number of plates and talons)</th>
<th>Enamel thickness (mm)</th>
<th>Lamellar frequency (mm)</th>
<th>Hypsodonty index (H/W)</th>
<th>Wear stage</th>
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<td>4.75</td>
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* restored number of plates; t — talon.
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 the crown and lamellar frequency, these forms partly overlap.

Tooth measurements of some lower teeth m3 of

<table>
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<th>m3</th>
<th>Length (mm)</th>
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<th>Lamellar frequency (mm)</th>
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<td>–</td>
<td>t11t</td>
<td>3.5</td>
<td>4.25</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>OP-1452</td>
<td>290.0</td>
<td>91.0</td>
<td>95.0</td>
<td>t12t</td>
<td>3.2</td>
<td>4.0</td>
<td>1.04</td>
<td>4</td>
</tr>
<tr>
<td>OP-1458</td>
<td>&gt;256</td>
<td>90.4</td>
<td>95.0</td>
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<td>4.0</td>
<td>1.05</td>
<td>4</td>
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<tr>
<td>OP-1459</td>
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<td>105.8</td>
<td>121.0</td>
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<td>3.4</td>
<td>4.25</td>
<td>1.14</td>
<td>4</td>
</tr>
<tr>
<td>L-119</td>
<td>320.0</td>
<td>103.0</td>
<td>–</td>
<td>t12t</td>
<td>3.5</td>
<td>3.9</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>L-125</td>
<td>328.0</td>
<td>108.0</td>
<td>–</td>
<td>t12t</td>
<td>3.6</td>
<td>4.0</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>L-591</td>
<td>288.0</td>
<td>106.0</td>
<td>–</td>
<td>t11t</td>
<td>3.1</td>
<td>4.13</td>
<td>–</td>
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</tr>
<tr>
<td>L-1426</td>
<td>287.0</td>
<td>99.0</td>
<td>&gt;127</td>
<td>t12t</td>
<td>3.3</td>
<td>4.5</td>
<td>–</td>
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<tr>
<td>L-1497</td>
<td>266.0</td>
<td>104.0</td>
<td>–</td>
<td>t12t</td>
<td>3.5</td>
<td>4.75</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>L-1702</td>
<td>258.0</td>
<td>90.0</td>
<td>–</td>
<td>t12t</td>
<td>3.7</td>
<td>4.25</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>ZIN no</td>
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<td>92.0</td>
<td>–</td>
<td>t13t</td>
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<td>4.5</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>Sablya</td>
<td>SMZ 20701/1</td>
<td>236.0</td>
<td>95.60</td>
<td>115.0</td>
<td>t11t</td>
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<td>4.50</td>
<td>1.20</td>
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<tr>
<td>GIN 4358-306/70</td>
<td>341.0</td>
<td>112.0</td>
<td>129.0</td>
<td>t12t</td>
<td>3</td>
<td>4.7</td>
<td>1.15</td>
<td>3</td>
</tr>
<tr>
<td>GIN 4358-10-308/70b</td>
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<td>96.6</td>
<td>–</td>
<td>t11t</td>
<td>4</td>
<td>4.0</td>
<td>–</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 2

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 (Bagyusheva 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 Mammutthus 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 Elephantinus gen., Pliocrocuta perrieri, Homotherium crenatidens, late Anancus arvernensis alexeevae, large and slender Equus (Allohippus) livenzovensis, Elasmotherium chaprovincum, small Paracamelus alutensis, Eucladoceros dicranios ssp., Arvernooceros cf. verestchagni, and Cervus (Rusa) philisi (Gromov, 1948; Bagyusheva, 1971; Titov, 2008). The major part of large animal’s bones as the holotype of A. m. gromovi occurs from the bottom of alluvial crosses 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

<table>
<thead>
<tr>
<th>Measurements</th>
<th>M3</th>
<th>Measurements</th>
<th>m3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>min</td>
<td>M</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>16</td>
<td>216.0</td>
<td>258.43</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>31</td>
<td>87.8</td>
<td>102.05</td>
</tr>
<tr>
<td>Height (mm)</td>
<td>20</td>
<td>92.0</td>
<td>122.80</td>
</tr>
<tr>
<td>Number of plates</td>
<td>18</td>
<td>10</td>
<td>11.94</td>
</tr>
<tr>
<td>Number of plates (excluding talons)</td>
<td>17</td>
<td>12</td>
<td>13.94</td>
</tr>
<tr>
<td>Enamel thickness (mm)</td>
<td>31</td>
<td>2.60</td>
<td>3.23</td>
</tr>
<tr>
<td>Lamellar frequency (mm)</td>
<td>33</td>
<td>3.50</td>
<td>4.55</td>
</tr>
<tr>
<td>Hypsodonty index (H/W)</td>
<td>19</td>
<td>0.94</td>
<td>1.20</td>
</tr>
</tbody>
</table>
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, N2 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 Otteni 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 dp2 (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.


Archidiskodon meridionalis: Osborn, 1942, p. 969.


**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).

**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 (collections of SMZ, and PKM), and Psekups (a collection of GIN RAS). The material includes 11 upper and lower molars.

**Archidiskodon 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*,...
Changes in number of plates, lamellar frequency, enamel thickness, and hypsodonty index of last molars generations M3/m3 of different age subspecies of Eucladoceros orientalis

Table 4
Tooth measurements of upper and lower teeth M3/m3 of Eucladoceros orientalis

<table>
<thead>
<tr>
<th>Measurements</th>
<th>M3</th>
<th>m3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>min</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>5</td>
<td>253.0</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>6</td>
<td>104.0</td>
</tr>
<tr>
<td>Height (mm)</td>
<td>2</td>
<td>125.0</td>
</tr>
<tr>
<td>Lamellar frequency (mm)</td>
<td>6</td>
<td>3.08</td>
</tr>
<tr>
<td>Enamel thickness (mm)</td>
<td>6</td>
<td>2.7</td>
</tr>
<tr>
<td>Number of plates (excluding talons)</td>
<td>4</td>
<td>14</td>
</tr>
<tr>
<td>Enamel thickness (mm)</td>
<td>6</td>
<td>3.08</td>
</tr>
<tr>
<td>Height (mm)</td>
<td>2</td>
<td>125.0</td>
</tr>
<tr>
<td>Lamellar frequency (mm)</td>
<td>6</td>
<td>3.08</td>
</tr>
<tr>
<td>Enamel thickness (mm)</td>
<td>6</td>
<td>2.7</td>
</tr>
<tr>
<td>Number of plates (excluding talons)</td>
<td>4</td>
<td>14</td>
</tr>
</tbody>
</table>

Hypsodonty index (H/W) 2 1.19 1.32 1.46 3 1.0 1.21 1.44
Lamellar frequency (mm) 6 4.25 4.79 5.0 4 5.0 5.31 5.75
Enamel thickness (mm) 6 2.7 3.08 3.6 4 3.15 3.28 3.5
Height (mm) 2 125.0 148.5 172.0 3 102.0 127.33 147.0
Lamellar frequency (mm) 6 4.25 4.79 5.0 4 5.0 5.31 5.75
Enamel thickness (mm) 6 2.7 3.08 3.6 4 3.15 3.28 3.5
Number of plates (excluding talons) | 4 | 14 | 14.0 | 4 | 14 | 14.0 |

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 Psekuks 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.


Selective synonymy:


Archidiskodon tamanensis: Garutt and Tikhonov, 2001, p. 54.

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)) Zulkalova Balka, Mariupol (= Zhdanov), 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, Pontocrocuta 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 mammothoides. 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
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), Ubediya (Israel), Psepek (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 craniofacial characteristics, have a similar tooth 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 – “Phanogor-olodon mammouthoides” and Elephas (Palaeoloxodon) “ausonius” with similar tooth morphology (Garutt, 1986). It is possible that the teeth samples from the Sinyaya Balka may contain remains of one of these non-trogontheriid 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 trogontheriid 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.

### 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 5

<table>
<thead>
<tr>
<th>Measurements</th>
<th>Archidiskodon meridionalis tamanensis, <em>n</em> = 5/7</th>
<th>Elephantidae form 2, <em>n</em> = 2/3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of plates (including talon)</td>
<td>15 – (16.25) – 17</td>
<td>16 – (17.2) – 18</td>
</tr>
<tr>
<td>Lamellar frequency</td>
<td>4.4 – (5.25) – 5.5</td>
<td>5.5 – (5.9) – 6.5</td>
</tr>
<tr>
<td>Enamel thickness, mm</td>
<td>2.5 – (2.9) – 3.4</td>
<td>2.1 – (2.4) – 2.6</td>
</tr>
</tbody>
</table>

### Table 6

<table>
<thead>
<tr>
<th>Measurements</th>
<th>Archidiskodon m. gromovi, Liventsovka, Khapry</th>
<th>Archidiskodon m. tamanensis, Sinyaya Balka/Bogatyri</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length, mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width, mm</td>
<td></td>
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<tr>
<td>Height, mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of plates (excluding talon)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lamellar frequency</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of single plate, mm</td>
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<tr>
<td>Enamel thickness, mm</td>
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<tr>
<td>Hypsodonty index (H/H/W)</td>
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</tbody>
</table>

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), Ubediya (Israel), Psepek (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 craniofacial characteristics, have a similar tooth 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 – “Phanogor-olodon mammouthoides” and Elephas (Palaeoloxodon) “ausonius” with similar tooth morphology (Garutt, 1986). It is possible that the teeth samples from the Sinyaya Balka may contain remains of one of these non-trogontheriid 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 trogontheriid 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.

### 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
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 differ (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 Pseukups and Georgievsk (n = 5), and *A. m. tamanensis* from Sinyaya Balka (n = 5). Findings from Tuluçeşti, 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 Akhchagylian") instead of “Middle Akhchagylian” (Lebedeva, 1978; Tesakov, 2004) or early Late Akhchagylian (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 chronospecies 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 Pleocene — 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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