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# A HISTORY OF ELEPHANTS OF THE ARCHIDISKODON-MAMMUTHUS PHYLOGENETIC LINE ON THE TERRITORY OF THE USSR

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### ABSTRACT

On the territory of the USSR archidiskodont elephants existed in the Pliocene and Eopleistocene. The genus Archidiskodon was represented by a single species with three morphologically and stratigraphically clearly distinct subspecies: Archidiskodon meridionalis meridionalis (Nesti), A. meridionalis taribanensis Gabunia et Vekua and A. meridionalis tamanensis Dubrovo.

The genus Mammuthus is known from the Pleistocene. In the early Pleistocene it is represented by Mammuthus trogontherii trogontherii (Pohlig), in the lower part of the middle Pleistocene—by M. trogontherii chosaricus Dubrovo, in the upper part of the middle Pleistocene and in the late Pleistocene—by M. primigenius (Blumenbach).

Evolution of the elephants of Archidiskodon—Mammuthus phylogenetic line proceeded in the direction of adaptation to severe climatic conditions and feeding on forage becoming increasingly tough.

Elephants are a very interesting group of mammals which underwent great evolutionary changes in a relatively short period of time. In some two million years there arose not only various species and subspecies but also new genera of the subfamily Elephantinae.

On the territory of the USSR elephants of the Archidiskodon-Mammuthus phylogenetic line existed from the late Pliocene\* to the late Pleistocene and palaeoloxodonts lived in the early and middle Pleistocene.

It was considered for a long time that *Protelephas planifrons* (Falc. et Cautl.) existed in the Pliocene of Europe as well as in that of India. It has been established by S. Schaub (1948) however, that in Western Europe there are no remains of this species.

Some jaws and teeth of Elephants known from Moldavia, Sea of Azov coast and the Caucasus were described as belonging to *Protelephas planifrons*. The absence of this species in Western Europe (Bout, 1960) and the doubts expressed by some investigators concerning the existance of the genus *Protelephas* in Eastern Europe forced us to reconsider the known data on *P. planifrons* specimens found in the USSR. Our study (Dubrovo 1964a) of the Soviet collections and literature sources has resulted in referring to *A. meridionalis* (Nesti) all the remains pre-

viously related to *P. planifrons*, *P.* cf. planifrons and *P.* aff. planifrons (Burchak-Abramovich, 1951; Gromov; 1948; Pavlow, 1910; Sherstukov, 1954, 1958, and others). Complete number of ridge plates on these teeth is more and the enamel is less thick than it is indicated for *P. planifrons* while the laminar frequency is greater. The subspecies of *P. planifrons* described from the Caucasus as *P. planifrons groznensis* (Sherstukov) is not to be valid. The diagnosis of this subspecies suggested by Sherstukov (1954) includes only general elephantine features. Large complete number of plates and the great laminar frequency on the penultimate and last teeth of "*P. planifrons groznensis*" suggest their belonging to *Archidiskodon* and not to *P. planifrons*.

It was supposed (Nikonov et al. 1971) that P. planifrons might have existed in the late Pliocene of Tajikistan. Extremely fragmentary remains of the elephant from Kuruksay locality were referred to Archidiskodon aut P. planifrons; but the occurrence of the latter in the Pliocene of Tajikistan seems doubtful. The remains apparently belong to the genus Archidiskodon, some teeth, incomplete skull and some bones of a postcranial skeleton of which were known from the late Pliocene deposits of Tajikistan (Beliajeva, 1936; Dubrovo, 1963a, 1963b).

The elephants first appeared on the Black Sea Coast in the late Pliocene. Thus, an elephantine skull with dp<sup>4</sup> and M<sup>1</sup> was unearthed from the lower horizon of the Kryzhanovka locality, near Odessa, which is dated back to the Kuyalnitsky age. The skull was preliminary

<sup>\*</sup>The present work follows the stratigraphic scheme suggested by I. I. Krasnov and K. V. Nikiforova (1973). The Neogene-Anthropogene boundary is taken to correspond to 1,800,000 years ago; the Anthropogene being subdivided into the Eopleistocene (1800 000—700 000 years ago) and the Pleistocene (700 000—10 000 years ago).

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referred to the genus *Palaeoloxodon—P.* cf. ausonuis (Gromov et al., 1961) and permitted to suppose the appearance of *Palaeoloxodon* on the territory of the USSR in Plicoene.

The study of teeth structure of the Kryzhanovka specimen however, shows that it cannot belong to *Palaeoloxodon*.

The molars of Palaeoloxodon are characterized by a high and narrow crown which distinguishes them from the low and broad teeth of Archidiskodon, but the crown of the teeth in the fossil skull from Kryzhanovka is both absolutely and relatively low. The height of M1 is 88 mm. and the height/length index of the tooth does not exceed 50%. The narrowness of the crowns which has just been mentioned is only seeming: the absolute width of M1 is 67 mm. but the width/length index is about 39% and the width/height index is 76%. The upper molars of Palaeoloxodon are considerably higher and narrower. Thus, the width/height index of its teeth is less than 55%. The proportions of M1, complete number of plates (8-9) and their frequency, which is 4, 5-5, make it possible to consider the incomplete Kryzhanovka skull as belonging to Archidiskodon.

The elephants of the *Palaeoloxodon* genus are not known from the Pliocene of the USSR.

Of similar geological age seem to be Archidiskodon specimens from the Kosyakinsky sand-pit and the Kamyshevakha localities, northern Caucasus, USSR (Gabunia, Vekua, 1967). Also from Pliocene but perhaps from somewhat later deposits the finds of Archidiskodon teeth are known on the territory of Moldavia, the coast of the sea of Azov and the Caucasus (Alexeeva, 1965; Dubrovo, Tshepalyga, 1967; Lebedeva, 1974; Pavlow, 1910, and others).

Apart from a great number of localities known to have yielded single remains of A. meridionalis, in the USSR there are two localities, Khapry and Liventsovka, which have already given rich material on late Pliocene Archidiskodon. The Upper-Akchagylian sands are exposed on these both localities, which are near the city Rostov-on-Don. Plentiful material obtained from here during a series of years made it possible to carry out detailed study of fossil mammals remains of the Khaprovian Faunal complex (Alexeeva, 1961, 1965; Bayguscheva, 1971; Dubrovo, Bayguscheva, 1964; Gromov, 1948; Gromova, 1948, and others). The Proboscides from this locality were originally referred by Gromov (1948: 451) to "an already highly evolved form of E. planifrons which properly speaking can be considered even as a primitive E. meridionalis."

Scientific treatment\* of a large series of penultimate

and last molars of the elephant from Khapry and Livent-sovka sandpits made it possible to establish that all these remains belong to a single species. The variational curves of all main diagnostic characters plotted for the elephant teeth from these localities are distinctly monoapical (Dubrovo, Bayguscheva, 1964). The range of variability of all characters do not exceed those common to other species.

The study of the only known specimen of adult male skull from Liventsovka sand-pit and its comparison with the description and photographs of the typical A. meridionalis skulls from Val d'Arno, Italy, failed to reveal any distinctions.

The skulls of fossil proboscideans are found quite rarely, the taxonomy of Proboscidea is based mainly on the characters of their penultimate and especially last molars. To determine exact systematic position of the fossil elephant from Liventsovka and Khapry its molars were compared with the similarly positioned teeth of A. meridionalis from the typical locality of this elephant from Italy.

Comparison of data reported in the literature on molars of the typical Archidiskodon from Italy (Mayet et Deperet, 1923; Osborn, 1942; Pohling, 1889; Weithofer, 1890, and others) with those obtained by the study of abundant serial material from Liventsovka shows that they are almost completely identical (Table I). This allows to refer the Liventsovka elephant to the nominative subspecies A. meridionalis meridionalis (Dubrovo, 1964b).

The assignment of the late Pliocene proboscideans from the USSR to an independent species, A. gromovi Garutt et Alexeeva (holotype adult skull from Liventsovka), cannot be accepted, for morphologically they do not differ from A. meridionalis of equal geological age of Italy.

The authors of A. gromovi pointed out the following specific characteristics: the skull is not high and sagittally elongated, the forehead is narrow, the occipital prominences are feebly marked, the occipital plane and the long axis of the skull are laying at right angle; molars are broad and low, M<sup>3</sup> consist of 12-13 plates with a frequency of 3.5-5, the enamel is 3-5 mm. thick, P<sup>4</sup> is present (Alexeeva, Garutt, 1965).

The study of the adult elephant skull from Liventsovka (holotype of "A. gromovi") and its comparison with A. meridionalis skulls from Italy do not confirm the distinction pointed out for these species. Thus, the absolute height of the holotype skull of "A. gromovi" and that of the lectotype skull of A. meridionalis and their occipital height/width are much the same, i.e. about 950 mm. and 89% in Liventsovka skull and 980 mm and 91%, in the Italian one respectively.

Practically the skulls are equally sagittally elongated so, the diameter/height index in the skull of "A. gromovi"

<sup>\*</sup>Measurement procedures for crania and teeth and a detailed description of all characters of elephantine teeth were given in the work of I. A. Dubrovo (1960).

Table 1

Measurements (mm.) and indices (%) of M³ of 
Archidiskodon meridionalis

Characters	A.	meridionalis	meridionalis	A. meridi- onalis tamanensis
		Italy	USSR	USSR
Tooth length		240—2981	229—303	252—317
		220—320	257—325	259—328
Tooth width		85—122	86—112	85—115
			80—109	82—122
Grown height			116—145	127—185
			104—124	115—150
Complete number of plates .		11—13	10—13	12—17
		11—14	11—13	12—17
Laminar frequency .		4.5—5	45	4.5 - 6.5
		45	3.5—5.5	46
Enamel thickness .			3—4	2.5 - 3.5
			3—4	2.5—4
Height/length index .			41.5—47.2	42.3—69.5
		-	25.7—40.3	41.4—51
Width/length index		3444.6	31.4—44.2	29.8—53.8
		31.8—42.5	28.9—34.5	27.2—42.2
Width/height index .			71.5—91.3	58.6—95.8
			76—84.6	62.7—86.8

<sup>&</sup>lt;sup>1</sup> Data on M<sup>3</sup> are on the line and data on M<sub>2</sub>, under the line.

is 86% and that of the lectotype of A. meridionalis meridionalis, 89%.

The relative width of the forehead in "A. gromovi" and that in the typical A. meridionalis meridionalis are the same, the index of the least forehead width to the occipital width being 29% both in Liventsovka skull and in Italian lectotype skull.

The angle between the occipital plane and the long axis of the skull, as well as the degree of development of occipital prominences in the typical A. meridionalis meridionalis from Italy, are considerably variable, these features being quite different even in the lectotype and cotype skulls (Osborn, 1942, fig. 865). In the latter, as well as in Liventsovka skull, the occipital prominences are hardly marked.

Comparison of other characters of skull structures also fails to reveal any features to distinguish the species

described by L. I. Alexeeva and V. E. Garutt (1965) from A. meridionalis meridionalis.

Besides the holotype a calf skull with pd<sup>4</sup> from Livent-sovka (Alexeeva, Garutt, 1965) was referred to "A. gromovi". A vertical pd<sup>4</sup>—P<sup>4</sup> replacement is seen in this skull and in those of P. planifrons of the same individual age from India. This character is considered to be archaic one and was previously indicated only for P. planifrons. As has already been stated the study of large series of teeth from Khapry and Liventsovka forbids any conclusion about their belonging to two species or even subspecies of elephants. Laminar frequency, enamel thickness, complete number of M³ plates beyond any doubt rule out the possibility of referring the fossils from this locality to P. planifrons which is recognized to possess M³ with smaller complete number of more widely spaced plates.

This makes us follow V. I. Gromov, L. I. Alexeeva and V. E. Garutt in supposing that the skull with pd<sup>4</sup>-P<sup>4</sup> vertical replacement may belong to the genus *Archidiskodon*.

Except for this skull we did not know other skulls or fragments of upper jaw bones with teeth of Archidiskodon of this individual age. Consequently, one cannot say how the replacement of pd<sup>4</sup> proceeded in the typical A. meridionalis, in vertical direction as in more ancient P. planifrons, or horizontally, as it was the case in more later elephants. It is also not excluded that the vertical pd<sup>4</sup>—P<sup>4</sup> replacement, characteristic of Mastodonts and P. planifrons, and observed only in the skull of just one individual of Archidiskodon due to atavism. In elephants the atavism seems to find its reflection in the presence of tusks in the lower jaw of A. celebensis Hooijer (Hooijer, 1954).

Considering all mentioned above vertical replacement of pd<sup>4</sup>—P<sup>4</sup> in only one skull from Liventsovka cannot be regarded as a character distinguishing the Khapry elephant, i.e. "A. gromovi", from the typical A. meridionalis from Italy.

The pd<sup>4</sup> replacement in the lower jaws of the Liventsovka calves proceeded horizontally and P<sup>4</sup> is missing.

The molars of "A. gromovi" and the typical Archidiskodon from Italy possess a wide and low crown and a thick layer of enamel. Complete number of M³ plates (12-13) indicated for "A. gromovi" is not distinguished from that characteristic of A. meridionalis meridionalis from Italy.

Thus, the comparison of the diagnostic characters of "A. gromovi" with those of A. meridionalis meridionalis from Italy shows their identity, "A. gromovi" being a junior synonym.

Absence of differences in the skull structure and dentition of the elephant from Liventsovka and other late Pliocene localities of the USSR including the remains 36 I. A. DUBROVO

described as *P. planifrons* and *A. gromovi* and in those of typical *Archidiskodon* of Italy suggests that these elephants to the same nominative subspecies *A. meridionalis* (Nesti).

The validity of "A. gromovi." has been questioned by V. I. Gromova (1965), L. K. Gabunia and A. K. Vekua (1967).

Probably, A. meridionalis taribanensis Gabunia et Vekua may be considered as somewhat later subspecies of Archidiskodon. Only one nearly complete adult male skeleton with a skull is known to be found in the upper Akchagyl-lower Apsheron deposits near the village of Taribana in the Caucasus (Gabunia, Vekua, 1963).

Taribana skull differs from that of A. meridionalis meridionalis in a number of characters. It has a wide forehead and an elongated postrostral portion (Gabunia, Vekua, 1963). Thus, the calculated index of the smallest forehead width to the width of the occiput is 47% in A. meridionalis taribanensis and about 30%, in A. meridionalis meridionalis from Val d'Arno and Liventsovka. The index of the distance between the occipital summit and the lower edge of the nasal opening (along the median line of the skull) to the extreme occipital width makes up 74% in Taribana elephant, near 60% in Liventsovka individual and probably even somewhat less in the holotype of Archidiskodon meridionalis meridionalis.

The interalveolar depression in the frontal portion of the Taribana skull extends almost up to the nasal opening and in A. meriodionalis meridionalis its end lies considerably lower.

All the distinctions stated certainly do not exceed the rank of subspecies. There are no absolute distinctions in M3 structure in Taribana elephant and in that of the typical Archidiskodon. It can be only pointed out that the index of the relative crown width of the last molars in Taribana elephant is close to the upper limit of this index in A. meridionalis meridionalis.

The relatively small width of molars, great number of conelets of the upper portion of their plates and elongated post-rostral portion of the skull could probably be considered as features of slightly more advanced A. meridionalis taribanensis. It agrees well with its geological age, probably a little more late than that of the typical Archidiskodon (Lebedeva, 1974).

It is A. meridionalis tamanensis Dubrovo (Plate I, Fig. 1), that is an evolutionary more progressive and geologically more late form of Archidiskodon.

This species has been established (Dubrovo, 1964b) by a lot of serial materials from the Siniaya Balka locality in the Taman Peninsula, the type locality of the Taman fauna complex (Gromov, 1948). The study of all molar characters with highly elaborated techniques (Dubrovo, 1960) precluding from any errors which might arise from neglecting the position of teeth, the degree of wearing

out, etc., resulted in establishing the variability limits of these characters. A great number of identically ordered and positioned teeth, got from one and the same locality, made possible their biometric study (Dubrovo, 1963c).

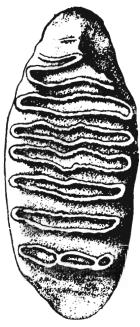


Fig. 1. Archidiskodon meridionalis tamanensis Dubrovo, Holotype M<sup>2</sup> N 1358-57, v. Siniaya Balka, Taman Peninsula, USSR; Eopleistocene. × 2/5 approx.

Biometric treatment of data on more than 250 penultimate and last molars has revealed that the variational curves of the principal diagnostic characters (number and frequency of plates, size and proportions of teeth, enamel thickness) are of distinctly monovertex type. It proved all the remains to belong to a single species. The molars of elephants from Siniaya Balka are characterized on the average, by a large complete number of somewhat more closely spaced plates having a less thick layer of enamel, the crowns being often narrower and higher (see Table 1). All this witness to the specimen from Siniaya Balka being more advanced than the typical Archidishodon.

In the number of plates 75% of  $M^2$  and  $M^3$  from Siniaya Balka differ from all corresponding molars of A. meridionalis meridionalis from Italy and Liventsovka; 50% of  $M_3$  from Siniaya Balka differ from all Liventsovka  $M_3$  as well as from  $M_3$  of A. meridionalis meridionalis described from Italy.

According to E. Mayr (Mayr et al., 1953) these distinction suffice for a species to be divided in two sub-species. The coefficient of distinction (CD) in the number of plates of M³ in A. meridionalis meridionalis and A. meridionalis tamanensis is 1.8 and it is recommended (Mayr et al., 1953), if the coefficient of distinction

exceeds 1.28, to refer two populations to two distinct subspecies.

The only skull found in Siniaya Balka belongs to an adult female. Certain distinctions become apparent from its comparison with the female skull of the typical *Archidiskodon* originally described as belonging to a separate species, *A. lyrodon* (Weithofer).

Very few skulls known to belong to A. meridionalis, most of which being either incomplete, like those from Italy, or essentially restored, like the skull of adult elephant from Liventsovka, do not permit to establish the individual variability of their characters. Therefore, it is quite possible that with new materials some of subspecific distinctions established by the skull characters may well turn out to be only individual ones.

First appeared on the territory of the USSR in its south-europian part the latest Pliocene and Eopleistocene representatives of the genus *Archidiskodon* are also known from the Middle Asia, Kazakhstan and Siberia (Beliajeva, 1948; Dubrovo, 1953, 1961; Zhilkibayev, 1963, 1972; Vangengeim, 1975; etc.).

In the late Pliocene subspecies of A. meridionalis meridionalis was common in the Europian and Asiatic parts of the USSR; in the Eopleistocene—that of A. meridionalis tamanensis.

The subspecies A. meridionalis taribanensis is known only from the latest Pliocene—early Eopleistocene of the Caucasus.

Distribution of elephants become even wider in the Pleistocene of the USSR.

During the late Pliocene, Eopleistocene and Pleistocene the elephants constantly evolved adapting to the changing environment, i.e. cooling of climate, becoming of more continental type and change of vegetation leading to changes in forage reserves.

In the early Pleistocene the first representatives of the genus Mammuthus appeared; the earliest of them being M. trogontherii (Pohlig) represented by two subspecies (see Table 2), the early Pleistocene M. trogontherii trogontherii (Pohlig) and the middle Pleistocene M. trogontherii chosaricus Dubrovo (Dubrovo, 1966).

M. trogontherii was first described by the remains from Süssenborn, an early Pleistocene locality in Germany. To the same species Pohlig (1889) referred yet an other elephant, the one from Rixdorf, geologically more late locality. The lectotype of M. trogontherii is M<sub>3</sub>, from Süssenborn.

Examining the remains of an early Pleistocene elephant from Tiraspol, the locality in Moldavia, USSR, M. Pavlow (1910) defined it as a new species, E. wüsti Pavlow, pointing out that it was identical to the specimen from Süssenborn but different from the Rixdorf specimens. According to the rules of zoologic nomenclature when dividing a species the old name is preserved by the species

Table 2

Measurements (mm.) and indixes (%) of M<sub>3</sub><sup>3</sup> of Mammuthus trogontherii

Character	M. trogontherii trogontherii M. trogontherii chosaricus			
Characters	Susseborn, GDR	Tiraspol, USSR	USSR	
Tooth length	246—400²	303—370	310	
	225—383	300-410	225—370	
Tooth width	73—120	86—115	86—108	
	74—114	79—115	74—98	
Crown height	129—212	160—211	160—180	
	127—167	130—173	120—144	
Complete number of plates	18—23	1622	20—21	
	16—21	16—21	18—24	
Leminar frequency	4—7	5—7	5.5—7	
	4-7.5	4—7	5.5—7	
Enamel thickness	2—3	23	2-2.5	
	2—3	2—3	2-2.5	
Height/length index	47—61.8	50.6; 51.7	••••	
	38.5—47	37—43	34.4—47	
Width/length index	27.8—36.3	29.1; 33.8	••	
	25.2—30.5	23.8—29.9	25.6—37.7	
Width/height index	4869.8	46.1—63.7	52.9—62.5	
	56—71.7	59.7—67.5	59.7—75.5	

<sup>&</sup>lt;sup>2</sup>Data on M<sup>3</sup> are on the line and data on M<sub>3</sub>, under the line.

that retains the former lectotype. So even in the case of dividing Pohlig's species in two the species from Tiraspol should be named *M. trogontherii* (Dubrovo, 1963b).

The Tiraspol elephant is referred to this species by A. I. David (1964), I. A. Dubrovo (1963, 1971), V. I. Gromova (1965), N. K. Verescagin (David, Verescagin, 1971) and most West-Europian paleontologists. In the Soviet, mostly in geological literature, however, the name Wusti's elephant is rather common. In this connection comparative study (Dubrovo, 1971) of all materials on the Tiraspol and Süssenborn specimens was conducted (see Table 2) which included biometric examination of molars and gave the quite conclusive proof that the elephants from both localities are taxonomically identical and belong to a single subspecies, M. trogontherii trogontherii.

While the Süssenborn elephant is generally recognized as belonging to the genus *Mammuthus*, the Tiraspol elephant is considered by some scientists to be a species of

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the genus Archidiskodon, V. E. Garutt (1971, p. 86) suggests to refer "the early primitive form of Trogontherian elephant to the genus Archidiskodon whereas the late advanced form, to Mammuthus". But the structure of the lower jaw and the non-serial disposition of the carpal bones support the reference of Tragontherian elephant to the genus Mammuthus (Dubrovo, 1963b, 1971).

Neither can we agree with V. E. Garutt (1971 p. 86) who assigns the Tiraspol elephant to a separate subspecies, A. trogontherii wiisti (M. Pavl.) on the assumption that "there are enough grounds (geographical remoteness of Süssenborn from Tiraspol, differences in the composition of the associating faunas, etc.) to retain Wiistian elephant as a geographic subspecies of Trogontherian elephant". The indicated characters of taxonomic differences between the Tiraspol and Süssenborn elephants, which are morphologically non-distinguishable (Dubrovo, 1971; Garutt, 1971) can not be accepted. The common areal distribution of M. trogontherii trogontherii is also supported by finds in Poland (Kubiak, 1965, and

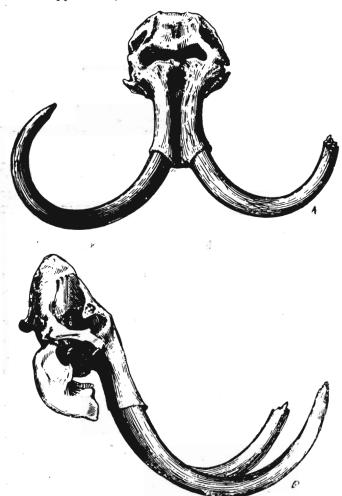


Fig. 2. Mammuthus trogontherii chosaricus Dub:ovo. Holotype skull with the lower jaw, v. Cherny Yar, Lower r. Volga region, USSR. Middle Pleistocene. (a) front view; (b) side view; both × 1/20 approx.

others). Moreover, the study of fossil mammals remains from Tiraspol and Süssenborn has revealed the affinity of Equidae, Cervidae, Bovidae and other groups of mammals from these localities (Gromova, Dubrovo, 1971; Flerov, 1969; Kahlke, 1971, and others).

The Tiraspol elephant has no diagnostic characters different from those of the typical Süssenborn M. trogontherii trogontherii, and its belonging to the genus Mammuthus is beyond doubt.

The late form of *M. trogontherii*, i.e. *M. trogontherii* chosaricus Dubrovo (figs. 2, 3), is characterized by somewhat more progressive structure. The distinctions between the two subspecies of *M. trogontherii* were established by the molar characters only, as there are no data on the skull of *M. trogontherii trogontherii*. There are differences in the number of plates, their frequency, enamel thickness and crown width (see Table 2). All distinctions are transgressive (Dubrovo, 1966), the rank rising of Chosarian elephant from subspecies to species, suggested by some authors, could not be, therefore, accepted. *M. trogontherii chosaricus* is known from the middle Pleistocene both of European and Asiatic parts of the USSR.



Fig. 3. Mammuthus trogontherii chosaricus Dubrovo. Holotype M<sub>3</sub>. v. Cherny Yar, Lower r. Volga region, USSR; Middle Pleistocene. × 2/5 approx.

Next in the phylogenetic succession is the Mammoth, M. primigenius (Blumenbach). There are numerous remains of Mammoth on the Territory of the USSR. In

the late Pleistocene it lived almost all over the country, from the Novosibirsk Islands in the North to the Crimea in the South and from the western State boundary areas to Kamchatka peninsula in East.

Two forms of *Mammuthus* are distinguished now quite clearly: the early and the late one. They differ both morphologically and stratigraphically. The latter form has molars with a greater number of more closely spaced plates higher crown and thinner enamel. All this formed very strong grinding apparatus and pointed to a higher degree of specialization.

Elephants of the phylogenetic line Archidiskodon—Mammuthus evolved undoubtedly very rapid. Within approximately two million years elephants developed from such form as Archidiskodon, which lived in a warm and damp climate and feeded on soft and lush vegetation, to Mammoth, a form adopted to live in cold and rather dry tundra-steppe and to feed on tough forage.

This rapid evolution was conditioned by the drastic climatic changes during Anthropogene, which in relatively short period of time, completely altered the environments of elephants in Europe and northern Asia.

#### REFERENCES

- ALEXEEVA, L. I. 1961. The oldest mammalian Anthropogene fauna of the south-european part of the USSR. In Geologicheskie problemy Anthropogena. 31-34.
- ALEXEEVA, L. I. 1963. Stratigraphic review of the Eopleistocene Proboscidea. In Chetvertichnyi period i ego istoriya.
- ALEXEEVA, L. I. and GARUTT, V. E. 1965. New data on the evolution of Archidiskodon. Bull. Comissii po izuch. chetvert. Perioda. 30: 161-166.
- BAIGUSHEVA, V. S. 1971. Fossil mammals fauna from the Liventsovka sand-pit, north-eastern region of the Azov Sea coast. In Materialy po faune Anthropogena SSSR. 3-29.
- Beliajeva, E. I. 1936. On the fossil Elephas found in Tajikistan.

  Trudy Paleozool Inst. AN SSSR. 5: 103-107.
- Beljajeva, E. I. 1948. On the fossil Elephas (Archidiskodon) meridionalis
   Nesti and Mastodon borsoni Hays found in the Chkalov region,
   USSR. Bull. Comissii po izuch. chetvert. perioda. 12: 78-84.
- Bour, P. 1960. Le villafranchien du Velay du bassin hydrographique moyen et superieur de l'Allier Le Puy.
- Burchak-Abramovich, N. I. 1951. Protelephas planifrons Falc. and related forms in Transcaucasia. Izv. Ak. Nauk Az. SSR. 2: 75-81.
- DAVID, A. I. 1964. Elephantine remains from the Anthropogene deposits of Moldavia. Trudy III Confer. Molod. Uchen. Moldavii. 13-15.
- DAVID, A. I. and VERESCHAGJN, N. K. 1967. The state of the facts and further tasks in investigation of fossil faunas from Moldavia. Mesto i znachenie iskopaemykh mlekopitauschich Moldavii v Kainozoe SSSR. 10-37.
- Dubrovo, I. A. 1953. On the first specimen of Elephas meridionalis

  Nesti found in northern Siberia. Bull. Comissii po izuch. chetvert.

  perioda. 17: 76-79.
- Dubrovo, I. A. 1960. Ancient Proboscidea of the USSR. Trudy Paleont. Inst. AN SSSR. Moscwa. 85: 1-78.
- Dubrovo, I. A. 1961. On the teeth of Archidiskodon meridionalis (Nesti) found in Kazakhstan, USSR. In Materialy po istorii fauny i flory Kazakhstana. 3: 58-61.

- Dubrovo, I. A. 1963a. New data on the late Genozoic mammals of Tajikistan. Paleontol. Journ. 2: 155.
- Dubrovo, I. A., 1963b. On systematic position of "Elephas wusti". Paleontol. Journ. 4: 95-102.
- Dubrovo, I. A. 1963c. New data on the Taman faunal complex of vertebrates. Bull. Mosk. Obstchest. Ispyt. Prirody. Otd. Geol. 6: 94-99.
- Dubrovo, I. A. 1964a. On the existence of Protelephas planifrons (Falc. et Cautl.) on the territory of the USSR. Soobstch. Ak. Nauk Gruz. SSR. 34(3): 599-603.
- Dubrovo, I. A. 1964b. Archidiskodon of the USSR. Paleontol. Journ. 3: 82-94.
- Dubrovo, I. A. 1966. On systematic position of fossil elephant from the Khozarskyf aunal complex. Bull. Comissii po izuch, chetvert perioda. 32: 63-74.
- Dubrovo, I. A., 1971. The order Proboscidea. In Pleistocene Tiraspolya. 92-108.
- Dubrovo I. A. and Baygusheva, V. S. 1964. Elephants of the Khaprovskiy faunal complex (on the materials from Liventsovka sand-pit). Bull. Mosk. Obstchest. Isypt. Prirody, Otd. Geol 39(5): 133-136.
- Dubrovo, I. A. and Tshepalyga, A. L. 1967. The remains of fossil elephants in the Dniester terraces and their stratigraphic significance. In Paleontologiya, geologiya i polesnye iskopaemye Moldavii. 191-203.
- FLEROV, K. K., 1969. On fossil bisons from the Tiraspol faunal complex. Tesisy dokl. k Mezhdunarodnomu Gollokviumu po geologii i faune niznnego i srednego Pleistocena Evropy. 11-12.
- GABUNIA, L. K., and Vekua, A. K. 1963. Fossil elephant from Taribana. Tbilisi.
- GABUNIA, L. K. and VEKUA, A. K. 1967. On new find of southern elephant remains in the northern Gaucasus. In Fauna Keinosoya Gruziii i ee geoistoricheskoe znachenie. 101-103.
- GARUTT, V. E. 1954. On southern zlephant Archidiskodon meridionalis, (Nesti) from the Pliocene of the northern coast of the Sea of Azov. Trudy Comissii po izuch. chetvert. perioda. 10(2): 1-7
- GARUTT, V. E. 1971. To the history of the discovery of intermediate forms within the phylogenetic line. *Archidiskodon-Mammuthus* In Chronologia lednikovogo veka. 78-88.
- Gromov, V. I., 1948. Palaeontological and archaeological substantiation of the stratigraphy of the Quarternary continental deposits of the territory of the USSR. Trudy I.G.N., Ser. Geol. 64 (17): 1-591
- Gromov, V. I. 1972. The Tiraspol faunal complex. In Geologiya i fauna nizhnego i srednego Pleistocena Evropy. 168-177-
- Gromov, V. I., Krasnov, I. I., Nikiforova, K. V. and Shantser, E. V. 1961. The state of the problem on the lower boundary and stratigraphic subdivision of the Anthropogene (Quarternary) system. In Voprosy geologii Anthropogena. 7-19.
- GROMOVA, VERA I. 1948. The history of horses (genus Equus) in the Old World. Trudy Paleontol. Inst. 17 (1): 1-374.
- Gromova, Vera I. 1965. Brief review of the Quarternary Mammals in Europa. "Nauka" Moskwa.
- Gromova, Vera I. and Dubrovo, I. A., 1971. Family Equidae Gray, 1871. In Pleistocene Tiraspolya. 108-127.
- Hooijer, D. A. 1954. Pleistocene vertebrates from Celebes. XI.

  Molars and tusked mandible of Archidiskodon celebensis Hooijer.

  Zool. Mededelingen. 33(15): 103-120.
- ZHILKIBAEV, K. ZH. 1963. Fossil remains of Elephants in the collections of the Institute of Zoology of the Ac. Scil of Kazakh. SSR. In Materialy po istorii fauny i flory Kazakhstana. VI. 66-76.
- ,ZHILKIBAEV K. ZH. 1971. Anthropogene elephants from Kazakhstan. Avtoreferat kandid. diss. Alma-Ata.

- Kahlke, G. D, 1971. The family Cervidae Gray, 1821. In Pleistocene Tiraspolya. 137-156.
- Krasnov, I. I. and Nikiforova, K. V. 1973. Stratigraphical scheme of the Quarternary (Anthropogene) of the USSR specified according to materials of the last years. In Stratigraphiya, paleogeographiya i lithogenes Anthropogena Evrasii. 157-188.
- Kubiak, H. 1965. Fossil elephants of South Poland. Folia Quaternaria. 19: 1-43.
- Lebedeva, N. A. 1974. Correlation of continental and marine deposits of the Eopleistocene and lower Pleistocene of the Post Caspian region. Avtoreferat doktor diss. Moskwa.
- MAYR, E. LINSLEY, E. and USINGER, R. 1953. Methods and principles of systematic zoology. New York.
- MAYET, L., et DEPERET, C. 1923. Les elephants pliocenes. Ann. de l'Univ. de Lyon, nouv, ser. 1(43): 1-213.
- NIKONOV, A. A., PEN'KOV, A. V., TROFIMOV, B. A., VANGENGEIM E. A., DMITRIEVA, E. L. and SOTNIKOVA, M. V. 1971. New data on the geology and fauna of the upper Pliocene and lower Pleistocene mammals of southern Tajikistan. Bull. Mosk. Obst-chest. Ispyt. Prirody. Otd. Geol. 6: 129.
- OSBORN, H. F. 1942. Proboscidea, a Monograph of the Discovery, Evolution and Extinction of the Mastodonts and Elephants of the World. 2. The Amer. Mus. Press, New York.
- Pavlow, M. 1910. Les elephants fossiles de la Russie. Nouv. mem. Soc. Natur. (Moscou). 27(2): 1-56.

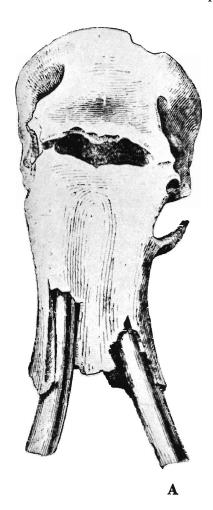
- PAVLOWA, M. 1931. Fossil elephants of the southern part of the USSR: *Elephas planifrons* Falc. and others. Sbornik pamyati Tutkovskogo P. A. 2. 67-85.
- Pohlic, H. 1889. Dentition und Kraniologie des Elephas antiquus Falc. mit Beitrage uber Elephas primigenius Blum. und Elephas meridionalis Nesti. Nova Acta d. ksl. Leop.-Carol. Deutsch. Ak. s Naturfor. 53(1): 1-280.
- Schaub, S 1948. Das Gebiss der Elephanten. Verhandl. d. Naturforsch. Gesellsch. im Basel 59: 89-112.
- SHERSTUKOV, N. M. 1954. Description of the fossil elephantine remains found in the Checheno-Ingush Autonomous Soviet Socialist Republic. Trudy Est-Ist. Museya AN Az. SS. 8: 227-261.
- SHERSTUKOV, N. M. 1958. On a new find of a fossil jaw of Protelephas planifrons in the Checheno-Ingush ASSR, Caucasus, in Asia-Vertebr. Palasiat. 2(4): 254-258.
- VANGENGEIM, E. A. 1975. Palaeontological substantiation of stratigraphy of Anthropogene deposits in the northern Asia (by mammals). Avtoreferat dokt. diss.
- Verescagin, N. K. and David, A. I. 1971. Mamma lia in the time of the formation of Tiraspol gravel deposits. In Materialy pofaunam Anthropogena SSSR. 30-43.
- WEITHGER, K., 1890. Die fossilen Proboscidier der Arnotales in Toscana. Beitr. Pal. Osterr.-Ung. 8: 107-240.

## EXPLANATION OF PLATE

## PLATE I

Fig. 1. Archidiskodon meridionalis tamanensis Dubrovo. Holotype, female skull N 1358-57; Siniaya Balka, Taman Peninsula, USSR. Eopleistocene. (A) front view, × 1/12 approx.; (B) side view, × 1/10 approx.





 $\mathbf{B}$