The phanagorian elephant *Phanagoroloxodon mammontoides*Garutt, 1957 from the Pliocene of the north-western Caucasus.2

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SUMMARY

In 1957 the author detected in the collection of the Yekaterinodar (Krasnodar) Historical and Archeological repository-museum the skull of an extinct elephant, of a previously unknown form. The skull had been found at the end of the last century in the north-western Caucasus, on the bank of the river Psekups, in the district of the village Saratovskaya. The form got the denomination *Phanagoroloxodon mammontoides* Garutt, 1957. Its probable age is Late Pliocene or Early Pleistocene.

Craniological and odontological characters of the new form served to the author as a reason for including it into the sub-family Elephantinae and the tribe Phanagoroloxodontini established by Garutt (1991). According to their morphological characters, the representatives of this tribe occupied a nearly intermediate position between the tribes Elephantini and Mamuthini belonging to the same subfamily. The author advances a supposition that the tribe Phanagoroloxodontini could be the progenitor of these two filial tribes.

SAMENVATTING

In 1957 ontdekte de auteur in de collectie van het Yekaterinodar (Krasnodar) Historische and Archeologisch Museum de schedel van een uitgestorven, tot nu toe onbekende soort olifant. De schedel was gevonden aan het eind van de vorige eeuw in het noordwesten van de Caucasus, aan de oevers van de rivier de Psekups, in het district van het dorp Saratovskaya. De soort kreeg de naam *Phanagoroloxodon mammontoides* Garutt, 1957. De schedel is waarschijnlijk van Laat Pliocene of Vroeg Pleistocene ouderdom.

Morfologische kenmerken van schedel en gebit pleiten voor de indeling van deze nieuwe soort in de subfamilie Elephantinae en het tribus Phanagoroloxodontini, welke werd opgericht door Garutt (1991). Uitgaande van de morfologische kenmerken, moeten de leden van dit tribus een tussenpositie tussen de tribi van de Elephantini en de Mamuthini uit dezelfde subfamilie hebben ingenomen. De auteur verdedigd de stelling dat het tribus Phanagoroloxodontini het voorouder tribus kan zijn van de twee andere tribi uit de subfamilie Elephantinae.

Introduction

During his investigatons of paleontological collections at the Historical-Archeological repository-museum of Yekaterinodar (Krasnodar) in 1957, the author detected a skull of an extinct elephant. The label for this exhibit had been lost, yet on the basis of indirect data (ancient photographs of the museum exposition as well as the catalogue of collections published by K. Zhivilo in 1909) it was possible to ascertain that the skull had been found in the north-western Caucasus, on the bank of the river Psekups (the left tributaru of the Kuban river) in the district of the village Saratovskaya. It was delivered to the museum by I.N. Chistyakov in 1885.

Description

The osseous matter of the skull is considerably mineralized, and this may serve as the evidence of its great antiquity. The surface was in many spots covered with a crust formed by carbonate-cemented sand of a polymictic composition. Identical rock fills the skull cavities. Most probably the sand has an alluvial origin. This is evidenced by the variegated mineral composition of the sand (quartz, microcline-perthite, acid plagioclase, hydrated biotite a.o.) and by its rather typical roundness. One may suppose that the crust formation on the skull was connected with the activity of phreatic waters which

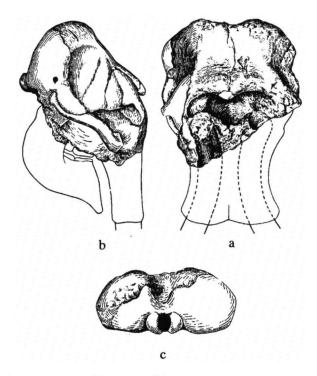


Fig. 1: The skull of *P. mammontoides* Garutt, 1957. a) frontal view b) lateral view c) occipital view.

Fig. 1:Schedel van *P. mammontoides* Garutt, 1957. a) frontaal aanzicht b) lateraal aanzicht c) occipitaal aanzicht.

circulated in these sands as shown by the hydrated bio-

The initial study of the elephantine skull from Psekups was accomplished by the author in Yekaterinodar (Krasnodar). For a further, more detailed examination it was transported to St.-Petersburg, to the Zoological Institute of the Russian Academy of Sciences. There the skull was subjected to a careful preparation: it was cleaned of the rock that covered it. As a result, there became accessible for investigation the formerly invisible parts of the skull (Fig. 1).

The skull is damaged: it lackes occipital condyles (condyles occipitales) and both cheek-bone arces (arcus zygomaticus) of which there remain only the cheek-bone processes (processus zygomatices) of the temporal and upper-jaw bones of the left side. On the right side the suborbital process (processus suborbitalis) has also been lost. Damaged are also the right half of the occiput surface, both intermaxillary bones (ossa intermaxillares). Better preserved is the left bone bearing the base of the tusk. The first hind-molar theeth (dentes molares) - M1 - also reveal traces of damage: their masicatory surface has been crumbled (Fig. 2).

The skull preparation was carried out by the author and I.F. Rumyantseva. After the preparation was finished, the missing parts of the skull were reconstructed by the sculptress E.A. Urlina, under the author's guidance. It consisted of the reproduction of the damaged parts of one half of the skull according to its mirror-reflected other side, which had remained undamaged. Therefore the correctness of the reconstruction arouses no doubts. Arbitrary is only the reconstruction of the occipital condyles (condylorum occipitalium), and of the cheek-bones (ossium zygomaticum). The damaged intermaxillary bones did not undergo reconstruction in order to leave the base of the right tusk and the alveole of the left one accessible for examination.

According to its combination of morphological characters the Psekups skull differs from the skulls of other, previously known forms of elephants, extinct as well as extant. In consideration of such data the author (GARUTT, 1957, 1958) deemed it possible to describe this finding as a type of a new elephantine species and genus, denominated Phanagorian - Phanagoroloxodon mammontoides - and later on included by him (GARUTT, 1991) in an independent tribe - Phanagorodontini.

The Systematic part

Order Proboscidea Illiger, 1811
Suborder Elephantoidea Osborn, 1921
Family Elephantidae Gray, 1821
Subfamily Elephantinae Gray, 1821
Tribus Phanagorodontini Garutt, 1991

The denomination of the tribe is derived from the name

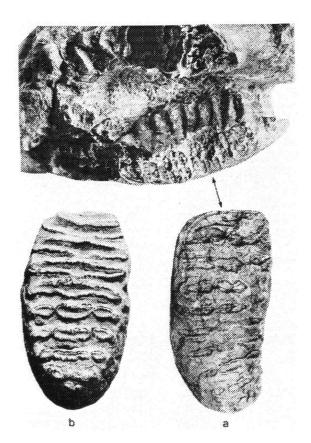


Fig. 2: The first upper molar (M1) of a) P. mammontoides and b) A. meridionalis

Fig. 2: Eerste bovenkaaksmolaar (M1) van a) P. mammontoides b) A. meridionalis.

of the ancient Greek town Phanagoria which was situated in VI-IV centuries B.C. on the Asiatic shore of Bosporus Kimmerian (the Taman peninsula).

The description: The cranium (Fig. 1, Table 1) is somewhat stretched in longitudinal direction. The surface of the occiput is almost flat; the occipital tubercles representing paired prominences, symmetrically situated on both sides of the occipital fossa, are feebly developed. The top of the skull, whether examined from the anterior side or from behind, has the outline of a semicircumference with a well developed saddle-formed groove (incisura cranii) in its middle part. The temporal fossae with their distinct borders are clearly seen. The frontal surface is low and broad, slightly concave in the longitudinal as well as the transverse direction; the frontal protuberance is not developed. The nasal process is feebly prominent relative to the frontal surface, rounded at its end, oval in section at its base. The nasal orifice, situated abve the level of the upper borders of the orbits, is broad and has the shape of a crescent with lateral edges pointed and slightly lowered downwards. A lateral view of the skull shows that the anterior borders of the orbits slightly protrude relative to the front of the skull and the intermaxillary bones. The supraorbital processes are moderately developed; the skull breadth in this region is smaller than the breadth of the occipital region. The tubercles of the Lachrymal bones are feebly

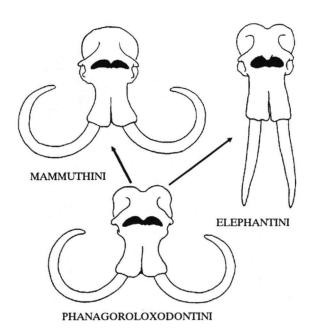


Fig. 3: Scheme of phylogenetic relationships of the Elephantinae. Fig. 3: Schema van de phylogenetische relaties van de Elephantinae.

developed. The intermaxillary bones, whether seen from the anterior or posterior side, have an X like shape: They are broad at the base, at the level of the supraorbital foraminae, tapering gradually in their middle part, and widening again towards the anterior borders

of the tusk alveoles. The tusks have a distinctly visible spiral curvature; on leaving the alveole they are directed downwards and sidewards, then they gradually turn upwards and inwards, their ends nearly meeting. The hind molar teeth (table 2, Fig. 2a) are relatively broad, the figures of laminae obliteration on the masticatory surface are developed after the types lat.lam., med.ann. that may be graphically expressed as ___. __. The laminae slightly damaged by obliteration, have the figures developed after the type lat.ann., med.lam., that is . . .

Comparison (Fig. 3). - According to their morphological characters, the elephants of the tribe Phanagoroloxodontini occupy a somewhat intermediate position between two other tribes, belonging to the subfamily Elephantinae: the elephants of the mammoth line - Mammuthini (genera Archidiskodon, Mammuthus, Parelephas) and the elephants in the strict sense of the word - Elephantini (genera Elephas, Hypselephas, Platelephas).

The resemblance to the Elephantini is revealed in the structure of the skull top (the presence of a saddle like groove), by distinctly developed temporal fossae, a concave frontal surface, the rounded shape of the nasal process, feebly developed supraorbital processes and lachrymal tubercles. The new tribe approaches the representatives of Mammuthini by the structure of the occipital section of the skull, almost devoid of tubercles, by the cresent like outlines of the nasal orifice and by the shape of the intermaxillary bones as well as by the spirally curved tusks and the hind molar teeth with obliteration figures on the laminae, expressed after the type

1)Length of skull: from anterior edge of orbits to the posterior edge of the c	ondyles. ca 523
2)Height of skull: from top of skull to masticatory surface of upper molars	ca 540
3)1/2	97
4)Height of cranial arch: from top of skull to ventral edge of external acousti	ic duct 260
5)Height of occiput: from top of skull to ventral edge of condyles	ca 342
6)Width of occiput	530
7)5 / 6	65
8) Distance from top of skull to ventral edge of nasal orifice	352
9)Minimal width of facial surface of the skull	310
10)Width of skull at the level of the supraorbital proces-ses	510
11)10/6	96
12)Height of orbit	ca 136
13)Width of nasal orifice	343
14)Maximum height of nasal orifice	91
15)Minimum distance from nasal orifice to the temporal fossa	83
16)Width of skull at the level of the proc. zygomaticum of the temoral bone	530
17)Width of skull at the level of the proc. zygomaticum of the maxillary bone	360
18)Width of intermaxillary bones at the level of suborbital foramina	345
19)Length and width of articulation surface for the lower jaw	96*77

Table 1: Measurements (mm) and indices (%) of the skull of *Phanagoroloxodon mammontoides*.

Tabel 1: Maten (mm) en verhoudingen (%) van de schedel van *Phanagoroloxodon mammontoides*.

. _____. All this gives us the right to advance the supposition that the elephants of the tribe Phanagoroloxodontini (its early representatives) could be the progenitors of two filial tribes: Mammuthini and Elephantini.

The composition of the tribe:

Genus Phanagoroloxodon Garutt, 1957.

Synonimum: ?Elephas; Aguirre, 1969, p. 347.

Type species: *P. mammontoides* Garutt, 1957; late Pliocene or early Pleistocene of the northwestern Caucasus. For the description and comparison see description and comparison of the tribe.

The composition of the species is monotypic.

The expanse of the species is from the Late Pliocene to the Early Pleistocene of the north-western Caucasus.

Phanagoroloxodon mammontoides Garutt, 1957 - The Phanagorian elephant.

Tables 1, 2, Fig. 1, 2.

?Elephas mammontoides Aguirre, 1969, p. 347.

The holotype. The skull of a female elephant (?) with the first upper molars (without lower jaw). The Yekaterinodar museum of history and regional studies, no. 40. The north-western Caucasus, the river Psekups, the village Saratovskaya. Late Pliocene or Early Pleistocene.

For the description see the description of the tribe.

The comparison of the skull. Its comparison has been given previously in the discussion of the peculiarities of the tribe Phanagoroloxodontini. Here we analyze the question concerning the comparison of the dental system. In the structure of its hind molar teeth *P. mammontoides* has almost no difference from the representative of the Mammuthini tribe, *Archidiskodon meridionalis* (NESTI, 1825). This may be ascertained by a visual comparison of the teeth of these elephants (Fig. 2) as well as by a juxtaposition of their numeral exponents (Table 2).

Observations. Such a similarity in the teeth structure may be explained as the result of their convergent de-

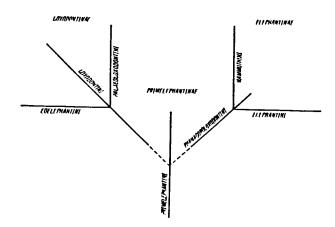


Fig. 4: Scheme of phylogenetic relationships of the elephantinae.

Fig. 4: Phylogenetisch relatiediagram van de Elephantidae.

velopment in the elephants of different origin but existing under analogous natural conditions and adapted to analogous vegetative nutrition. This was recorded by Vaufrey (1955) for several taxons of Proboscidae. For their occurence see the description of the genus.

The origin and the evolutionary course of the elephants of the tribe Phanagoroloxodontini

The ancestral birthplace of elephants is in Africa. Just in the east of its equatorial part there have been detected the reamains of the most ancient and archaic representatives of this family (MAGLIO, 1970, 1973), which got the denomination *Primelephas gomphoteriodes*. The remains of this species are connected with deposits formed in the second half of the Miocene, their age being approximately defined as 5.5 to 5.0 million years. To jedge from the tooth structure, this elephant lived in humid tropical forests and its nutrition consisted of soft succulent vegetation (GARUTT, 1977, 1986).

The aridization of the African climate, occurring in the Pliocene, led to a considerable reduction of woodland areas and to the expansion of savannah and prairie

	P. mammontoides	A. meridionalis			
	M 1	N	Min	Max	M
Length of crown	163	6	137	166	151
Width of crown	71	11	64	87	70.4
Number of laminae	10	6	9	11	10
Frequency of laminae per 100 mm	6-6.5	17	5.5	8	6.3
Average length of laminae	16.3	17	13.2	17.0	15.4
Enamel thickness	2.0	18	1.5	2.8	2.1
Laminae patterns	-· -		_	·_	

Table 2: Measurements of the first upper molar (M1) of Phanagoroloxodon mammontoides and Archidiskodon meridionalis.

TAbel 2: Maten van de eerste bovenmolaar (M1) van Phanagoroloxodon mammontoides en Archidiskodon meridionalis.

landscapes. The elephants became adapted to the changing conditions of the surrounding medium, to the nutrition with rough forage (branches, leaves) and herbaceous plants. In their search for pastures the elephants are constantly moving from one place to another, and as the result of this these animals spread widely over the whole continent adapting themselves to different climatic conditions and landscapes. Already in the Early Pliocene one may come across elephants with tokens of the beginning differentiation process. In the middle of the Pliocene there existed in Africa representatives of two filial branches, side by side with their progenitor group, Primelephantinae. Evidently, to the same period one should assign the beginning of the elephantine migration from Africa to Eurasia over the Suez isthmus and probably also over the "bridge" which existed then at the place of the Gibraltar strait.

Spreading over the vast territory of Africa, Eurasia, and later on of North and Central America, the isolated phylogenetic elephantine branches continued their independent development, giving rise to a large diversity of forms.

According to the author's notions the family Elephantidae comprises three subfamilies (Fig. 4): Primelephantinae, Loxodontinae, and Elephantinae. The subfamily Primelephantinae includes the tribe Primelephantini (with the genus Primelephas). The subfamily Loxodontinae includes three tribes: the initial one, Loxodontini (Protoloxodonta, Loxodonta, and Paraloxodonta) and two filial tribes: Eoelephantini (Eoelephas and Protelephas) and Paleoloxodontini (Omoloxodon and Paleoloxodon). The subfamily Elephantinae also includes three tribes: the initial one Phanagoroloxodontini (Phanagoroloxodon) and two filial tribes: Elephantini (Elephas, Hypselephas, and Platelephas) and Mammuthini (Archidiskodon, Mammuthus, and Parelephas).

At present we have not at our disposal sufficiently reliable data about the origin of the elephants belonging to the tribe Phanagoroloxodontini. With some probability one may place at its base the elephant, the remains of which (found in Virginia, South Africa) which have been described by A. Meiring (1955). In addition to the skull fragments and teeth, the findings include a tusk with clearly expressed spiral curvature. On the grounds of the similarity in the tooth structure the new form was related by Meiring (1955) to the elephants of a mammoth line, and it got the denomination Mammuthus (Archidiskodon) scotti; later on V. Maglio (1979) included this elephant into the synonym A. subplanifrons.

The ancient, archaic forms of elephants, with distinctly different craniological attributes, are characterised by teeth of similar structure. According to L.K. Gabunia and A.K. Vekua (1963), such a similarity must be the result of a momeomorphic development when the representatives of different phylogenetic lines still possess the initial primitive structure of an organ (teeth in this

case), inherited from a common, though remote, ancestor. One may suppose that at the earliest stages of the elephantine phylogenetic development the representatives of diverse lines differed only by craniological attributes. The probable similarity of the vegetative forage composition in the dwelling places of these elephants did not evidently subject their dental system to any considerable alterations. The reconstruction of the elephantine dental system takes place later on, when the quality of the vegetative nutrition changes due to the influence of altered climatic conditions and also as the result of migrations. Here it is quite possible (like in the above investigated instance with the Phanagorian and the southern elephants) to admit convergence in the development of the dental system resulting from the adaptation of elephants, different by their origin, to the nutrition with similar vegetation (GARUTT, 1977).

The division of the initial tribe Phanagoroloxodontini into two filial tribes (Mammuthini and Elephantini) occurred approximately 4.5 to 5.0 million years ago. The most ancient representatives of the tribe Mammuthini apparently is A. subplanifrons Osborn (1920), from South Africa. As for the tribe Elephantini, its initial African form has not yet been established.

The representatives of the tribe Mammuthini had a skull, the top of which was normally characterised by the absence of a medial cavity. However, a single species is known in which this cavity, though insignificantly, is developed. This phenomenon apparently should be considered as an atavism. Therefore it is possible to suppose that the ancient ancestors of the Mammuthini had a skull with a bifurcate top. It is probable that the migration of these elephants from Africa to Eurasia began soon after the desintegration of the Phanagoroloxodontini into filial tribes. The representatives of the tribe Elephantini, continuing their evolution, gave rise to several forms in Eurasia. The most ancient and archaic among the representatives of this tribe, known to us at present, is Hypselephas hysudricus (Falconer and Cautley, 1845) from deposits of the Late Pliocene of Pakistan, India and Burma. The absolute age of this elephant is 2.3 to 1.4 million years. The last representative of the tribe is the recent asiatic elephant, Elephas maximus Linnaeus (1758).

The most ancient representative of the tribe Mammuthini in Eurasia was the Rumanian elephant Archidiskodon rumanus (Stefanescu, 1924) from deposits in southeastern Europe dated to the Late Pliocene. Its absolute age is approximately 2.5 to 2.3 million years. The last representatives of the Mammuthini were the Eurasiatic Mammuthus primigenius (Blumenbach, 1799) and the North American Parelephas jeffersonii (Osborn, 1923).

As for the initial tribe Phanagoroloxodontini, its representatives had also migrated from Africa. The above mentioned finding of the skull belonging to *P. mammontoides* in the Caucasus serves as a confirmation of

this migration. One may suppose that the Phanagoroloxodontini did not attain a wide expansion in Eurasia and became extinct sometime during the earliest Pleistocene, apparently being unable to withstand the concurrence with their progeny, the Mammuthini and Elephantini.

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