

SUMMARY

The Khapry Faunal Unit is the famous east European analogue of Middle Villafranchian faunas. Localities of the fauna are associated with alluvial layers that are excavated in sand pits and exposures along the northeast coast of the Sea of Azov and the right bank of the lower stream of the Don River near Rostov-on-Don and Taganrog cities (south of Russia). Main sites include Khapry, Liventsovka (the stratotype and the parastratotype of the Khapry faunistic complex), Mokriy Chaltyr', Morskaya, Volovaya Balka and others.

Most of the large mammal bones from Khapry and Liventsovka sand pits were found in lower layers of alluvium. Based on analysis of species composition and sample preservation, the Khapry megafauna association is indivisible chronologically. After recent revision, the Khapry complex includes 84 vertebrate taxa, including 30 small and 34 large mammal taxa.

The full list of large mammals includes: *Nyctereutes megamastoides*, *Canis* cf. *senezensis*, *Ursus* cf. *etruscus*, *Lutra* sp., *Pannonictis nestii*, Mustelidae gen., *Pliocrocota perrieri*, *Pachycrocota brevisrostris*, *Homotherium crenatidens*, *Lynx issiodorensis*, *Acinonyx pardinensis*, *Anancus arvernensis alexeevae*, *Archidiskodon meridionalis gromovi*, *Hipparion moriturum*, *Equus* (*Allohippus*) *livenzovensis*, *Equus* sp., *Stephanorhinus* ex gr. *megarhinus-kirchbergensis*, *Elasmotherium* cf. *caucasicum*, *Sus strozzii*, *Paracamelus alutensis*, *Paracamelus* cf. *gigas*, *Cervus* (*Rusa*) *philisi*, *Eucladoceros* cf. *dicranios*, *Arvernoceros* sp., Cervidae gen. indet., *Libralces gallicus*, *Palaeotragus* (*Yuorlovia*) *priasovicus*, *Leptobos* sp., *Gazellospira gromovae*, Tragelaphini gen. indet., Tragelaphinae gen. indet., *Gazella* cf. *subgutturosa*, Gazellinae gen. indet. (Bajgusheva, 1971; Titov, 2000; Nikolsky, Titov, 2002; Sotnikova et al., 2002).

The majority of samples pertains to *Anancus*, *Archidiskodon*, *Equus*, *Paracamelus*, *Arvernoceros* and *Eucladoceros*; these animals were inhabitants of steppe and forest-steppe landscapes. All of these animals required regular watering-places.

Systematic paleontology of some representatives of the association

PROBOSCIDEA Illiger, 1811

Gomphotheriidae Hay, 1922

Anancus Aymard, 1859

Anancus arvernensis (Croizet et Jobert, 1828)

Anancus arvernensis alexeevae Bajgusheva, 1971

H o l o t y p e : ROMK, № L-103, a right upper jaw with M²-M³ in the collection of Rostov local museum (Russia).

T y p e l o c a l i t y : Liventsovka, northeast Sea of Azov Region, Russia.

A g e o f t h e t y p e l o c a l i t y : Upper Pliocene, Middle Villafranchian, MN 17.

M a t e r i a l : A number of upper and lower jaws with teeth, isolated teeth, and postcranial bones were discovered in some Khapry fauna localities.

Description and comparison: The number of transverse ridges is 4 on M^2 and 4 or 5 on M^3 , excluding anterior and posterior talons. The upper dentition has 2-5 additional tubercles (conules) in anterior valleys. Inner and outer cones are alternating, not opposite. Cement is present between cones. The anterior talon on M^3 is well developed and consists of a compact row of tubercles. There is a tendency for the formation of a sixth loph on M^3 . Tubercles on the posterior talon are quite large, and have a separate root. The cingulum is well developed on the inner and outer parts of the crown. Lower jaws are relatively small with a short, downturned rostrum. The height of the horizontal ramus behind M_3 is 118,0-133,0 mm. Lower tusks were not found. M_2 has 4 lophids and M_3 has 6. Additional intermediate conules are not numerous. Crown lengths are: dp_3 — 46,0 mm, dp_4 — 79,0 mm, M_1 — 100,0 mm, M_2 — 135,0 mm, M_3 — 199,0-210,0 mm.

The dentition of *Anancus* from Liventsovka is similar to that of representatives of the genus from Lower Pliocene deposits of Europe (Perrier, Toscana, Trevox, Spoleto etc.). However, in comparison with the typical subspecies *A. arvernensis arvernensis*, lower jaws of *Anancus* from the Khapry association are less massive, the rostrum is shorter, and the teeth are smaller. From *A. arvernensis arvernensis* and *A. arvernensis brevirostris* the Khapry association mastodon differs by the addition of tubercles and well developed cement on the crowns, and the absence of lower milk tusks (Bajgusheva, 1971).

Anancus from Liventsovka is larger than *A. arvernensis chilhiacensis* Boeuf (Boeuf, 1992) from Chilhac (early Pleistocene, France) and *A. arvernensis falconeri* Osborn (late Pliocene, United Kingdom), and has fewer conules. *A. arvernensis alexeevae* differs from *A. arvernensis sinensis* Hopwood (Ruscinian, China) in having smaller and broader teeth with more secondary elements.

Results and discussion: It is possible to attribute to *A. a. alexeevae* some findings from late Pliocene – early Pleistocene sites from the territory of Northern Caucasus: Psekups, Malgobek (Mozdok), Liapino (Mariupol), Sablia, Tsimbal (Tamanian peninsula; Dubrovo, 1963; Bajgusheva, 1971).

At the end of the Pliocene anancoid mastodonts disappeared from nearly all the territory in Asia where previously they had been widely distributed. However, remains of the genus *Anancus* are frequently found in middle-upper Pliocene and lower Pleistocene deposits of Europe. They are found at: Yukari-Sogutonu (Turkey; Becker-Platen et al., 1975), Etouaires, Vialette, Rocca Neyra, Villaroya, Pardines, Olivola, Saint-Vallier, Valdarno, Chilhac (France, Boeuf 1992), Sesklon, Polyakkos (Greece; Koufos, Kostopoulos; 1997), Eastern Scheld Estuary (Netherlands; Van Essen, Mol, 1996), and Great Britain (Osborn, 1936; Alexeeva, 1986). All of these forms differ from the type subspecies, *A. arvernensis arvernensis*, from the early Pliocene.

Dwarfing of late forms of *Anancus*, the usual presence of the sixth loph on M^3 , and the occurrence of additional tubercles and cement in tooth valleys was probably a response to climatic aridification that began in the terminal Pliocene and resulted in the change of vegetative communities. Further drying and temperature decrease led to extinction of mastodons within Europe.

Elephantidae Gray, 1821
Archidiskodon Pohlig, 1889
Archidiskodon meridionalis (Nesti, 1825)
Archidiskodon meridionalis gromovi Garutt et Alexeeva, 1964

H o l o t y p e : ROMK, № L-113, the cranium of an adult male in the collection of the Rostov local museum (Russia).

T y p e l o c a l i t y : Liventsovka, northeast Sea of Azov Region, Russia.

A g e o f t h e t y p e l o c a l i t y : Upper Pliocene, Middle Villafranchian, MN 17.

M a t e r i a l : The material includes about 380 teeth and postcranial bones from various Khapry fauna localities. There are 148 samples of upper and lower molars.

D e s c r i p t i o n a n d c o m p a r i s o n : The cranium is relatively low and elongated in the sagittal direction (the ratio of the length to the height — 0,86). The forehead is concave and exhibits notable narrowing (the ratio of the forehead's weight to the skull's weight in the occipital area — 0,29). The occiput is wide and its angle with the tooth occlusal surface is nearly 90°. The top of the cranium is weakly convex. The intermaxillary bones are slightly elongated anteriorly. The mandibular rostra are long and wide and antero-ventrally directed (Alexeeva, Garutt, 1965; Garutt, Baigusheva, 1981). These features distinguish the skull *A. m. gromovi* from other representatives of *Archidiskodon*. During excavation the cranium, ROMK № L-113, was damaged across the top. According to V. E. 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 low and wide (the crown width is 80-85 % of its height). The height of the unworn tooth plate at the centre of crown is only 97 mm. *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.

Elephants from Khapry deposits have a greater number of enamel plates in the teeth, and on average a higher lamellar frequency than does more archaic *A. m. rumanus*. *A. m. rumanus* has a greater length for a single plate (28,4 mm) than does *A. m. gromovi* (15,8-25,6 mm).

Molars of *A. m. gromovi* are similar in lamellar frequency and enamel thickness to the teeth of “southern elephants of primitive type” from Norwich Crag (England), Laiatico, San Regolo, San Miniato, Inchiza Belobo (Italy; Azzaroli, 1977), Aszod (Hungary; Voros 1985), Ferladany (Moldova; Pavlowa, 1910), Podpusk (Kazakhstan; Vislobokova, 1996) and Kuruksay (Tajikistan). These “southern elephants” were referred by Maglio (1973) to *A. meridionalis* “Laiatico stage”. But 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*. Some of eastern European “primitive” elephants may be ascribed to *A. m. rumanus* (Lister, Essen, 2003).

The teeth from Khapry and Liventsovka have on average a smaller number of plates on $M^3/3$, and a smaller lamellar frequency than do teeth of typical *A. meridionalis meridionalis* from Upper Valdarno (Italy), Seneze, Chagny (France), Georgievsky quarry (Russia) and other Late Villafranchian localities of Europe (Garutt, Safronov, 1965; Azzaroli, 1977; Maglio, 1973; Dubrovo, 1989; Lister, 1993, 1996). 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*.

Comparison of *A. m. gromovi* $M^{3/3}$ with those of Early Pleistocene *A. m. tamanensis* from Sinaya Balka (Tamanian peninsula, Russia) and other sites showed that in such parameters as length of the crown and lamellar frequency, these forms partly overlap. But elephants from Liventsovka have a lower number of plates, and on average, a smaller lamellar frequency (Bajgusheva, Titov, 2001).

Postcranial bones of *A. m. gromovi* have similar dimensions and proportions to those of “southern elephants” 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 small forms of woolly mammoth, but differs from them by more slender limb bones and elongated humeri. The last fact may suggest that their diet included a considerable amount of food from the upper vegetation layer.

R e s u l t s a n d d i s c u s s i o n : Because of significant differences in tooth parameters, skull, and postcranial characteristics between “southern elephants” and other representatives of the “mammoth line” (altogether 28 differences by Garutt, 1998) we think it reasonable to separate these groups at the genus level. All taxa of “meridionalis” elephants are related to the genus *Archidiskodon*. The first appearance of the genus *Mammuthus* (including “steppe”, “chosaricus” and “woolly” mammoth) is marked by the Trogontherii elephant.

Taking into consideration the large variability seen in cranial, dental, and postcranial characteristics, we view the following subspecies of *Archidiskodon meridionalis* from eastern Europe and the northern Caucasus as valid: *A. m. rumanus* (early-middle Villafranchian), *A. m. gromovi* (middle Villafranchian), *A. m. meridionalis* (middle? – late Villafranchian), *A. m. taribanensis* (late Villafranchian; Transcaucasus), and *A. m. tamanensis* (Late Villafranchian – Early Galerian; the Sea of Azov Region).

In view of several differences from typical *A. meridionalis*, we consider that the Khapry association elephant is a distinct subspecies. The presence of a primitive “southern elephant” in Europe was noted by several investigators (Ramaccioni, 1936; Azzaroli, 1977; Maglio, 1973; Lister, 1993, 1996). However, its taxonomic status has been controversial. Looking at dental characteristics of early and late meridionaloid elephants we can see their gradual conversion from early to Late Villafranchian types. So, it is inexpedient to pick out the “rumanus” type elephant as the separate specific taxon.

Observed variability in skull structure of different *Archidiskodon* testifies to their various specializations and to their significant diversity. Taking into account the landscape-climatic differences between various regions within the geographic area of “southern elephants” in Eurasia, the presence of several geographical subspecies on this territory during the Plio-Pleistocene is possible. This is confirmed by the taxonomic variety shown by related proboscideans woolly mammoths. Several taxa of *Mammuthus* are known in the Pleistocene, differing in the morphology of the teeth and the skull.

All diagnostic measurements (crown length; number of plates (with and without the talon); lamellar frequency) overlap between the different forms of “southern elephants”. Comparisons between different subspecies of *Archidiskodon meridionalis* that use only minimal and maximal values are insufficient. Mean values, determined for different samples, are also necessary for the analysis. Another problem is that some researchers included in the dental formula plates that form the talons, while others did not.

Measurements taken on highly worn teeth also present problems when comparisons are made. Removal through wear of the anterior talon and some of the succeeding plates changes the length and width of the crown. For example, the M^3 of *A. m. meridionalis* from Upper Valdarno, attributed by V. J. Maglio (1973) to the “Montevarchi stage” (specimens IGF-46, IGF-Na5, IGF-1054 type), has the same number of enamel plates as *A. m. gromovi* according to the table (11+talon, 12+talon, 12+talon correspondingly). However, based on measurements, these teeth are highly worn. Thus the anterior talon likely were destroyed and was not included in the dental formula. It thus appears that the minimum number of plates on the upper teeth of the “Gromov’s” elephant and the “southern” elephant differs on average by 2.

According to Alexeeva and Garutt (1965), one of the diagnostic species characters of “*A. gromovi*” is the unvarying presence of the last permanent upper premolar, which is considered a primitive feature. That tooth is actually present, but reduced, on the skull from Khapry (specimen GIN, № 300/122, collection of Geological institute RAS, Moscow) and consists of a variable numbers of tubercles. The presence of simultaneously functioning “ P^4 ” and M^1 caused V. I. Gromov (1977) and Garutt (Garutt et al., 1977) to suppose a possibility of vertical replacement of first generation of teeth. Such feature is typical for more primitive proboscideans and unknown at *A. m. meridionalis*. There is information that such a peculiarity is present on the skull from Olteni in the museum of Kraiova (Rumania; V. E. Garutt, pers. com). Other researchers consider that feature as an individual atavism (Dubrovo, 1989), rudiment (Titov, 2001), or abnormal development of dp^2 (Maschenko, 2002).

PERISSODACTYLA Owen, 1848

Equidae Gray, 1821

Equus Linnaeus, 1758

Equus (Allohippus) livenzovensis Bajgusheva, 1978

H o l o t y p e : ROMK, № L-4, the cranium of an adult female in the collection of Rostov local museum (Russia).

T y p e l o c a l i t y : Liventsovka, northeast Sea of Azov Region, Russia.

A g e o f t h e t y p e l o c a l i t y : Upper Pliocene, Middle Villafranchian, MN 17.

M a t e r i a l : The material includes about 250 specimens — skulls, upper and lower jaws, teeth and postcrania from some Khapry fauna localities.

D e s c r i p t i o n a n d c o m p a r i s o n : The skull is large and relatively narrow. The estimated basal length is about 570-580 mm (sample ROMK, № L-4), and 600 mm (sample ZIN, № 31078, collection of Zoological institute RAS, S.-Petersburg). The facial part of the skull is elongated and deflected downward about 25° relative to the cerebral part (sample ZIN, № 31078). The ratio of incisor arcade width to the breadth of the forehead behind the posterior edge of the eye-socket is 0,32 (ROMK, № L-4) and 0,314 (ZIN, № 31078). The caudal border of the narial notch is above P^2 . The orbits are elongated and their upper edges are just below the frontal bone surface. The external auditory meatus is high and straight. The sagittal crest is low and bifurcated at the level of the os occipitale.

The upper incisive row is curved. The chewing surface of little worn incisors is oval and in heavily worn incisors is prismatic. The female C^1 is tiny compared to the male

C¹. An alveolus for a rudimentary P¹ is present. The upper cheek teeth are characterized by significant enamel plication that is especially pronounced on the inner side of the anterior fossette. On highly worn teeth the complexity of the enamel plication is simplified. The protocone is relatively short and boot-shaped. The index of protocone length to width is 34,7 and 52,8 for P³ and P⁴, respectively, and is 31,0 and 46,4 for M¹ and M², respectively. The length of the chewing surface is 32,0-49,0 mm for P², 30,0-36,4 mm for P³⁻⁴, 25,0-32,6 mm for M¹⁻², and 27,0-35,0 mm for M³. The hypocone is wide and on the posterior end is rounded or has "a beak". The hypoconal groove is comparatively deep and narrow. The lingual border of the hypocone is level with the protocone base. The pli caballin is notably long and usually single on teeth in mid-wear. The parastyle is wide, round, and tends to bifurcate on large premolars. The mesostyle is relatively narrow. The ratio of premolar row length to molar row length is 1,03 (specimen ZIN, № 31078).

The lower jaw is narrow and elongated. The angle between the horizontal and vertical ramus is 110° on specimen ROMK, № L-1911, and 121° on specimen AKM, № 1535. The lower border of the mandible is straight and the symphysis is long. The range in length of P₂ is 34,0-41,5 mm, P₃₋₄ — 28,0-36,0 mm, M₁₋₂ — 26,5-36,0 mm and M₃ — 35,0-38,5 mm. The double knot is of "stenonis" type. Metaconids and metastylids are usually rounded. The postflexid is greatly plicated on the premolars and little-worn molars. The index of postflexid length is 37,9-52,8 for P₃₋₄ and 27,2-58,7 for M₁₋₂. On premolars the ectoflexid is rather shallow and during wear it closely approaches the isthmus of the double knot but does not penetrate it. On the molars the ectoflexid enters the isthmus on little-worn teeth, and on highly-worn ones it joins the linguaflexid. Linguaflexids are "V-shaped" and become deeper during wear. The pli caballinid is single and may vary in shape. The protostylid is not expressed.

The horse from the Khapry alluvium is smaller and has less plicated tooth enamel, a smaller protocone, and slender metapodials in comparison with *E. süssenbornensis* Wüst (Süßenborn, Germany) and *E. verae* Sher (Kolyma lowland). *E. livenzovensis* has larger bones and teeth than the Eurasian species *Equus (Allohippus) stenonis* Cocchi, *E. sanmeniensis* Teilhard de Chardin et Piveteau (Nihewan, China), *E. altidens* Reichenau (Germany), *E. sivalensis* Falconer (Siwalik), and *E. nomadicus* Falconer et Cautley (India).

E. livenzovensis shares several features with typical stenonid horses. These include an elongated muzzle, a narrow forehead, and the shape of the protocone and double knot (Azzaroli, 1990). In addition to larger size, distinguishing characteristics of the horses from Liventsovka and Khapry include narial notch above P² but not above P³, as in *Equus stenonis*, and preorbital fossa strongly developed. The incisor breadth of *E. livenzovensis* is smaller (70 mm) than *E. stenonis vireti* Prat from Saint-Vallier have (78-82 mm). The ratio of incisor arcade breadth to forehead breadth in *Equus* from Liventsovka is 0,321 and 0,35 in the horse from Saint-Vallier.

In comparison with typical *Equus stenonis*, the horse from Liventsovka has longer and more slender metapodials and proximal phalanges. Metapodial proportions for this horse (the average of the index of diaphysis massiveness for Mc III is 14,4 and for Mt III is 13,3) are similar to recent savanna *Equus burchelli boehmi* (Mc III — 14,97, Mt III — 13,2) and to the mountain zebra, *E. zebra hartmannae* (Mc III — 14,76, Mt III — 12,97). We think that the main habitats frequented by *E. livenzovensis* were steppe areas of forest-steppe landscapes, hill and valley slopes, and flood-lands.

Results and discussion: The dental characteristics of the large horse from the Khapry association are similar to those of *Equus* of the combined group

E. major – *E. bressanuss* – *E. robustus*. But measurements and limb bone proportions differ in these forms. Metapodials of *E. livenzovens* are less massive than those of *E. major* – *E. bressanus* from Seneze (France), East-Runton (Italy), Wurzburg-Shalksberg (Germany), Kislang (Hungary) and Moiseevka (Kazakhstan) (Azzaroli, 1990; Forsten, 1998). Horses similar to *E. livenzovens* have been found at Tataurovo, Psekups (Russia) and probably from Novie Tanatry, Dolinskoe, Oasele (Moldova), Kryzhanovka (Ukraine), Tegelen (Nederland), Sidestrand (Great Britain), Bacton (Italy), Podpusk-Lebiazhensky (Kazakhstan) (Vislobokova, 1996; Forsten, 1998). Specimens from Middle Villafranchian localities (Montopoli (Italy), Huelago, Rincon-1 (Spain)), which were attributed to *E. livenzovens* differ from the Khapry horse in having shorter and slenderer metapodials according to A. Forsten (1998).

Forsten (1998) thought that there were two large horses in the Khapry complex, *E. livenzovens* and *E. major* Boule. V. Eisenmann (2004) called in question of cranium ROMK № L-4 the precision as a holotype of *E. livenzovens*. She suggests that it is better to make the holotype of such taxon one of the largest limb bones. Eisenmann doubts the homogeneity of *stenonis* horses in Khapry fauna and marks out 5 different forms. But there are no their detailed characteristics, and only one taxon *A. mygdoniensis* is singled out in this paper. Her opinion is based on the supposition about the heterogeneity of Khapry complex and on the inference of Forsten about the presence of *E. aff. altidens* besides two large *stenonis* forms. We think that there are no obvious dental and skeletal differences to support such multiformity of horses in localities of Khapry layers.

Equus sp.

Description and comparison: Average-sized horse. Upper molars are characterized by the absence of strong enamel plication, by a narrow, antero-posteriorly flattened and undoubled mesostyle, a wide parastyle, a short, rounded protocone (the index of protocone length is 23,8 on P⁴ and 25,0-27,3 on M¹), a round hypocone, a shallow hypoconal groove, and absence of the pli caballin.

In the lower teeth the metaconid and metastylid are roughly equal in size. The plication on the postflexid is less complex than in the teeth of the large horse from the Khapry deposits. The ectoflexid is deep. On little-worn premolars it only reaches to the double knot isthmus. On molars however, significant penetration by the ectoflexid into the isthmus is typical, such that the ectoflexid commonly touches the linguaflexid.

Limb bones are smaller and more slender than in *E. livenzovens*. The dimensions of the metapodials exceed those of all monodactyl horses of the late Pliocene and early Pleistocene except those of giant forms of the *E. major* – *E. bressanus* – *E. robustus* group. Longer metapodials and larger teeth with a very short protocone distinguish the “smaller horse” of the Khapry complex from European *E. stenonis* and *E. altidens*.

Metapodial massiveness of this horse (the index of diaphysis massiveness Mc III is 13,9 on average and Mt III — 11,6) is similar to that of the desert zebra, *E. grevyi* (Mc III—13,8, Mt III — 11,75). Very likely then, this horse dwelled in open landscapes.

Rhinocerotidae Gray, 1821

Elasmotherium Fischer von Waldheim, 1808*Elasmotherium chaprovicum* Shvyreva, 2004

Description and comparison: The skull is elongated. The width of the large cupola-shaped eminence on the frontal bones is more than 257 mm. Occipital condyles are large and oval.

The horizontal ramus of the lower jaw is massive. Upper teeth are distinguished by the presence of a closed postfossette basin and irregular enamel plication. The protocone on the heavily worn P⁴ is oval. An antecrochet is present. On M¹ the protocone is double-bladed. Crochet and antecrochet are contiguous. The M² has open roots. The protocone is three-bladed. Crista and antecrochet are strongly developed. There is a cristella on the ectoloph. The crochet is small. Upper teeth have the following measurements (length/breadth): P⁴ — 53,5/46,0 mm; M¹ — 72,0/53,0 mm; M² — 83,0/54,0 mm. M₂ and M₃ have a tendency for closure of the roots. Alveolar length of M₂ is 67,0 mm, breadth — 40,6 mm. Length of M₃ is 82,0 and width — 42,0 mm.

The width of the malar arch, and the sizes of the occipital foramen and condyles on specimen ROMK, № L-257 are slightly greater than the finds from Tokmak, Svetly Yar, Zelenokumsk (Shvyreva, 1995), Serepty (Burchak-Abramovich, 1953), Luchka and Rohmanovka (Khromov, 1999), and various other sites. The absence of complete skulls of these animals from the *E. caucasicum* Borissiak site at Sinaya Balka (Tamanian peninsula), and unstudied sexual dimorphism in *Elasmotherium* complicates the comparison.

The upper teeth of *Elasmotherium* from the Khapry complex are larger than those of *E. sibiricum* Fisher and overlap in size those of *E. caucasicum* and *E. peii* Chow. The M² from Khapry is narrower (width/length ratio = 78,6), than the M² from Caucasian (width/length ratio = 85,52) and Siberian *Elasmotherium* (width/length ratio = 89,27) and is similar in proportion to *E. peii* (width/length ratio = 79,64) from China (Shvyreva, 1995).

The closed postfossette basin, irregular enamel plication and the three-bladed protocone on M² are similarities shared between the upper molars of *Elasmotherium* from the Khapry association and those of *E. caucasicum*. *E. sibiricum* and *E. peii* differ from *Elasmotherium* from Liventsovka in having an open postfossette throughout life, well-ordered enamel plication, and a two-bladed protocone (Shvyreva, 1995). The width to length ratios of the lower teeth from Liventsovka (W/L is 60,5 for M₂ and 51,2 for M₃) differ from those of *E. caucasicum* (W/L — 54,55 and 48,1 correspondingly), *E. sibiricum* (W/L is 49,76 and 48,87 correspondingly) and *E. peii* (66,0 and 46,8 correspondingly).

The limb bones of *Elasmotherium* from Liventsovka are shorter than those of Caucasian *Elasmotherium* and are close in length to those of Siberian *Elasmotherium*. Distal limb elements are comparable in size to those of *E. sibiricum*, but are more massive. The same tendency is observed in carpal and tarsal bones from Novie Tanatry and Zubov Sad (Alexeeva, 1977; Shvyreva, 1995).

Results and discussion: *E. chaprovicum* is present in late Pliocene faunas of some sites from the northern Caucasus, Moldova and Asia and displays differences with Siberian and Caucasian *Elasmotherium*. However their remains are rare. It is likely that *E. chaprovicum* was widespread in pre-Pleistocene faunas.

ARTIODACTYLA

Camelidae Gray, 1821

Paracamelus Schlosser, 1903*Paracamelus alutensis* (Stefanescu, 1895)

H o l o t y p e: Lower jaw with teeth, Museum of geology and paleontology of Bucharest (Rumania), collection number is not mentioned.

T y p e l o c a l i t y: Rumania, Slatina.

A g e o f t h e t y p e l o c a l i t y: ? Lower Pleistocene, Late Villafranchian.

M a t e r i a l: The material includes about 230 specimens — skulls, upper and lower jaws, teeth and postcranial bones from some Khapry fauna localities.

D e s c r i p t i o n a n d c o m p a r i s o n: The skull of an adult male (specimen ROMK, № L-936) is relatively small. The facial part of the cranium is elongated and makes up 77,4 % of the basal length of the skull. The nasal passageway is narrow and insignificantly expanded in the middle of its length. Its posterior edge is above the anterior third of the P³-P¹ diastema. Premaxillary bones are large and unfused. The nasal and premaxillary bones are somewhat inflated. The preorbital (ethmoidal) foramen is anteriorly placed, and most likely is single. The facial crest is not expressed. Nasals are short and relatively flat. The ratio of muzzle height to basal skull length is 0,217. Eye-sockets are closed and they are directed anterolaterally. The anterior edge of the orbit is located above the back third of M² (specimen ROMK, № L-261) or between M² and M³ (specimen ROMK, № L-936). The lachrymal vacuity is narrow and long. The malar arch is insignificantly curved ventrally. The palatine notch extends to the posterior border of M². The maxillary fossa is large (10×5 mm), and is located above the back half of P⁴. The occipital crest is high, thin, and considerably overhangs the occipital bones. The sagittal crest is continuous, low and intersects the occipital crest.

Teeth are mesohypsodont. The tooth rows are nearly parallel to the sagittal plane of the skull, forming only a weak arch. The upper teeth include I³, C¹, P¹ and P³-M³. The small caniniform I³ is located laterally on the premaxillary bone. The I³-C¹ diastema is 12,5 mm (specimen ROMK, № L-936). The canines are large (15,4×11,3 mm), with an oval cross-section. There are sharp longitudinal ridges on the anterior and posterior edges of the canine. P¹ is small and caniniform and is separated from the other premolars and the canine by long diastemas. P² is absent. On P³ the anterior valley is open. The P⁴ is molarized. Premolars and molars have ribs and strongly developed styles (especially the parastyle and mesostyle) on their labial surfaces. The length of P³ is 23,1 mm, width — 12,7 mm. P⁴: length of a chewing surface — 21,2 mm, width — 17,6 mm. M¹: length — 32,5 mm, width — 24,3 mm. M²: length — 34,0 mm, width — 23,0 mm. M³: length — 32,8 mm, width — 20,0 mm.

The body of the mandible is low and inflated. The angular process is small, situated at the level of the base of the tooth crowns, and slightly medially inflected. The angle between the horizontal and ascending rami varies from 93° to 114°. The diastemal crest is sharp. P₁ is caniniform and P₂ is absent. The P₁-P₃ diastema is about 60 mm long. P₄ has an open anterior valley. The lingual surfaces of the teeth are rather smooth except for having weakly developed entostylids. Well-worn M₂ and M₃ have anteroexternal plicas on 29 out of 36 jaws, but plica development varies greatly.

Metapodials are slender. Metatarsals are slightly longer on average than metacarpals. Proximal phalanges are slender, too, and have large W-shaped suspensory ligament scars

on their back surfaces that extend for two fifths of the diaphyseal lengths. The restored length of the vertebral column is about 200 cm.

P. alutensis from the Khapry alluvium is smaller than other Plio-Pleistocene camels of the genus *Paracamelus* (*P. gigas*, *P. trofimovi*, *P. praebactrianus*, *P. khersonensis alexejevi* and *P. longipes*).

Results and Discussion: *P. alutensis* from the Sea of Azov Region has a number of similarities in the skull, teeth and postcrania in common with the larger form from the early Pliocene of the Ukraine *P. khersonensis alexejevi*. It is thought that *P. khersonensis alexejevi* is ancestral to *P. alutensis* (Havesson, 1954; Alexeeva, 1977).

P. alutensis differs from species of *Camelus* in having an elongated facial part of the cranium, a more developed P³, the presence of P₃, and a long and low mandible, among other features. This small late Pliocene camel has slender limb bones and greater bifurcation of the metapodial distal articular condyles.

The little camel of the Khapry Faunal Unit has slender and elongated limbs and neck, a lengthened facial part of a skull, a small nasal passageway and relatively low-crowned teeth compared to other large herbivores of the association. Apparently, this form was a mixed feeder. Pliocene representatives of *Paracamelus* likely were inhabitants of mesophytic steppe and forest-steppe landscapes, which were widespread in the northern Black Sea Coast and Sea of Azov Region since the end of Miocene.

Cervidae Goldfuss, 1820

Eucladoceros Falconer, 1868

Eucladoceros sp.

Description and comparison: Skulls are represented mainly by braincase pieces, and fragments of the frontal and parietal bones with antler pedicles. Characteristics of *Eucladoceros* skulls include the following: the frontal surface behind the orbits is only slightly concave, sagittal interfrontal suture is smoothed, and in young specimens it is more convex, the part of the skull behind the antler is wide and short, the mastoid is narrow, the occiput is high, the supraoccipital is trapezoidal and convex, and the occipital crest is low (Bajgusheva, 1994).

Pedicles are massive and rounded in cross section, and their length is quite variable. Older individuals have shorter and more massive pedicles. The angle of pedicle divergence is 70° in young animals and 85° in adults. The distance between pedicles bases is equal to or less than pedicle width.

Antlers are large. The burr is large and rounded. The cross section of an antler base varies from oval to subtriangular. In adult animals with large, massive antlers the first anterior tine is situated near the burr. But this tine may be some distance from the base in young individuals. As a rule this outer tine is long, flattened, and unbranched, but may be palmate in old deer. One or two additional unbranched tines with round cross sections may be present on the antlers of mature individuals. In young animals such tines may be represented by the tubercle. Above the outer tine the beam deviates posteriorly and laterally (the angle is 83-135°). All tines branch from the anterior surface of a beam and bifurcate. The cross section of the beam varies from round to subtriangular and the distal part is flat.

The antler dichotomous branching sequence of *Eucladoceros* from the Khapry association resembles that of *E. dicranios* from Upper Valdarno (early Pleistocene, Italy) and *E. orientalis* Radulesco and Samson from Psekups (terminal Pliocene, Russia). Antlers from the Khapry deposits have a similar degree of flattening as in *E. dicranios*.

The better preserved antler in the collection (ROMK, № L-531) differs from that of typical *E. dicranios* by lesser length, fewer tines and greater flattening. Moreover, on massive antlers from Liventsovka the first outer tine is situated near the burr while on the specimen from Upper Valdarno it diverges higher on the shaft. The angle of pedicle divergence is larger in the samples from the Khapry alluvium. The basioccipital is less massive and flattened (Bajgusheva, 1994).

Giraffidae Gray, 1821

Palaeotragus Gaudry, 1861

Palaeotragus (Yuorlovia) priasovicus Godina et Baigusheva, 1985

H o l o t y p e : ROMK, № L-904, distal part of the humerus in the collection of Rostov local museum (Russia).

T y p e l o c a l i t y : Liventsovka, North-east Sea of Azov Region, Russia.

A g e o f t h e t y p e l o c a l i t y : Upper Pliocene, Middle Villafranchian, MN 17.

M a t e r i a l : A fragment of the braincase, horn, lower jaw fragment, and limb bones.

D e s c r i p t i o n a n d c o m p a r i s o n : Parietal bones of the skull are wide, and have a weak dorsal concavity. Well expressed parietal crests overhang the temporal area of the parietal bone. The frontal-parietal part of the cranium is rather flat and wide. The surface of the occipital bone is expanded upwards, and has a concavity and well expressed median crest. The occipital crest is wide and overhangs the occipital part of the skull. The basioccipital is large, with anteriorly situated tubercles; it is anteriorly extended relative to the articular condyles. The horn is almost straight, and in the upper third the inside curve is visible; in cross section the horn is subtriangular. The length of the horn is about 200 mm and the basal diameter about 60,0 mm. Lower teeth are brachydont, with wrinkled enamel. The mandible shows swelling below M_1 - M_2 , and the molar row is oriented obliquely to the longitudinal axis of the jaw.

The humerus is massive. The axis of the head and neck is a little inclined relative to the axis of the shaft. The ratio of the greatest diameter of the medial part of the proximal extremity relative to the diameter of the lateral part is 1,311. The transverse crest extends high above the lateral portion of the coronal fossa. The humerus has a feebly marked dorsal triangular depression on the head. The olecranon fossa is deep and low.

The metacarpal bone has a considerably broadened distal end. Metacarpal III is a little shorter than metacarpal IV. The median crests on the articular surfaces are well expressed. The metatarsal bone is slender with an expanded proximal end. A small Mt II (length 36 mm) and a groove for articulation with Mt V are present on either side of the proximal end of the metacarpus.

The horn of the giraffe from the Khapry alluvium differs from that of *Palaeotragus (Yuorlovia) asiaticus* Godina from western Mongolia (Godina, 1979) in having a subtriangular cross section and in its inside curvature. From *P. (Y.) microdon* (Koken) it differs in slightly greater length and curvature. *P. (Y.) priasovicus* has relatively slender

and larger limb bones in comparison with other representatives of the subgenus (Godina, Bajgusheva, 1985).

Results and discussion: In size and some morphological features the giraffe from the Sea of Azov Region is similar to large *Palaeotragus* of the subgenera *Yuorlovia* and *Achtiaria*. The majority of characters indicate a closer relationship to species of *Yuorlovia*. In absolute size and similar contour the horn from Liventsovka resembles that of *Macedonotherium martini* Sickenberg from the Volax sites (Macedonia). However the horn of the Khapry association giraffe is less rounded in cross section.

In comparison to horns of *Sogdianotherium kuruksaense* from Kuruksay (late Pliocene, Tajikistan) the horn of *P. (Y.) priasovicus* is shorter, straighter, has an additional surface ornament and has a subtriangular cross section.

Palaeotragus was widespread in the forest-steppe zone of Eurasia from the end of Miocene to the Middle Pliocene (Godina, 1979). During the increasing aridification of the terminal Pliocene and beginning Pleistocene, this ecological form survived mainly in the Mediterranean subarea — Macedonia, Greece (*Macedonotherium martini*; Koufos, Kostopoulos, 1997) and neighboring territories — Turkey (*Palaeotragus* sp.; Sickenberg, Tobien, 1977), Romania (*Mitilanootherium inexpectatum* Samson et Radulesco; Alexeeva, Motuzko, 1985; Radulesco, Samson, 1990), Tajikistan (*Sogdianotherium kuruksaense* and *Sivatherium* sp. (Godina, 1980; Sharapov, 1986).

Late Pliocene giraffes probably were more highly adapted to dwelling in forests than the modern *Giraffa*. Based on features of their skeleton, many of them, including *P. priasovicus*, had ecological adaptations similar to those of recent *Okapi* (Godina, 1979; Sharapov, 1986).

Correlation and paleoecology of the Khapry Faunal unit

Khapry strata are reversely magnetized and, based on the composition and stage of evolution of the Khapry fauna, they are correlated with the pre-Olduvai part of the Matuyama epoch of the magneto-chronological scale. The following taxa from the Khapry Faunal Unit allow an age determination to be made.

1. Forms that had a wide stratigraphic range for most of the Villafranchian: *Pannonictis*, *Pliocrocuta perrieri*, *Homotherium crenatidens*, *Lynx issiodorensis*, *Acinonyx pardiensis*, *Sus strozzii*, *Paracamelus gigas*, *Leptobos*.

2. Taxa that first appeared in the Middle Villafranchian, thereby providing a maximum age for the Khapry association: *Equus (Allohippus)*, *Elasmotherium*, *Cervus (Rusa) philisi*, *Libralces gallicus*.

3. Taxon that are unknown after the Middle Villafranchian (*Nyctereutes megamastoides*), thereby providing a minimum age for the Khapry Faunal Unit.

4. Forms with an evolutionary stage consistent with a Middle Villafranchian age: *Anancus arvernensis alexeevae*, *Archidiskodon meridionalis gromovi*, *Equus livenzovensis*, *Homotherium crenatidens*.

Small mammals' remains were extracted from all levels of Liventsovka sand pit thickness. Rodents from the base of Khapry layers are presented by *Pitymimomys* sp., *Borsodia praehungarica praehungarica*, *Mimomys hintoni livenzovicus*, *M. polonicus*, *Dolomys milleri*, *Pliomys ucrainicus*, *Allactaga* sp. Such complex allows to assume the beginning of

the alluvial thickness forming at the end of middle Pliocene. All known large mammal fossils from the Liventsovka sand pit were found in the lower part of alluvial thickness in bed gravel-sand facies. The megafauna is accompanied by a rich small mammal association, including *Mimomys praepliocaenicus*, *Borsodia praeungaricus cotlovinensis*, *Mimomys* ex gr. *reidi* and other species (Bajgusheva et al., 2001; Tesakov, 1993, 1995, 2004). Taken together, these faunal elements correlate the Khapry association to the middle Villafranchian. In the top part of Khapry strata (without any known large mammal remains) there is an association of rodents *Borsodia* ex gr. *arankoides-fejervaryi*, *Mimomys* aff. *reidi*, *M.* aff. *pliocaenicus*, *Cletrionomys kretzoi*, *Ellobius* sp., characteristic for the end of zone MN 17 and the beginning of MN 18 (=MN 18 by C. Guerin scheme). The small mammal fauna from the top part of Khapry thicknesses is compared to fauna from site Psekups (Northern Caucasus), including *Archidiskodon meridionalis meridionalis*, and relates to the beginning of Late Villafranchian (Tesakov, 1995, 2004).

The time of accumulation of Khapry alluvium was rather long. Overall, the large mammal complex from Khapry layers resembles Middle Villafranchian faunas from Eastern Europe, such as Saint-Vallier, and is correlated with mammal zone MN 17. Possibly, the time of formation of the Khapry large mammal taphocoenosis includes most of MN 17, excluding the earliest Middle Villafranchian. We think that its age range is in the interval 2,6–2,2 Ma, taking into consideration that the lower boundary of the MN 17 is corresponding with the boundary of C2An/C2r chrons of magnetostratigraphic scale.

The Khapry association has some particularities in comparison with western European analogs. We can say that *Canis* cf. *senezensis*, *Pachycrocuta brevirostris*, *Cervus (Rusa) philisi* cf. *philisi*, *Eucladoceros* cf. *dicranios* and *Libralces gallicus* appeared earlier in eastern Europe because of the closer relationship of the Khapry association with Asian faunas and in consequence of the better developed steppe landscapes in this area. In western Europe, these forms appeared later — in the terminal Pliocene and in the beginning of the Pleistocene.

The appearance of large hyena *Pachycrocuta brevirostris* was fixed in Africa at the level about 3,0 Ma. There are findings of such forms from late Pliocene localities of India (*P. brevirostris*), China (*P. b. licenti*), and Kazakhstan. In Asia *Canis* aff. *etruscus* appeared in Early Villafranchian. Similar dogs are known from late Pliocene of China, Tajikistan and Kazakhstan (Sotnikova et al., 2002).

On the other hand, there are few forms in Khapry association, which someone may suggest to be older than late Pliocene. For example, genus *Arvernoceros* was earlier known only from Early Villafranchian sites (Etouaires, Villaroya, Vialette, Kvabebi; MN 16a zone). But now representatives of this genus are known from several upper Pliocene and early Pleistocene localities of Moldova (Chishmikiy, Salci), Georgia (Dmanisi), and Greece (Apollonia 1). Thus, genus *Arvernoceros* has wide stratigraphical spreading within limits of Villafranchian of Europe.

In late Pliocene east European faunas there are some zoogeographical groups:

1. Taxa with widespread Eurasian distributions: *Nyctereutes*, *Pannonictis*, *Pliocrocuta*, *Homotherium*, *Acinonyx*, *Lynx*, *Anancus*, *Equus (Allohippus)*, *Gazella*, *Cervus (Rusa)*, and *Eucladoceros*.

2. Forms that were mainly restricted to the western Eurasian and to the Mediterranean area in the middle Villafranchian: *Archidiskodon*, *Hipparion moriturum*, *Equus (A.)* cf. *stenonis*, *Sus strozzi*, *Arvernoceros* and *Libralces*.

3. Animals with distributions mainly in the Asian part of the Eurasian: *Elasmotherium*, *Paracamelus gigas*.

4. The small camel *Paracamelus alutensis*, evidently endemic in the late Pliocene to the Black Sea territory.

The late Pliocene faunas of the Black Sea and the Sea of Azov Regions are united with those of western Kazakhstan and western Siberia on the basis of the abundance of *Archidiskodon*, the presence of large *Paracamelus*, *Elasmotherium*, and two horse species. For Khapry type faunas, *Paracamelus alutensis* and *Palaeotragus (Yuorlovia)* are typical. These forms are not known from the Asian late Pliocene. It's possible that some animals of open habitats had an unbroken distribution in an area that covered the Black Sea Region and Kazakhstan until the late Pliocene. Faunas of this age from the Black Sea Region and the Northern Caucasus were transitional between typical Mediterranean associations on one side and middle Asian and Kazakhstan associations on the other. That territory included the western limits of the distributions of *Struthio*, *Elasmotherium* and *Paracamelus*, genera that were widespread in Asia. *Villanyia* was also abundant, as was a variety of jerboas and gophers (Topachevsky et al., 1987). Taking into account features of faunistic communities of the Pliocene of southeastern Europe, this area may be distinguished as the Black Sea Region province within the European-Siberian paleozoogeographical subarea.