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Quaternary megafauna from the Dnieper alluvium near Kaniv (central Ukraine): Implications for biostratigraphy

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ABSTRACT

Subfossil remains of the Quaternary megafauna from two Ukrainian natural history collections stored at Kaniv Nature Reserve and the National Museum of Natural History NAS of Ukraine were examined. Most of the bones were collected in 1965–1966, in the building pit and the gateway of the Kaniv hydroelectric power plant. The fauna is represented at least by ten taxa (*Gulo gulo, Mammuthus trogonterii chosaricus, Mammuthus intermedius, Coelodonta antiquitatis, Megaloceros giganteus, Alces alces, Bison priscus, Cervus elaphus, Capra* cf. *ibex,* and *Equus ferus*). Skeletal parts are represented mainly by skulls, long bones, horns, and tusks. Based on the species composition of proboscideans, at least part of the faunal assemblage is dated by the end of the Middle Pleistocene (Dnieper Stage = Saale, Warta, MIS 6), but majority of bones could be older or younger (Late Pleistocene and Holocene age) due to the alluvial origin of accumulation.

1. Introduction

The construction of the hydroelectric power plant on the Dnieper River near Kaniv (central Ukraine) started in 1963–1964. The deep pit excavated for the fundaments of gateways and the plant building uncovered thick Quaternary alluvial deposits of the Dnieper River (Fig. 1). These strata contained numerous faunal remains. In 1965–1966, the special palaeontological expedition of the Institute of Zoology of the Ukrainian Academy of Sciences collected there a significant bone material. Part of the collection was stored in the Museum of Nature, Kaniv Nature Reserve (Fig. 2), while the rest of it was taken to the Institute of Zoology in Kyiv, and now it is included into the collections of the Department of Palaeontology, National Museum of Natural History at the National Academy of Sciences of Ukraine. Until now, only a handful number of publications were dedicated to these collections, containing mainly the general species determination.

In general, the faunal assemblage was typical for the Late and Middle Pleistocene cold landscapes: mammoth, woolly rhino, bison, giant and red deer, reindeer, and horse. The geological age of the fauna was estimated as Late Weichselian. Since the 1960s, our knowledge on Pleistocene faunal assemblages have significantly improved allowing a detailed revision of the collection with a more precise determination of its age and taxonomic composition.

In 2017, a joint team of researchers examined the collection stored in Kaniv Museum and a part of the collection stored in Kyiv. Not all specimens were measured, thus we consider this article as a preliminary analysis of the Kaniv collection. The obtained data provide some keys to the biostratigraphy of the Kaniv fossil-bearing site (Table 1).

1.1. Literature review

The first special communication about the faunal composition of the site was made by Svistun (1966). He determined the remains of several large and small mammal species (353 bones in total), and three species of birds (52 bones). The collection also contained 116 bones of domestic animals. The megafauna was represented by *Coelodonta antiquitatis, Equus* sp., *Megaloceros giganteus ruffi*, *Cervus elaphus*, *Capreolus capreolus*, *Rangifer tarandus*, and *Bison priscus*. All remains of Proboscidea were

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identified as *Mammuthus primigenius*. In addition, *Sus scrofa* and *Sus domestica* were determined. As the ^{14}C dating was unavailable at that time, there was an attempt to date the bones by the so-called "collagen method" proposed by Pidoplichko (1952). The method is based on burning a piece of the examined bone in a muffle furnace, with its weighing before and after burning. It was considered that burning of the bone at 800 °C removes the organic compounds from its composition. The older a bone, the less organic matter (represented mainly by collagen) remains in its composition. Based on this method, the geological age of most of the bones from Kaniv was estimated as Late Würm, and only a few were dated to Riss-Würm in the Alpine scale. Domestic species were associated with the uppermost part of the alluvium (Svistun and Lomayev, 1967). Later, Pidoplichko (1974) noticed that 873 mammoth bones belonging to 46 individuals were collected in the construction area of the Kaniv HPP. In this case, he also meant bones collected by the employees of local museums from Kaniv and neighbouring villages. More recent publications considered the description of some species from Kaniv (Kovalchuk and Ryzhov, 2011; Kovalchuk et al., 2011; Marciszak and Kovalchuk, 2011).

In 1969–1971, I. Pislariy collected flint tools and animal bones with signs of artificial damage in the construction pit at the central part of the dam, about 10–15 m deep from the pit top (Pislariy, 1972). These artefacts were stratigraphically associated with the bottom of Würm loams. Faunal remains were determined only as "long bones, ribs, and mandibles of woolly rhino and mammoth". The stone industry was recently attributed as Micoquian (Pislariy et al., 1999).

The first description of the geological setting and taphonomy of the site was presented by Svistun and Lomayev (1967). According to this study, bones were bedded through the entire thickness of alluvial sands. Sometimes, bone accumulations were found in the "basal horizon of the alluvium", bedding on black-green boulder loam or striped lacustrine-alluvial sandy loams. The bottom of the alluvial formation was 20–30 m deep. Because the bone-bearing sands were washed out with a hydrojet, the exact stratigraphical position of each bone was not registered. The bones were bedded *in situ,* not in anatomical connection, and belonged to different individuals, i.e. they were transported for a short distance. Other researchers (Goretskiy, 1961; Romodanova et al., 1969; Paliyenko et al., 1971; Kukhtiy, 1972) also presented the geological description of the area near Kaniv, but the most complete description based on the geological survey for the Kaniv HPP construction was done by Goretskiy (1970). More recent publications consider mainly the alluvial sediments (Matoshko et al., 2002, 2004) and the general state of the art (Tsyba et al., 2012).

2. Regional (geographical and geological) setting

The studied area is tectonically located on the north-eastern slope of the Ukrainian crystal shield, steeply descending to the Dnieper-Donets depression, covered by Mesozoic and Cenozoic sediments (Fig. 3). The Dnieper valley near Kaniv is incised into Mesozoic and Oligocene deposits. The very specific feature of this region is the area of Kaniv dislocations, the folded zone on the right bank of the Dnieper, considered as the area of glacial dislocations of the Dnieper Glacial (Lavrushyn and Chugunnyi, 1982; Popova et al., 2018).

Considering the relief of this part of the valley, its main element is the Shevchenko Depression of glacial exaration and erosion, which extends along the Kaniv dislocations, from Pereyaslav to Cherkasy. This depression continues the series of the same depressions upstream the Dnieper valley. The depression bottom is uneven with raised and more incised areas; its altitudes vary from – 52.5 to 13.0 m a.s.l. The depression is filled with till, fluvio-glacial, and lacustrine-glacial sediments, and overlayered with the alluvium. According to the State Geological Map (Tsyba et al., 2012), the Dnipro unit ($P_{II}dn$) consists of the following types of sediments. Fluvio-glacial undertill sediments ($fP_{II}dn^i$), represented with unsorted quartz sands, sometimes with pebbles of crystalline rocks. Lacustrine-glacial undertill sediments ($lgP_{II}dn^i$), composed mainly of loams, sandy loams, with lenses of sands, and have thin horizontal stratification. Till ($gP_{II}dn$) consists of yellow-pale, yellow-gray, and reddish-pale loams with pebbles, gravel, and boulders of sedimentary and crystalline rocks up to 5–6 cm in diameter. Moraine deposits also include large local glacial xenoliths of dislocated Jurassic, Cretaceous, and Paleogene rocks. Fluvio-glacial above-till sediments ($fP_{II}dn^s$) are represented mainly by unsorted sands, while the lacustrine-glacial above-till sediments ($lgP_{II}dn^s$) – mostly with loams and sandy loams with sandy lenses and interbeds (Tsyba et al., 2012).

Cherkasy alluvial deposits ($a^4P_{III}\check{c}r$) are represented mainly by quartz and feldspar sands with a well-defined oblique and horizontal bedding,

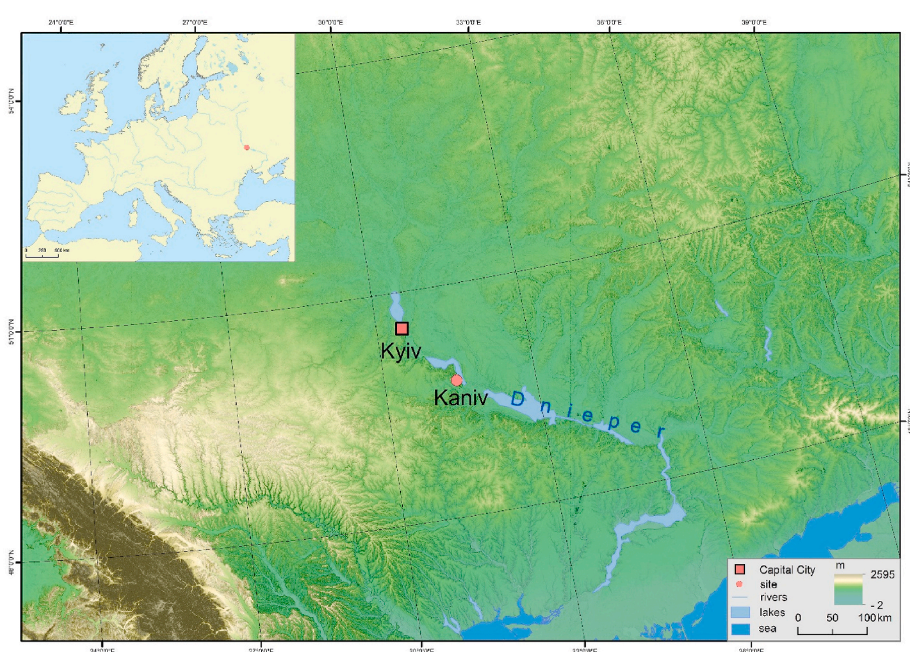

Fig. 1. Location of the Kaniv site.

and with the pebbles and gravel of crystalline rocks (up to 0.4–0.8 cm in diameter) at the lower part. This alluvium is spread in the areas of till-free terraces and the Shevchenko exaration depression, where they form the fourth (Cherkasy) above-floodplain terrace. The thickness varies from 26.3 to 49.0 m (Tsyba et al., 2012).

The alluvium of the third and second terraces, Trubizh and Vilshany Stages ($a^{3-2}P_{III}$tb-vl) correlates with the Vytachiv interstadial (MIS 3). The thickness of these deposits varies from 11.2 to 43.0 m. Within the Shevchenko Depression, they are deposited on lacustrine and lacustrine glacial sediments of the Dnieper Stage (Tsyba et al., 2012).

The alluvium of the first terrace, Desna Stage ($a^{1}P_{III}$ds), is represented by quartz and feldspar sands, sometimes with pebbles of crystalline rocks, with oblique stratification in some places. The thickness of these sediments is up to 21.3 m, but it equals 7–10 m in average. They overbed the alluvial of the second and third terraces, and sometimes fluvial and lacustrine-glacial sediments of the Dnieper Stage. The Holocene alluvium (aH) consists of sands, sometimes including gravel and pebbles, can be up to 12 m in the Dnieper valley (Tsyba et al., 2012).

3. Material and methods

The material described here is represented by isolated bones and their fragments stored in the Museum of Nature, Kaniv Nature Reserve (acronym K), as well as in the Department of Palaeontology of the National Museum of Natural History (NMNHU-P), National Academy of Sciences of Ukraine in Kyiv. These specimens were measured with an electronic calliper with 0.01 mm precision. The measuring scheme and abbreviations follow von den Driesch (1976) for horses, deer, and bisons, van der Made and Tong (2008) for the giant deer, as well as Made (2010) for the rhino remains. All values are presented in millimetres. Characteristics of mammoth molars were presented according to standard techniques (Dubrovo, 1960; Garutt and Foronova, 1976). Dimensions of a crown (length, width, and height), plates' frequency per 100 mm, an average length of one plate, enamel thickness, and character of the erasure figures on the occlusal surface were analysed. The mammoth species/subspecies determination based on teeth measurements follows Foronova (2001b), 2007, 2014). Lowercase and uppercase letters (p/P for premolars, and m/M for molars) were used for the abbreviation of lower and upper teeth, respectively.

4. Results of the study

Family Mustelidae G. Fischer von Waldheim, 1817
Genus *Gulo* Pallas, 1780
Gulo gulo (Linnaeus, 1758).

A fragment of the right maxilla with P3–P4 of a large wolverine is so far the only described in detail carnivore from Kaniv (Marciszak and Kovalchuk, 2011). The crown of P3 is 11.0 mm long, conical in shape and has a well-developed ridge on its buccal side. A well-visible cingulum at the lingual and posterior part is present; the tooth has two roots. The surface of P4 is partially erupted, but, in general, the tooth is rather well preserved. The total length of the crown is 22.40 mm, the width of the crown at the base of the protocone equals 13.70 mm, and the width at the base of the metacone is 9.50 mm. The tooth has three massive roots. The total length of P4 from Kaniv exceeds values given by (Döppes, 2001) for males from the recent population of Fennoscandia (17.4–21.5 mm, n = 60). It is widely accepted that Late Pleistocene wolverines were on average 8–20% larger than modern ones (Döppes, 2001). Considering all of the above, the wolverine remains from Kaniv belong to a very large individual, most probably a male.

Order Proboscidea Illiger, 1811
Family Elephantidae Gray, 1821
Genus *Mammuthus* Brookes, 1928

The genus is represented in the material from Kaniv by at least three taxa: *Mammuthus trogonterii chosaricus* (Dubrovo, 1966) by one right m3 (K 101), *Mammuthus intermedius* (Jourdan, 1861) by one maxilla with two M3 (K 224), and *Mammuthus primigenius jatzkovi* (Golovko, 1958) by one right M3 (K 102). All teeth measurements are given in Table 2.

Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758
Equus ferus Boddaert, 1785

Material. One left p2, one left P2, two isolated upper molars, one cervical vertebra (K, all unnumbered), one complete right humerus (K 181) and its fragment (K, unnumbered), one left (K 169) and one right part of the pelvis (K, unnumbered).

Measurements. *Teeth:* p2 (L 29.56; W 12.09), P2 (L 32.13; W 19.70), upper molars (L 25.46; W 17.27; L 33.09; W 21.87). *Cervical vertebra:* PL 83.88. *Humeri:* Dp 105.06; Bd 87.66, 96.88; Bt 80.13; Dd 90.88. *Pelvis:* GL 426.11; SB 25.64, 30.86; LS 132.19; LFP 69.08, 70.38; LAR 58.32, 59.01; LA 66.48, 67.58; GBTC 525.00; GBA 252.77; SBI 149.53.

Remarks. The obtained results of the osteometrical analysis were compared with the data from the literature and measurements of equine remains from our own research in Biśnik (Poland) and Emine-Bair-Khosar caves (Crimea, Ukraine) (van Asperen and Stefaniak, 2011; van Asperen et al., 2012). The size of the teeth and limb bones from Kaniv is smaller than that in the Early and Middle Pleistocene horse species *Equus stenonis* Cocchi, 1867, *Equus suessenbornensis* Wüst, 1901, *Equus verae* Sher, 1971, and *Equus mosbachensis* Reichenau, 1903. In the case of the humerus, however, it is in the lower range variability of *Equus ferus latipes* (Gromova, 1949) female from the Middle and Upper Pleistocene (Kuzmina, 1997, Fig. 20; tab. 17, 18, 19), and is larger than those in *Equus hydruntinus* (Regalia, 1907) (Fig. S1).

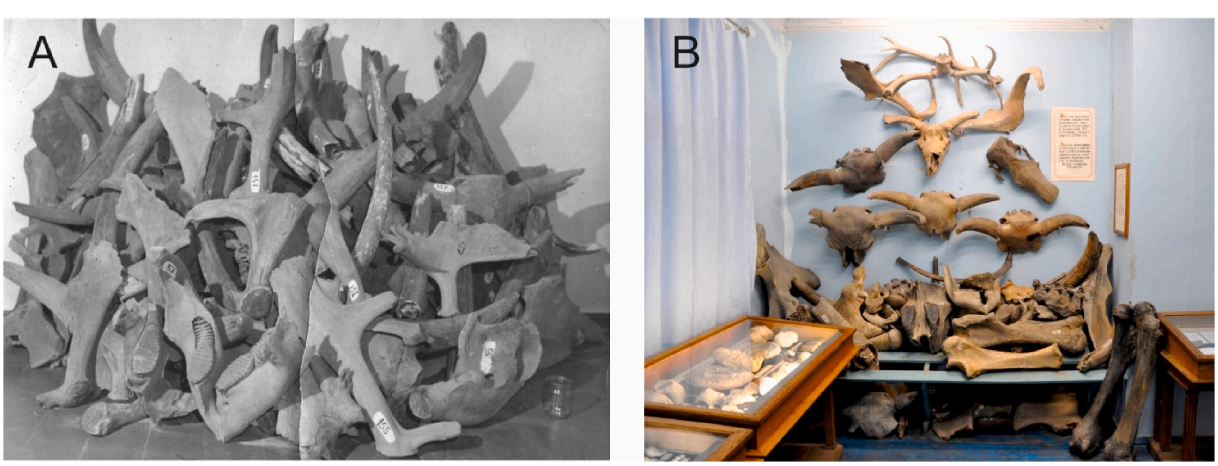

Fig. 2. Collection of bones in the Museum of Nature, Kaniv Nature Reserve: A – the view of the collections in 1960s; B – the modern view in the exhibition of the Museum of Nature.

Equus hydruntinus (Regalia, 1907).

Material. One left tibia (K 182).

Measurements. L 312.47; Bd 64.56; Dd 41.20; GL 349.99; SD 35.41, CD 135.00.

Remarks. The tibia is significantly smaller (see Kuzmina, 1997, Table 21) than that in *Equus ferus latipes*, and is clearly within the range of variation of *Equus hydruntinus* (Fig. S2).

Family Rhinocerotidae Owen, 1845

Genus *Coelodonta* Bronn, 1831

Coelodonta antiquitatis (Blumenbach, 1799).

Material. One skull (K 214), one upper and one lower molar (K, unnumbered), one left humerus (K 183), one right ulna (K, unnumbered), one right part of the pelvis (K 170), one femur (K 184).

Description. The skull is well preserved. Its dorsal side is almost complete. The outline of nasals is rectangular with a smooth surface. The frontal bones are also smooth. The occiput is complete, rectangular in the caudal view, and its edge seen from above is a straight line. The nasals are not widened and together with their smooth surface indicate that the anterior horn was small or very small. The same is true for the posterior horn based on the smooth surface of the frontals. The shape of the occiput, which is narrow closer to its base, comparable to the width of its dorsal part, shows that the neck musculature was not robust, probably because the head was not heavy. This specimen likely represents a subadult individual. The upper molar lacks a significant portion of its lingual side, making it impossible to obtain the width measurements, both anterior and posterior, or even to distinguish whether it is M1 or M2. The lower molar is poorly preserved; it is impossible to identify it more precisely. The humerus is preserved in half. Its proximal end is missing, together with a part of the shaft. The distal epiphysis is gracile. This bone could belong to a subadult individual or a female. The ulna is poorly preserved; only a part of the proximal epiphysis is present. A part of the pelvis is well preserved, with partly broken ilium and missing ischiatic tuber. The pelvic symphysis was not consolidated. It probably belonged to a subadult individual. The femur is the only complete bone belonging to an adult individual.

Measurements. *Skull* (numbers of measurements are presented according to the scheme in van der Made, 2010, Fig. 2): #5–117.80; #6–335.20; #8–405.40; #9–135.90; #15–200.30; #16–272.70; #17–62.60; #22–112.80; #23–173.80; #31–59.30; #32–155.00; #33–151.60; #37–46.00; #38–39.80; #39–82.60; #41–65.60; #42–55.20; #43–28.90; #45–172.30; #46–99.90; #47–89.50; #50–141.00. *Upper molar:* DAP 51.50. *Humerus:* DTd 169.70; DTdf 112.50; DAPd 132.90; R1 99.60; R2 58.60; R3 79.10. *Ulna:* DTm 96.60; DTfu 52.50. *Pelvis:* biggest diameter of acetabulum 109.50. *Femur:* L 506.00; DTp 217.20; DTd 158.10; DTdf 130.40; DAPd 158.30; DAPd’ 100.90; DAPpf 97.36.

Remarks. The calculated MNI is one, but the remains probably represent at least two individuals (the upper tooth does not seem to be a part of the skull, most of the bone remains seem to belong to a subadult individual, although the femur may belong to an older animal). Three pairs of measurements were chosen to compare the skull with other materials. Comparison of the width of the skull at the mastoid process (16) to the width of the occiput (15) depicts the shape of the occiput (Fig. S3). In this case, the value of measurement #16 is almost equal to the mean given by (Guérin, 1980). The width at the mastoid process (15) is close to the mean, not far below it. This result may be explained by the suspected subadult age, placing it below the fully-grown individuals and above the juvenile ones. Rhinos from various European sites (except for the Polish ones) have the biggest occiputs. There are also two above average specimens from the Ural Mountains and Western Siberia; however, most of the analysed rhino skulls are below the mean of both measurements #15 and #16 (except for a specimen from Tobolsk). The specimen from Kaniv is between the European rhinos with wide occiputs and those from the Ural Mountains and Asia with narrower occiputs.

Comparison of the skull width at the mastoid process (16) to the distance of the foramen magnum to the occipital crest (23) (Fig. S4) confirms the analysis of occiput’s width. The distance from the nasoincisive notch to the anterior rim of the orbit (9) and distance from the preorbital process to the occiput (8) allows comparing indirectly the lengths of incomplete skulls. The specimen from Kaniv is below average in terms of measurements #9 and #8 (Fig. S5). This is probably due to its relatively young age. Although this skull is shorter, unlike the width of the occiput, which is closer to the mean, this specimen seems to be a link between large European rhinos and the smaller ones from the Ural Mountains and Asia.

Family Suidae Gray, 1821

Genus *Sus* Linnaeus, 1758

Sus scrofa Linnaeus, 1758

Material. One left M3 (K, unnumbered).

Measurements. L 34.77; W 20.88.

Table 1

Stratigraphic distribution of *Mammuthus* species related to the Ukrainian Quaternary framework.

International stratigraphic chart of Quaternary (after Cohen et al. (2013))			Regional and local stratigraphical divisions of Quaternary sediments Compiled after Gerasimenko (2010) and Tsyba et al. (2012)				MIS[a]	*Mammuthus* species/subspecies and forms (adopted from Foronova (2001a))
System	Series	Subseries	Stage	Index	Strata	Index		
Quaternary	Holocene					*hl*	1	
Q	Pleistocene P	Upper P_{III}	Desna	*ds*	Prychornomoria	*pč*	2	*M. primigenius* (late form)
					Dofinivka	*df*		
			Vilshany	*vl*	Bug	*bg*		
					Vytachiv	*vt*	3	*M. primigenius* (intermediate thick-enamel form) or *M. p. jatzkovi*
			Trubizh	*tb*	Uday	*ud*	4	*M. primigenius* (intermediate thin-enamel form)
					Pryluky	*pl*	5a-c	
			Cherkasy	*čr*	Tyasmyn[b]	*ts*	5d	*M. primigenius* (early thick-enamel form)
					Kaydaky[b]	*kd*	5e	*M. primigenius* (thick-enamel form)
		Middle P_{II}	Khadzhybei	*hd*	Dnipro	*dn*	6	*M. primigenius* (early form) or *M. p. fraasy*
					Oril	*or*	7	*M. intermedius*
					Potyagaylivka	*pt*	8	*Mammuthus* sp.
					Zavadivka	*zv*	9–10	*M. trogonterii chosaricus*
							11	*M. trogonterii*
			Krukenytsia	*kn*	Tyligul	*tl*	12	
					Lubny	*lb*	13–17	
			Donetsk	*dc*	Sula	*sl*	18	
					Martonosha	*mr*	19–23	

[a] Correlation of regional divisions with MIS given after Gerasimenko (2010).

[b] Tiasmyn and Kaydaky units in Tsyba et al. (2012) were placed into the Middle Pleistocene (P_{II}), but Gerasimenko (2010) places Kaydaky into the Late Pleistocene.

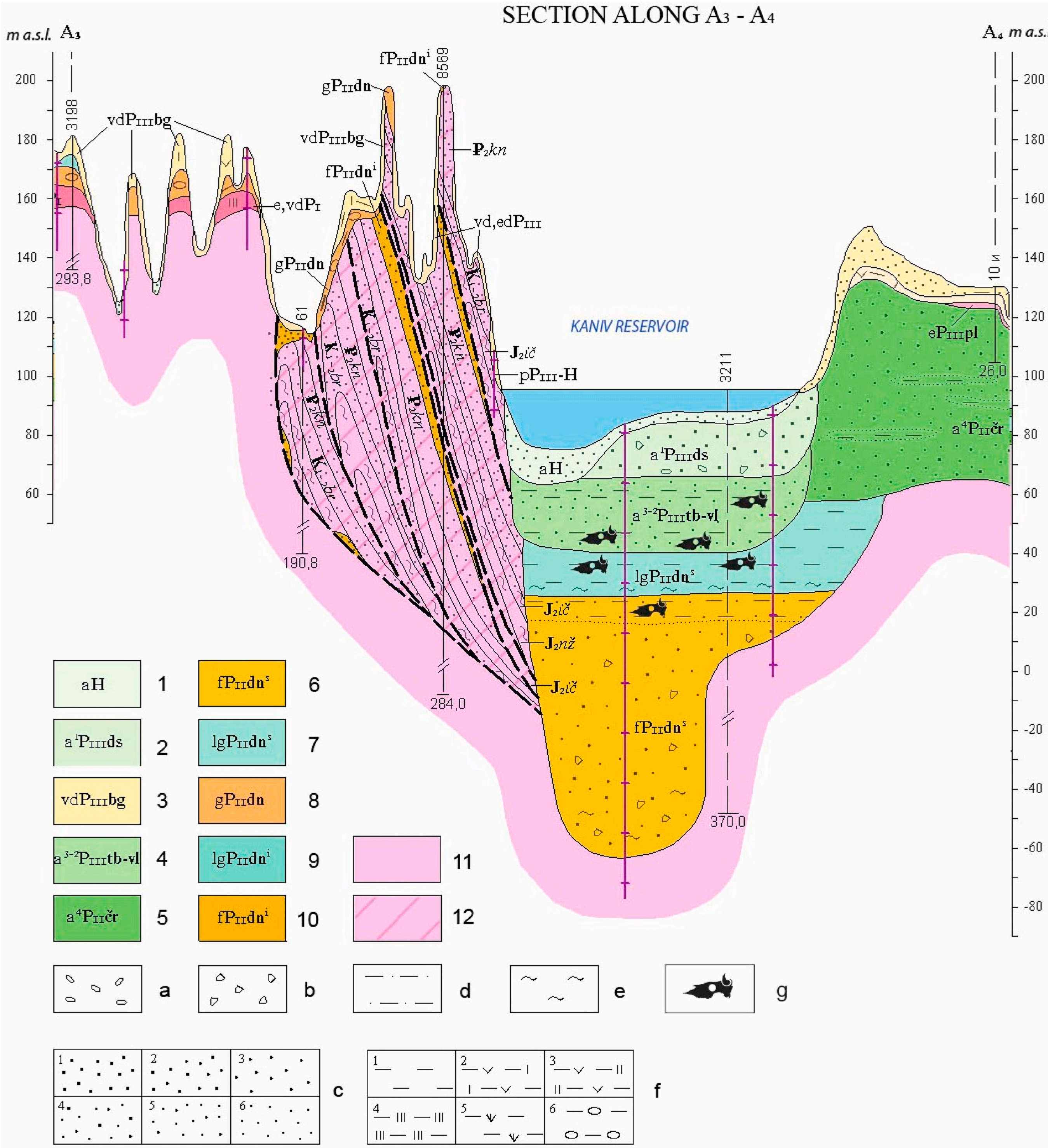

Fig. 3. Cross-section of the Shevchenko Depression in the Middle Dnieper valley (from SW to NE), 12 km north from Kaniv HPP dam (adopted from Tsyba et al., 2012): 1 – Holocene alluvium; 2 – Late Pleistocene alluvium, Desna Stage; 3 – Late Pleistocene aeolic-deluvial sediments, Bug Stage; 4 – Late Pleistocene alluvium, Trubizh and Vilshany Stages; 5 – Middle (?) Pleistocene fluvio-glacial undertill sediments, Cherkasy Stage; Middle Pleistocene, Dnieper Stage: 6 – fluvio-glacial above-till sediments; 7 – lacustrine-glacial above-till sediments; 8 – till; 9 – lacustrine-glacial undertill sediments; 10 – fluvio-glacial undertill sediments; 11 – pre-Quaternary sediments; 12 - pre-Quaternary sediments involved in the glacial dislocations. *Types of sediments*: a – pebbles; b – debris; c – sand: 1 –coarse; 2 – middle and coarse; 3 – middle; 4 – unsorted; 5 – middle and fine; 6 – fine; d – sandy loam; e – clay; f – loams: 1 – loam; 2 – light loess-like; 3 – middle loess-like; 4 – heavy; 5 – loam with peat interbeds; 6 – boulder loam; g – bone remnants.

Table 2
Measurements of the *Mammuthus* teeth (in mm).

Specimen	Plate number	Crown length	Crown width	Crown height	Average length of a plate	Plate frequency/100 mm	Enamel thickness	Species/subspecies
K 101	16	248.00	125.00	158.00	15.50	6.30	2.10	*Mammuthus trogonterii chosaricus*
K 102	18	212.00	119.00	163.00	11.70	8.40	1.90	*Mammuthus primigenius jatzkovi*
K 224s	18	227.00	93.00	–	12.60	8.50	2.00	*M. intermedius*
K 224d	18	226.00	91.00	–	12.50	8.00	2.30	*M. intermedius*

*The mean value of two M3 in the maxilla.

Remarks. Dimensions of the upper molar were compared with the available data from the literature (Pająk, 2020) and presented in the diagram (Fig. S6). The tooth is smaller than most of those from the analysed localities. It is similar in size to M3 from the Holocene sediments of Biśnik and the Niedźwiedzia caves, presumably from the MIS 3 period (Pająk, 2020).

Family Cervidae Gray, 1821

Genus *Megaloceros* Brookes, 1828

Megaloceros giganteus (Blumenbach, 1799).

Material. One near-complete skull (K 213), one right mandible with p4-m3 (K 116) (Fig. 5, A-D), twenty-five fragments of antlers (K 142–144, K 148, K 153, K 155–156, K 211–213, NMNHU-P 10-468 – 10-482, NMNHU-P 10–627); left metacarpus (K 186); right metacarpus (K 261).

Measurements. *Skull:* alveolar length of cheek teeth row 154.00; length of premolars (P2–P4) 59.00; length of molars (M1-M3) 95.00; ectorbitale-entorbitale 61.00; the greatest inner height of the orbit 58.00; least frontal breadth 145.00; greatest breadth across the orbits 210.00. *Mandible:* L (p2-m3) 159.00, L (p2-p4) 61.00, L (m1-m3) 98.00. *Metacarpi:* Bp 74.30; 71.70; Dp 43.90, 41.60; Bd 77.90; Dd 48.30. Measurements of the teeth and antlers are presented in Tables 3 and 4. (in mm, according to the scheme in Made and Tong, 2008)

Remarks. Most of the giant deer antlers from Kaniv are characterised by large rosettes, which are among the largest in Eurasia (Fig. S7) (Croitor et al., 2014; Malikov, 2015; Shpansky, 2011, 2014; Stefaniak, 2015). Mandibular teeth are within the range of measurements for this species from the territory of Ukraine, e.g. from Romankovo (MIS 3), and smaller than those from Bukovynka (MIS 3). Processed specimens are in the lower range of variation for those from Western Europe as well as *M. giganteus giganteus* from Poland. Antlers from Kaniv are within the range of the smaller *M. giganteus germaniae/ruffi* known from several cave sites and Middle Pleistocene localities in Poland (Stefaniak, 2015). The specimen from Kaniv had a relatively shorter row of cheek teeth similar in proportions to those of *M. giganteus germaniae/ruffi* from the MIS 3 of the Biśnik Cave. It was also smaller compared to the specimen from Bukovynka Cave and Romankovo (MIS 3) from the territory of Ukraine, as well as to the specimens from Moldova (Fig. S8). It was also smaller compared to typical Late Pleistocene representatives of *M. giganteus giganteus* from Western Europe. The material also contained fragments of the proximal and distal epiphyses of metacarpal. Their dimensions were smaller compared to other representatives of this species from Europe (Fig. S9). Croitor et al. (2014) and Stefaniak (2015), describing the remains of *M. giganteus* from Central and Eastern Europe, state that there were two forms of this species. The smaller occurred in the Middle and Upper Pleistocene in Eurasia and belonged to *M. giganteus germaniae/ruffi*. This form was present until the end of MIS 3. At the end of the last glaciation, a more massive *M. giganteus giganteus* appeared in this area. Remains of the giant deer from Kaniv belonged to *M. giganteus germaniae/ruffi*.

Genus *Alces* Gray, 1821

Alces alces (Linnaeus, 1758).

Material. One fragment of the right antler (NMNHU-P 10–483) (Fig. 5, E).

Measurements. DAPp 60.00; DTp 55.00; DAPb 59.40; DTb 61.00; DAPr 70.60; DTr 70.30.

Remarks. The elk antler from Kaniv belonged to the largest individual among those analysed by us (Fig. S10) (Breda, 2002; Stefaniak, 2015). Specimens from the Holocene of Poland are slightly smaller.

Genus *Rangifer* Smith, 1827

Rangifer tarandus (Linnaeus, 1758).

Material. Four fragments of antlers (NMNHU-P 10–484, 10–485, K 164–165) (Fig. 5, F, G).

Measurements. DAPp 41.00; DTp 37.70; DAPb 41.40, 41.00; DAPr 44.10, 50.60, 56.00; DTb 42.20, 32.70; DTr – 41.40, 45.70; CD 118.00, 138.00.

Remarks. Based on the comparison of the reindeer specimens from Kaniv with those from cave sites in Poland (Fig. S11), we can conclude that they belonged to large, massive females. Obtained results corroborated with the observations of Weinstock (2000), Croitor (2010a, 2010b), Stefaniak et al. (2012), Stefaniak (2015), who noticed that the specimens from Moldova and Ukraine are larger and more massive than those from central and north-western Europe.

Family Bovidae Gray, 1821

Genus *Bison* Hamilton Smith, 1827

Bison priscus Bojanus, 1827

Material. Eight near-complete skulls (K 132–136, K 215–216, 218, unnumbered) (Fig. 5, H), five humeri (K 188, 190, 192–194), seven radii (K 195–200, NMNHU-P 10–64), four tibiae (K 201–202, unnumbered, NMNHU-P 10–807), three scapulae (K 203–204, 289), one calcaneus (K 255) (Fig. 4, G-H).

Measurements. See Tables 5–9 for separate bones. *Calcaneus:* GL

Table 3
Measurements of lower teeth of *Megaloceros giganteus* from Kaniv (in mm).

Tooth	Coll. No.	Measurements				L occlusal surface	DTa (posterior part)
		W	D	Ta	DTa		
p2	K 116	21.60	50.00	–	–	–	–
p3	K 116	24.30	51.80	–	–	–	–
p4	K 116	28.10	53.20	–	–	–	–
m1	K 116	30.60	57.50	2.00	15.50	24.80	18.20
m2	K 116	31.30	58.60	2.10	19.30	29.00	19.80
m3	K 116	31.20	61.40	–	–	–	–
m3	K (unnumbered)	–	–	–	–	38.37	19.52

Table 4
Measurements of antlers of *Megaloceros giganteus* from Kaniv (in mm).

Coll. No.	DAPp	DAPr	DAPb	H_{ext}	H_2	DTp	DTr	DTb	CD
NMNHU-P 10-468	–	–	–	–	–	–	–	–	~210.00
NMNHU-P 10-469	88.10	102.40	97.50	80.20	–	82.00	90.80	80.20	292.00
NMNHU-P 10-470	89.00	105.30	99.60	64.60	390.00	77.80	92.70	80.40	294.00
NMNHU-P 10-471	90.50	105.10	102.40	50.30	430.00	77.50	90.80	75.80	305.00
NMNHU-P 10-474	93.20	107.40	100.80	65.30	410.00	91.10	105.30	81.10	306.00
NMNHU-P 10-475	90.60	105.20	101.00	61.80	380.00	83.40	88.00	82.10	305.00
NMNHU-P 10-476	86.70	94.10	93.40	62.70	380.00	74.00	84.70	74.40	288.00
NMNHU-P 10-477	90.00	97.20	93.90	61.30	–	88.30	100.20	81.30	292.00
NMNHU-P 10-478	92.10	102.20	98.80	82.20	–	88.00	102.00	92.70	305.00
NMNHU-P 10-479	92.10	106.00	104.70	66.20	–	84.40	87.00	86.60	304.00
NMNHU-P 10-481	78.70	87.10	85.20	52.60	–	62.70	70.60	63.00	236.00
NMNHU-P 10-627	–	111.60	–	–	–	–	97.26	–	330.00
K 142	80.00	91.20	89.30	77.20	–	79.40	92.60	93.30	–
K 143	90.60	116.80	100.20	84.00	415.00	91.30	118.60	103.50	–
K 144	78.40	89.00	80.70	75.20	360.00	86.40	99.80	100.40	–
K 148	90.40	112.70	108.10	62.60	410.00	90.70	113.20	108.70	–
K 153	83.90	93.40	93.00	62.20	410.00	83.20	96.20	98.10	–
K 155	94.60	117.40	111.50	80.00	470.00	97.80	116.20	117.10	–
K 156	85.60	112.30	99.40	65.20	390.00	85.80	114.20	116.00	–
K 211	85.40	112.70	97.10	64.80	400.00	84.10	113.80	98.30	–
K 212	88.40	112.20	95.00	67.40	400.00	89.40	112.90	96.70	–
K 213 (right)	84.40	93.20	92.70	59.00	360.00	81.90	96.10	86.60	255.00
K 213 (left)	85.00	93.10	92.00	51.50	350.00	80.70	90.20	83.40	253.00
K (unnumbered)	89.20	100.60	99.00	47.00	345.00	90.70	102.40	83.50	–

162.20; GB 65.20.

Remarks The results were compared with measurements from the literature (Flerov, 1976; Baryshnikov et al., 1996; Álvarez-Lao and García-García, 2006; Vasiliev, 2008; Croitor, 2010a; Vercoutère and Guérin, 2010; Shpansky et al., 2016). The dimensions of the skulls and other specimens from Kaniv are characteristic for those of the Late Pleistocene steppe bison of Europe and Siberia. They are similar in size to individuals, both males and females, from the Upper Pleistocene of Tomsk region (W Siberia) as well as Peschanaya Gorka (Yakutia, MIS 5) and Taubach (Germany, MIS 5e). Two males from Grigorievka (Kazakhstan, MIS 9–11) also have similar size, while two specimens from Kaniv are characterised by larger horncore sizes. The latter are similar to those from Langsdorf (Germany, MIS 3) and to the largest Late Pleistocene specimens from Poland. The smallest dorso-basal is characteristic for bison females from the Late Pleistocene of Krasny Yar (Tomsk Region, Siberia, MIS 2), Habbarra (France, MIS 2) and Lombardy (Italy). Processed remains belong to individuals of medium size. Bison skulls can be compiled into two groups, the first of which is characterised by short and straight horncores typical of the forest bison morphotype (Soubrier et al., 2016). It occurred in a warm and temperate climate. The second group is represented by high-vaulted massive skulls with long, curved horncores typical of representatives living in open areas of southern Siberia and Eastern Europe at the end of the Middle Pleistocene (Kahlke, 1999). The size of horncores (Fig. S12) is within the range of variation for Late Pleistocene Polish specimens and bison males from MIS 5e of Krasny Yar. Measurements of the smallest breadth of humerus diaphysis of the steppe bison (Fig. S13) show that individuals from Kaniv fall into the range of variation of specimens from the Middle Pleistocene Romain la Roche sites (France) and Krasny Yar (Tomsk Region, Siberia, MIS 5e and MIS 3). Bison individuals from the Middle Pleistocene of Spain have the most robust humeri, while the most gracile bones belong to those from Tarandanovo (Siberia, MIS 3) and females from Habbara (France, MIS 2). The ratio of breadth to the depth of the distal end of bison radii from Kaniv (Fig. S14) is similar to those from Romain la Roche and Krasny Yar (MIS 5e). They have large, massive distal ends of this bone compared to the specimens from Tarandanovo (Siberia) and MIS 3 of Poland. The smallest bison tibia from Kaniv (Fig. S15) is within the range of variation of bison females from Krasny Yar (Tomsk Region, Siberia, MIS 3), Poland (MIS 3), Orda (Siberia, MIS 2), as well as Habbara (France, MIS 2). Two medium-sized individuals from Kaniv are within the range of variation of those from Grigorievka (Kazakhstan, MIS 9–11), Krasny Yar (Tomsk Region, Siberia, MIS 5e), and MIS 3 of Siberia. One specimen from Kaniv and the other one from the Middle Pleistocene of Romain la Roche (France) and Taubach (Germany, MIS 5e) are the largest (together with that of bison female from the Late Pleistocene of Ofetinţi (Vykhvatyntsi), Republic of Moldova). The distal epiphysis of calcaneus from Kaniv is similar in size to those from Krasny Yar and the Middle Pleistocene of France.

5. Discussion

The stratigraphical position and geological age of bones from Kaniv remain uncertain. In his first publication, Svistun (1966) divided all finds into two groups. The first group contained geologically young remains of domestic animals such as "goat, sheep, cow, pig, horse, and dog", which originated from Holocene archaeological sites found on banks of rivers. The second group included such species as *Mammuthus primigenius, Coelodonta antiquitatis, Bison priscus, Megaloceros giganteus*, and *Cervus elaphus*, dated to the Late Pleistocene. The next publication contains some information about the bones bedding (Svistun and Lomayev, 1967). Bones were bedded through all thickness of alluvial sands, but sometimes bone accumulations were found in the so-called "basal horizon of alluvium", usually laying 20–30 m deep, and bedded above the blackish-green boulder loam (till) or on the sands and laminated sandy loams of lacustrine-alluvial origin. At the bottom, the sands are very ferruginated and change to the gravel interbed (Svistun and Lomayev, 1967). Goretskiy (1961) considered all sediments below the basal alluvial horizon as the Shevchenko Formation of the Middle Pleistocene, containing lacustrine, alluvial and glacial sediments. Based on the faunal data of Pidoplichko, G. Goretskiy considered that the Shevchenko Formation is not older than the Dnieper Glaciation (Goretskiy, 1970, p. 290).

The Shevchenko Formation *sensu* Goretskyi now corresponds to the above-till fluvioglacial ($fP_{II}dn^s$) and lacustrine-glacial ($lgP_{II}dn^s$) sediments/facies of the Dnieper unit (Fig. 2) (Tsyba et al., 2012). If the Dnieper Glaciation corresponds to the MIS 8, all the Kaniv fauna should be younger of this age.

The wolverine from Kaniv was considered previously as most probably of Late Pleistocene rather than Holocene age (Marciszak and Kovalchuk, 2011). Other carnivores from the site showed an admixture of Late Pleistocene and Holocene species, which recently occurred in the territory of Ukraine. However, Holocene specimens can be distinguished

Fig. 4. A – *Mammuthus intermedius,* maxilla (K 224), ventral view; B, B' – *Mammuthus trogonterii chosaricus,* right m3 (K 101), occlusal surface, lingual view; C, C' – *Mammuthus primigenius jatzkovi*, right M3 (K 102), occlusal surface, lingual view; D-E – *Coelodonta antiquitatis*, skull (K 214), dorsal view (D), left humerus (K 183), lateral view (E); F – *Mammuthus* sp., ulna (K 243), lateral view; G-H – *Bison priscus*, right humerus (K 193), lateral view (G), scapula (K 204), ventral view (H).

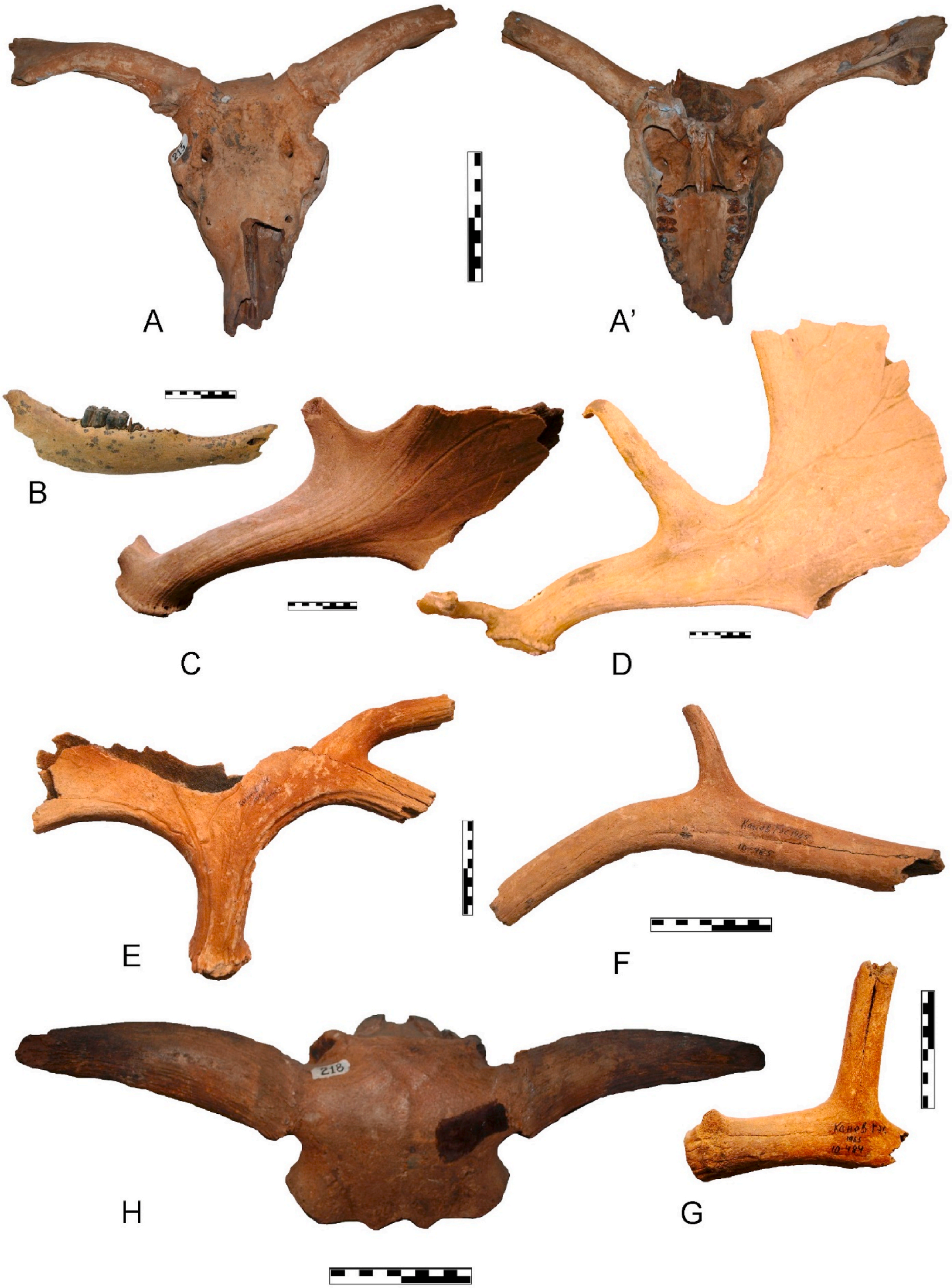

Fig. 5. A-D – *Megaloceros giganteus*, skull (K 213), dorsal (A) and ventral view (A′), right mandible (K 116), lateral view (B), antlers (C – NMNHU-P 10–470; D – K 211), lateral view; E – *Alces alces*, antler (NMNHU-P 10–483), lateral view; F, G – *Rangifer tarandus*, antlers (F – NMNHU-P 10–485; G – NMNHU-P 10–484); H – *Bison priscus*, skull (K 218), dorsal view.

Table 5
Skulls and horncore dimensions of the steppe bison *Bison priscus* from Kaniv[a].

Coll. No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Unnumbered	291.3	154.1	231.5	44.7	40.6	193.8	276.4	–	–	–	187.6	141.8	109.4/	108.3/	385/
K 132	315.7	152.9	234.5	42.3	45.1	185.1	–	–	–	–	–	–	110.7/	107.4/	378/
K 134	293.5	148.8	238.9	49.2	56.1	195.8	196.6	298.7	301.2	–	195.8	149.8	93.4/96.5	106.8/ 100.7	325/330
K 135	296.7	139.6	230.2	41.6	45.8	213.6	320.2	307.3	356.1	–	186.4	133.6	102.4/99.1	101.7/ 104.3/	340/388
K 136	–	–	–	–	–	–	–	–	–	–	–	–	/102.5	108.1	/346
K 215	303.7	145.8	229.8	35.5	37.8	216.2	311.4	320.5	355.8	–	197.8	139.2	124.1/122.1	113.4/ 114.5	392/390
K 216	322.5	142.2	236.4	44.3	45.3	225.9	351.8	334.1	365.8	214.1	209.8	166.2	125.3/116.9	118.4/ 114.2	393/382
K 218	303.4	145.7	233.3	38.1	49.2	209.6	289.0	306.4	337.9	–	185.3	136.9	110.4/106.1	103.9/ 106.3	361/375

[a] Measurements (in mm, according to the scheme in von den Driesch, 1976): 1 – greatest breadth: otion-otion; 2 – greatest breadth of occipital condyles; 3 – greatest breadth at the bases of paraoccipital processes; 4 – greatest breadth of the foramen magnum; 5 – height of the foramen magnum: basion – opisthion; 6 – least occipital breadth; 7 – least breadth between the bases of horncores; 8 – least frontal breadth: breadth of the narrowest part of the frontal aboral of orbits; 9 – greatest breadth across orbits: ectoorbitale – ectorobitale; 10 – least breadth between the orbits: entorbitale – entorbitale; 11 – greatest height of the occipital region; 12 – least height of the occipital region; 13 – dorsoventral breadth of the horncore base; 14 – cranio-caudal breadth of the horncore base; 15 – horn-core basal circumference.

Table 6
Measurements of humerus of the steppe bison *Bison priscus* from Kaniv[a].

Coll. No.	Age	Side	Gl	Bp	Dp	Bd	BT	Dd	SD
K 188	adult	right	–	–	–	104.40	103.70	107.60	–
K 190	adult	left	–	–	–	110.20	109.80	114.30	–
K 192	adult	right	–	–	–	125.90	116.30	116.60	64.90
K 193	adult	right	438.50	166.10	148.70	120.30	118.70	124.90	70.70
K 194	adult	left	–	–	119.10	122.90	118.10	–	67.60

[a] Measurements (in mm, according to the scheme of von den Driesch, 1976): Gl – greatest length; Bp – breadth of the proximal end; Dp – depth of the proximal end; Bd – breadth of the distal end; Dd – depth of the distal end; SD – smallest breadth of diaphysis.

Table 7
Measurements of radius of the steppe bison *Bison priscus* from Kaniv[a].

Coll. No.	Age	Side	Gl	Ll	Bp	BFp	Dp	Bd	BFd	BT	Dd	SD
10–64	adult	right	389.40	–	118.90	110.70	66.70	–	–	59.40	64.60	186
K 195	adult	left	403.20	372.90	122.50	114.90	–	110.70	100.50	70.90	77.30	240
K 196	adult	right	390.10	369.10	126.40	118.00	–	121.70	105.30	70.10	75.20	239
K 197	adult	left	–	–	127.10	116.30	–	–	–	–	–	–
K 198	adult	right	376.20	365.70	120.90	108.50	–	117.50	110.50	64.50	74.00	220
K 199	adult	left	400.60	371.20	114.80	113.40	–	–	99.50	72.16	72.30	205
K 200	adult	left	411.80	395.60	123.90	114.90	–	115.40	112.00	78.40	68.10	208

[a] Measurements (in mm, according to the scheme of von den Driesch, 1976): Gl – greatest length; Ll – length of the lateral part; Bp – breadth of the proximal end; BFp – greatest breadth of the facies articularis proximalis; Dp – depth of the proximal end; Bd – breadth of the distal end; BFd – greatest breadth of the facies articularis distalis; Dd – depth of the distal end; SD – smallest breadth of diaphysis; CD – smallest circumference of diaphysis.

Table 8
Measurements of tibia of the steppe bison *Bison priscus* from Kaniv[a].

Coll. No.	Age	Side	Gl	Ll	Bp	Dp	Bd	Dd	SD	CD
Unnumbered	adult	left	–	–	–	–	84.20	56.80	–	–
NMNHU-P 10-807	adult	right	459.50	422.70	135.90	122.20	86.90	64.80	58.30	158.00
K 201	adult	left	504.50	483.40	149.82	143.70	93.40	73.50	65.00	224.00
K 202	adult	left	465.90	424.80	140.30	119.00	83.40	68.70	–	–

[a] Measurements (in mm, according to the scheme of den Driesch and von, 1976): Gl – greatest length; Ll – length of the lateral part; Bp – breadth of the proximal end; Dp – depth of the proximal end; Bd – breadth of the distal end; Dd – depth of the distal end; SD – smallest breadth of diaphysis; CD – smallest circumference of diaphysis.

by a light colour and lower mineralisation. Remains of this species were reported from a number of Palaeolithic sites within Ukraine (Pidoplichko, 1940; Rekovets and Starkin, 1990). The presence of wolverines was noted even from recent times; however, most of them were migrated individuals. Due to the scarce material, carnivores cannot provide any reliable comments on the biostratigraphy of the site.

The teeth and humerus belonged to *Equus ferus latipes*, and the other humerus fragment belonged to the European wild ass *Equus hydruntinus*. Both species were widespread in Eastern Europe during the Middle and Late Pleistocene. These species occurred together in many Eurasian localities (Kuzmina, 1997; van Asperen and Stefaniak, 2011; van Asperen et al., 2012; Kovalchuk et al., 2020). The size of the examined remains indicates Late Pleistocene age. At the same time, the presence of *E. hydruntinus* indicates a warm climate (interglacial or interstadial), probably MIS 5 or MIS 3, which corresponds to the Late Pleistocene alluvium (Fig. 3).

Table 9
Measurements of scapula of the steppe bison *Bison priscus* from Kaniv[a].

Coll. No.	Age	Side	BG	GLP	SLC	LG
K 204	adult	left	70.70	98.60	95.40	86.20
K 203	adult	left	70.80	103.90	91.40	86.50
K 289	adult	left	69.30	97.90	75.60	86.20

[a] Measurements (in mm, according to the scheme of von den Driesch, 1976): BG – breadth of glenoid cavity; GLP – greatest length of processus articularis; SLC – smallest length of collum scapulae; LG – length of glenoid cavity.

The woolly rhino (*C. antiquitatis*) remains are not time specific, and the same specimens could occur during either the Middle or Late Pleistocene (Pidoplichko, 1940; Korneev, 1953). The scarce remains of the wild boar also cannot be used for the parallels from other periods. This species was quite common in Ukraine during the Pleistocene (Korneev, 1953; Pidoplichko, 1956).

The cervid material from Kaniv was dominated by the giant deer *M. giganteus* represented by *M. giganteus germaniae/ruffi* typical for this area (Pidoplichko and Svystun, 1963). In most cases, the antlers were quite large, while the teeth and the metapodial fragment were smaller compared to other specimens of this species from the territory of Ukraine. The giant deer indicates only time limits, no later than MIS 3, but the same subspecies existed during the Middle and most of the Late Pleistocene.

Krokhmal et al. (2002) reported the presence of reindeer during the terminal phase of the Middle Pleistocene of Ukraine. In addition, remains of this species were identified in materials of numerous Palaeolithic sites within Eastern Europe (Pidoplichko, 1940; Korneev, 1953; Pidoplichko and Topachevsky, 1953; Belan, 1983; Rekovets and Starkin, 1990; Sablin and Kuzmina, 1992; Croitor, 2010b, 2010c; Kovalchuk and Kochubei, 2011). According to Croitor (2010b), all these specimens belonged to *Rangifer tarandus constantini* Flerov (1934). Elk also occurred in the territory of Ukraine probably during the entire Pleistocene (Korneev, 1953; Pidoplichko and Topachevsky, 1953; Pidoplichko, 1956; Krakhmalnaya, 2008; Kovalchuk, 2011), but its range has subsequently declined, and now this species is rather scarce (Kovalchuk, 2010).

Bovid remains in materials from Kaniv are represented only by the steppe bison *Bison priscus*. They belonged to individuals of medium size and represent two morphological groups, one of which (massive skulls with long curved horncores) is characteristic for the end of the Middle Pleistocene (probably the end of Dnieper Glaciation), and the other (skulls with short and straight horncores) is related to a warm and temperate climate, most likely of the Kaydaky unit (Eem, MIS 5e). Studies on postcranial bones of adult bison skeletons show the same characteristics. The analysis of humeri, radii and tibiae shows the similarity of long bone dimensions to those from the Middle Pleistocene sites of Europe and Asia (Kahlke, 1999; Soubrier et al., 2016).

Even the scarce material of the teeth of proboscideans provides more reliable biostratigraphic benchmarks (Tables 1 and 2). The presence of *M. p. jatzkovi* does not contradict the stratigraphy described above. It can be associated with the Upper Pleistocene alluvium of Trubizh and Vilshany Stages ($a^{3-2}P_{III}$tb-vl), correlating with the Vytachiv interstadial (MIS 3). The presence of *M. intermedius*, according to Foronova (2014), indicates the inter-Saalian sediments (MIS 7), which could be correlated with the lacustrine-glacial above-till sediments ($lgP_{II}dn^{s}$). Other researchers (Golovachev and Titov, 2018) extended the occurrence of *M. intermedius* to MIS 5, claiming its co-existence with *M. t. chosaricus* and *Palaeoloxodon antiquus*.

The single tooth of *M. trogonterii chosaricus* in the collection (Table 2) contradicts to the claimed age of the bone-bearing strata – the end of Dnieper Glaciation – Late Pleistocene, but, on the other hand, it could get into the over-till sediments from the older alluvial due to glacial dislocations. Otherwise, the age of lacustrine-glacial strata ($lgP_{II}dn^{s}$) or the timespan of *M.t. chosaricus* existence in Eastern Europe should be revised.

6. Conclusions

Considering that the entire Kaniv collection was studied at the present stage, we can conclude that the collection is heterochronouss and originates from a few timespans of the Middle and Late Pleistocene, and Holocene. In this study, we did not analyse Holocene faunal remains, but their presence does not require confirmation. According to the faunistic analysis of several Pleistocene species, mainly proboscideans but also to a lesser extent equids and cervids, we can conclude that the bone accumulation near Kaniv took place during most part of the Late Pleistocene (MIS 5 – MIS 3) and the end of Middle Pleistocene. We suggest that the massive maxilla of *M. intermedius*, as well as other massive bones, could be correlated with bone accumulations in the so-called “basal horizon”, and is more likely dated to the interstadial MIS 7. The find of the isolated tooth of *M. trogonterii chosaricus* can evidence the presence of sediments older than the Dnieper Glaciation in the Shevchenko Depression, but this assumption should be supported by more numerous finds.

Author contributions

B.R. and O.K. designed research. B.R. completed regional settings and geological part of the discussion. Comparative analyses were performed, and the obtained data were analysed by A.M. (carnivores), B.R. (proboscideans), K.S. (equids, suids, and cervids), A.K. (rhinocerotids), and U.R.S. (bovids). B.R. and O.K. wrote the paper with input from all authors. U.R.S. prepared the map and photos. All authors approved the final version of the manuscript.

Data availability

The authors declare that all data supporting the finding of this research are available within the paper and its Supplementary Information.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2020.11.010.

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