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Glacial and post-glacial adaptations of hunter-gatherers: Investigating the late Upper Paleolithic and Mesolithic subsistence strategies in the southern steppe of Eastern Europe

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ABSTRACT

Diverse landscapes and ecosystems stretching across Europe led to diverse hunter-gatherer cultural records during the Upper Paleolithic and Mesolithic. In response to abrupt climatic forcing, starting around the Late Glacial Maximum and followed by climatic events such as the Bølling–Allerød and the Younger Dryas in the Terminal Pleistocene, archaeological data pertaining to cultural and behavioral shifts of hunter-gatherers continue to be explored on a regional and pan-regional scale. Here we present an initial summary, which includes new and published data on faunal analyses from multiple open air sites that span the Late Pleistocene to the Holocene, dated between the Late Upper Paleolithic and Mesolithic (20,000–6000 uncal ^{14}C BP) in the southern steppe of Eastern Europe. For this area, this is the first study to compile the cultural and faunal data with geo-referenced localization and radiometric dates of the archaeological sites. Taken together, faunal assemblages from the Epigravettian are characterized by low diversity and are often dominated by one species of large game, including bison and equids, whereas the Mesolithic diet is characterized by higher inter-site variability subsisting on large ungulate and greater emphasis on freshwater resources. This study contributes to the general knowledge concerning the last phases in the evolution of the Eurasian hunter-gatherers.

1. Introduction

The past adaptation of Paleolithic and Mesolithic hunter-gatherers in Europe is a result of their interaction with the diverse landscapes and ecosystems. Unlike other cultural transitions where the relationship between climatic forcing and human behavior remains to be demonstrated, the shift from the Late Upper Paleolithic and Mesolithic has been linked to and framed in terms of abrupt climatic changes occurring between the Late Glacial and the Holocene. In response to abrupt climatic forcing starting around the Late Glacial Maximum and followed by climatic events such as the Bølling–Allerød and the Younger Dryas in the Terminal Pleistocene, archaeological data pertaining to cultural and behavioral shifts of hunter-gatherers have been explored on a regional and pan-regional scale (Crombé et al., 2011; Donahue and Lovis, 2006; Huntley et al., 2013; Lovis et al., 2006). Within the

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framework of the INQUA Project 1404, this study presents an overview of our current knowledge of economic activities among foragers from the Late Upper Paleolithic and Mesolithic cultures in the southern steppe of Eastern Europe.

The paper considers the period from the Late Glacial Maximum (Greenland Stadial 2b: 19-18,500 uncal ^{14}C BP) over the Bølling–Allerød interstadial (Greenland Interstadial 1: 12,500 -11,000 uncal ^{14}C BP), Younger Dryas (Greenland Stadial 1, 11,000–10,000 uncal ^{14}C BP) and up until the Holocene warming ~6000 uncal ^{14}C BP. This interval is characterized by relatively abrupt climatic changes that preceded the beginning of the Holocene as well as the climatic amelioration, which followed thereafter (Birks and Ammann, 2000; Brooks and Birks, 2001; Davis et al., 2003). The Greenland ice core records indicate that climatic fluctuation was marked globally and led to large environmental shifts on a local scale, triggered by the decrease in sea level, increased humidity and temperature, as well as changes in the floral and faunal communities (Burke et al., 2014; Clark et al., 2012; Rosen et al., 2014; Thiagarajan et al., 2014; Yanko-Hombach, 2007). This instability drove Upper Paleolithic foragers to adapt to their changing environment, which is associated with the rise of the Mesolithic cultures.

Regions with a long history of hunter-gatherer occupations are often characterized by the abundance of karst systems, which resulted in comparatively good preservation and visibility. However, Eastern Europe has provided key archaeological records of human settlements and movement across open landscapes (Hoffecker, 2002). Thus, archaeological investigations of open air settlements have the potential to address the broader spectrum of hunter-gatherer adaptations and can complement our understanding of hunter-gatherer behaviors that is often biased towards cave and rockshelter sites. Drawing on this interest, we consider open air sites in the Late Upper Paleolithic and Mesolithic sites from the southern steppe of Eastern Europe.

This paper constitutes a review article based on a combination of original unpublished data from recently studied/revised collection and a summary of literature and new studies, which entail cultural and faunal data with geo-referenced localization and radiometric dates of the archaeological sites. Current data indicate that hunter-gatherers in the Late Upper Paleolithic continued to exploit large ungulates for subsistence, a pattern that deviated little over most of the Paleolithic period. Changes, when observed, reflect shifts in the commonly targeted species by hunters. Bison and horses are the most dominant fauna in the southern steppe, depending on the region and the time interval. In contrast, the Mesolithic record shows greater diversification in the choice of large game prey as well as greater emphasis on gathering/fishing practices, and as a whole reflects a shift to a more regionally variable diet.

2. Southern steppe of Eastern Europe

The current biome in Northwestern Eurasia consists of a mix of tundra, taiga, forest and steppe. Steppes stretch geographically from the lowlands of Inner Mongolia to the west coast of the Black Sea and parts of Hungary. It is one of the biologically and culturally rich environments that is threatened today by human impacts and has been the subject of multidisciplinary conservation efforts (Antonchikov et al., 2002; Korotchenko and Peregrym, 2012). It has been postulated that patches of relict from the Quaternary steppe exist today in Eastern and Western Beringia and the Altai-Sayan Mountains of Central Asia (Kienast, 2007; Pavelková Řičánková et al., 2014).

The past distribution of the steppe biome, which emerged roughly two million years ago, was larger than the present, as it originally covered most of mid-to-high latitude Eurasia, but the spatial diversity and temporal evolution of the prehistoric biome continue to intrigue paleoecologists and archaeologists alike. According to paleoenvironmental reconstructions, the steppe of the Pleistocene was locally heterogeneous, yet homogeneous on the continental scale (Pavelková Řičánková et al., 2014).

The tundra steppe is one of the most known biomes of the past, an ecological system that has received considerable interest in Quaternary research (Bigelow et al., 2003; Edwards and Armbruster, 1989; Guthrie, 1990; Hibbert, 1982; Kahlke, 1999; Kozhevnikov and Ukraintseva, 1999; Yurtsev, 2001; Zimov et al., 2012). Environmental conditions from middle to higher latitudes in the Pleistocene were characterized by a cold and dry continental climate (Kienast, 2007). However, we have yet to fully understand the past biome of Eastern Europe in the Pleistocene due to several issues, including the lack of systematic sampling of paleoenvironmental record with chronological depth, creating geographical biases, as well as the resolution of the paleoenvironmental records, which allows us to correlate multiple sampled sites for regional-scale data (but see Haesaerts et al., 2010).

The tundra and steppe vegetation is indicative of the diversity of the plant communities in northern Eurasia and attests to the existence of several zonal biomes that were intergraded in the past (Kozhevnikov and Ukraintseva, 1999). The vegetation is largely dominated by herbs including tufted grasses, sedges and dwarf shrubs, which are found in the steppes of middle to high latitudes and in the Arctic tundra today (Elias and Crocker, 2008). Furthermore, the extreme seasonal fluctuation of moisture is documented by grasses typically linked to meadows as well as littoral plants that inhabit the shores of small lakes with unstable water levels (Kienast, 2007).

The tundra steppe has also been linked to a faunal community with no modern analogs. A notable feature is the large biomass of grazing animals, epitomized by extinct woolly mammoths and woolly rhinoceroses, hence the term ‘mammoth steppe’ (Guthrie, 1982, 1990; Kahlke, 2014). Many East European sites are known for the rich presence of mammoth remains exploited for dietary needs and their use as raw material for artifacts and structures. One of the known examples of Paleolithic dwelling structure was constructed from cranial and post-cranial remains of mammoths at sites such as Mezin, Molodova I, Gontsy and Mezhyrich (Demay et al., 2012; Iakovleva et al., 2012; Péan, 2015; Pidoplichko, 1998; Soffer, 1985). However, while taphonomic and sampling biases must be taken into account, zooarchaeological and paleontological records show that the density of mammoth population varied across the steppic landscape in Eastern Europe (Ponomarev et al., 2013; Puzachenko and Markova, 2014; Velichko and Zelikson, 2005). Megafauna (woolly rhinoceros and woolly mammoth) are particularly scarce in the area that some have referred to as the southern steppe (or the Black Sea steppe) in the Final Pleistocene (Anthony, 2007).

In the present, the region between the north of the Black Sea and ~48 °N is characterized by the Pontic steppe (Korotchenko and Peregrym, 2012). The southern steppe of Eastern Europe extended eastwards from the Danube river and in the northern area of the North Sea below 48°N, traversing the Volga Valley and reaching Kazakhstan. Beginning at 32,000 uncal ^{14}C BP, the Black Sea underwent the last phase of regression, and the sea level reached 110 m below the present at LGM (Bahr et al., 2008; Shmuratko, 2007). Additionally, the change in the sea level led to the formation of a lake in the place of the current Black Sea while the Azov Sea was fully part of the continent, and the Crimea was geographically part of the rest of the landmass, making up the southwestern margin of Eastern Europe (Winguth et al., 2000). The transgression of the Black Sea occurred beginning at the Bølling-

Allerød phase with increased runoff (Bahr et al., 2008).

The southern steppe of Eastern European Plain, which is the focus of this paper, was a region that remained free of glaciers during the colder periods of the Last Glacial (Fig. 1). The notion of a steppe zone in archaeology was first conceptualized by Boriskovskii to describe an ecological and cultural entity associated with specific economic activities (Boriskovskii, 1993; Boriskovskii and Praslov, 1964). According to Boriskovskii, the area served as a refugium for multiple plant and animal species, possibly leading to diverse ecological communities. It was therefore assumed that the ecological communities differed from the typical tundra steppe of the higher latitudes and that the area served as a refugium for multiple plant and animal species, possibly leading to diverse ecological communities. According to microfaunal analyses, the zonation of mammalian assemblage supports the notion that this area was ecologically distinct from other parts of Eurasia where there was greater representation of tundra, corresponding the Euro-Kazakhstanian steppe assemblage in the Pleistocene (Markova and Puzachenko, 2007). During the Late Glacial Maximum, the distribution tundra element on the Russian Plain was limited to the north of 57 °N and while it is possible that tundra existed to the south, it was intergraded with the steppe vegetation, characterized by steppe forb and grass species (Tarasov et al., 2000). The steppe is composed of different taxa of *Artemisia*, grasses and xerophilous plants. The riverine and riverbanks were characterized by vegetation that included arboreal species such as alders and willows (Spiridonova, 1991). This is supported by the presence of arboreal species, namely willow and alder from Kamennaya Balka II (Leonova et al., 2006). This ecosystem is thought to have been relatively stable despite the interstadial-stadial fluctuations (Kienast, 2007). Another possible explanation of this pattern is that the paleoenvironmental record does not have the chronological resolution to track short term shifts. This remains to be demonstrated from controlled samples with increased chronological resolution.

For the mammalian record, some evidence of megafauna from the Rostov-on-Don, southern Bug and Lower Dnieper has been reported (Krotova, 2013; Leonova, 1994). However, it is puzzling that their occurrences in the southern steppe area are rare, as the exploitation of mammoth increased during the Upper Paleolithic in other regions of Eastern Europe (as described above). Their biogeographic distribution may have been influenced by the presence of glaciers and permafrost in higher latitudes although this will require future paleontological and archaeological investigations. Furthermore, it is possible that the ecological border at around 48°N between two vegetation biomes also shifted between the steppe in the south and the tundra steppe in the north over several glacial and interglacial intervals and that the megafauna were more abundant in the northern tundra steppe (Bolikhovskaya and Molodkov, 2006; Jary, 2009; Simakova, 2006). Megafauna also existed in the southern area including the Crimea and their distribution expanded and contracted over time, offering further clues to the complexity of the population history of mammoths and woolly rhinoceroses (Baryshnikov, 2003). Nonetheless, it is clear that the distribution of megafauna was not homogenous across all areas of the East European/Russian Plain and is partially a testament to the variability on the steppic landscape. To demonstrate this further, we will need to consider 1) if the absence is not a result of sample bias and 2) this absence correlates with some environmental condition in the region between the north of the Black Sea to ~48 °N.

The environment changed after the LGM when the forest element began to enter the steppe region. The transgression of the sea followed between 17 and 14,000 uncal ^{14}C BP. The warm period of the Allerød around 12-11,000 uncal ^{14}C BP is exemplified with the presence of oak, lime and maple. In other words, the Pleistocene-Holocene transition, occurring 13-10,000 uncal ^{14}C BP, was accompanied by warmer and wetter conditions (Cordova et al., 2011; Mudie et al., 2007; Novenko et al., 2015; Rousseau et al., 2001, 2011). Several pollen sequences with chronological framework provide insight into the floral spectra of the steppe mixed with forest, notably from Rogalik XII in eastern Ukraine (Gerasimenko, 2011). The core documents an increase in forests, especially pine trees, starting at the Allerød period, followed by a decrease during the Younger Dryas. The vegetation in the interval from the Preboreal to the Boreal (10,300 -8000 uncal ^{14}C BP) is characterized by

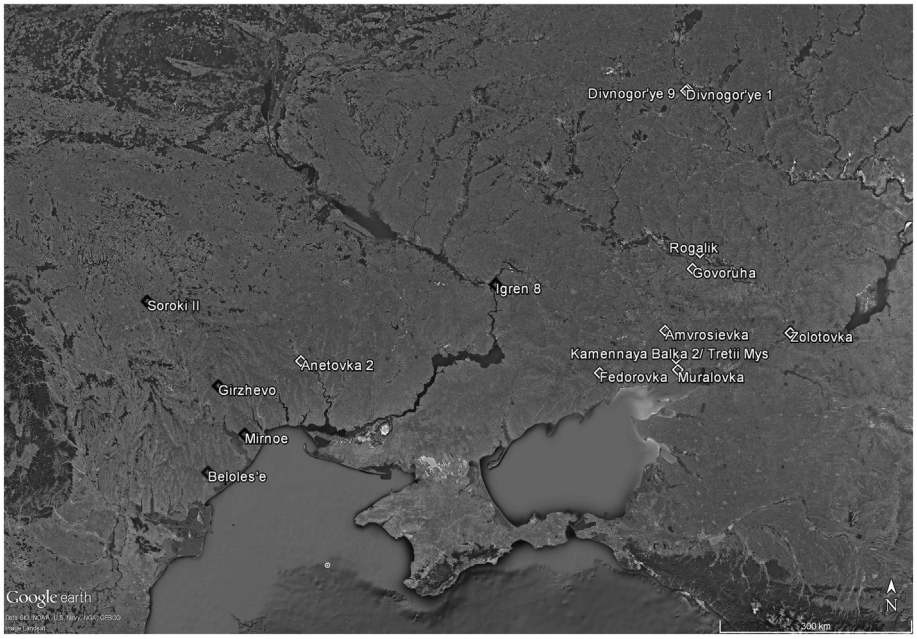

Fig. 1. Map of the sites of the southern steppe in Eastern Europe mentioned in this study. White squares = Epigravettian sites, black squares = Mesolithic sites.

sedges (*Carex)* and *Artemisia* (Kremenetsky, 1991). Forests began to spread from river valleys from ~9000 uncal ^{14}C BP, consisting of pine and birch in the earlier phase and shifting later to broad-leave trees such as oak and elm (Dergachev and Dolukhanov, 2007; Dolukhanov and Arslanov, 2009; Gerasimenko, 2011). During the Atlantic period (7500–5000 uncal ^{14}C BP), forests expanded in regions, which were previously dominated by steppe, as is documented at sites such as Beloles'e and Mirnoe in western Ukraine (Pashkevich, 1982). The forest consisted of pine and broad-leaved arboreal species (*Quercus, Tilia, Carpinus, Ulmus*) and concentrated in valleys of the large rivers such as Dnieper, Dniester, Bug, Donets and Don (Bibikova, 1982; Dolukhanov et al., 2009b).

3. Culture

Lithics in prehistoric archaeology play an important role in identifying cultural groups and linking tool types with economic activities (Gorelik, 2001; Krasnokutsky, 1999; Praslov et al., 1989; Smyntyna, 2007). Cultural traditions have been based on lithic assemblages containing tool types that serve as index fossils (Cohen and Gorelik, 1998). The economic activities in Eastern Europe are often discussed relative to the lithic industries, with an implicit assumption that a direct linear correlation between tool types and hunting strategies existed (Krasnokutsky, 1999; Praslov et al., 1989). For instance, the abundance of microliths associated with bison remains from sites such as Amvrosievka and Anetovka II has been linked to the use of bows and arrows (Krasnokutsky, 1999; Nuzhnyi, 1990). Thus, some maintain that certain lithic traditions can be ascribed to a particular cultural group and is related to specific functions related to resource exploitation (Praslov et al., 1989).

The tool assemblage from the southern steppes of Eastern Europe dating around ca. 22- 18/17,000 uncal ^{14}C BP includes carinated and nosed endscrapers, multifaceted burins and bladelets with a curved profile (ie. Dufour bladelets) (Ketraru et al., 2007; Praslov, 1972; Sapozhnikov, 2004). This tool assemblage has been defined as the Epiaurignacian and can be identified in several regions of Central and Eastern Europe, leading to a discussion of its cultural link to Aurignacian (Demidenko, 2008, 2009; Steguweit, 2009, 2010). Sites such as Sagaidak, Anetovka I, Muralovka and Zolotovka in Ukraine and southern Russia have been defined as Epiaurignacian.

The Epigravettian technocomplex refers to an archaeological culture that extended across Southern and most of East Europe, including southwestern France, Italy, the Balkans, the Caucasus, Ukraine and Western Russia. The Epigravettian existed between ca. 20-10,000 uncal ^{14}C BP (some argue for a shorter chronology, see Kozlowski, 1986), emerging before the onset of the LGM and persisting until the end of the Pleistocene. In Eastern Europe, the industry followed the Gravettian, showing technological continuity from preceding industries (Kozlowski, 1986). Despite the geographical variability, all variants of Epigravettian culture reveal a common trait, that is the dominance of microliths. Common tools that characterize the industry include backed blades, backed points, and bladelets with retouched ends (Olenkovskiy, 2010 and references herein). Functional and usewear analyses indicated that they served as weapons for projectiles and were also used for domestic uses (Boriskovsky, 1953; Leonova, 1994; Nuzhnyi, 1998; Sapozhnikova, 2003). The relationship of the Epiaurignacian and the Epigravettian remains unclear. The Epiaurignacian chronologically precedes the Epigravettian in most cases, and the sites with Epigravettian are more widespread compared to the Epiaurignacian, but a systematic comparison of the two industry cultures needs to be conducted in order to better understand the cultural dynamics of hunter-gatherers on a pan-regional scale.

There is a general consensus that regional variability within the East European Epigravettian existed but little agreement on the nature of this variability (Cohen and Gorelik, 1998; Krotova, 2013; Olenkovskiy, 2010). A number of local cultures during the LGM, including the Kamennaya Balka on the Lower Don, are consistent with the general definition and typology of the Epigravettian while others are not (Bessudnov, 2013). Some have noted that the lithic industry from Kamennaya Balka shows technological parallels to the Caucasus culture such as (Imeretinskaya culture) with a high relative abundance of microliths, especially pointed and backed bladelets (Leonova, 1994).

Organic artifacts are scarce during the Epigravettian in most regions, and the use of faunal material for artifact production is limited to perforated objects such as mollusks, which contrasts with the mammoth rich tundra steppe where ivory artifacts are abundant and Dniestr-Bug area where reindeer hunting characterized much of the subsistence (Djindjian et al., 1999). Further, the region of Rogalik-Peredelskoye provides evidence for two distinct lithic traditions (Gorelik, 2001). One consists of an industry with a relatively lower proportion of microliths and is characterized by truncated burins and blades manufactured using soft hammer percussion. The other has a relatively high proportion of geometric microliths with trapeze-like truncations and triangular points (Cohen and Gorelik, 1998; Gorelik, 2001).

The material culture of the Mesolithic is generally recognized as a local development of the Late Upper Paleolithic cultures in Eastern Europe, which responded to the abrupt climatic forcing of the Holocene, but uncertainties in the cultural and technological affiliation remain (Bessudnov and Bessudnov, 2017). A direct technological link between the Epigravettian and Mesolithic has yet to be established (Stanko and Kiosak, 2010). Specifically, the beginning of Mesolithic in some areas, such as the northwest area of the steppe, is not well documented. Nonetheless, the Pleistocene-Holocene transition in the southern steppe is marked by the transformation of local Epigravettian cultures into a series of Mesolithic cultures. Some argue that the microliths continue to increase in proportion compared to the Late Upper Paleolithic cultures from the Early to Late Mesolithic. Furthermore, certain tool types such as core-like scrapers and burins decrease in the Mesolithic (Korobkova, 1993). These industries are dominated by microliths, characterized by small prismatic blades, end scrapers, burins, lunates and trapezes (Demidenko, 2014; Dolukhanov and Shilik, 2007). Such features suggest continuity from the Epigravettian industries in the region of the northern Black Sea (Demidenko, 2014; Yanevich, 1993). The pattern lends support to the proposed idea that no large-scale migrations of Late Upper Paleolithic and Mesolithic hunters took place in the East European steppe (Boriskovskii, 1953; Demidenko, 2014; Dolukhanov et al., 2009a; Efimenko, 1953; Levenok, 1966).

Several Mesolithic cultures have been identified by Telegin, with the main distinction between the Early and Late Mesolithic in the steppe defined by the gradual decrease in abundance of microlithic tools (Telegin, 1982). Lithic analyses of Early Mesolithic, exemplified by assemblages such as Beloles'e, have been characterized by regular prismatic blades and infrequent geometric microliths (Stanko, 1982; Telegin, 1982).

Functional and typological analyses of lithic assemblages provide evidence that at least two Late Mesolithic technocomplexes existed (Dolukhanov et al., 2009b). The Kukrek culture from the Boreal and Early Atlantic period was characterized by a toolkit which consisted of truncated, notched blades as well as microliths including trapezes and triangles. Microlithic isosceles trapezes with retouched truncations, notched bladelets and Kukrek burins were also common (Biagi and Kiosak, 2010). This lithic tradition has been identified in sites around the Azov Sea, lower Dnieper Valley (including Igren 8) and lower southern Bug area (Biagi and Kiosak,

2010; Dolukhanov and Arslanov, 2009). Another cultural technocomplex, Grebeniki (Grebenyky), is documented in the southern steppe in areas between the mouth of the Danube and was distributed around the South Bug, Dniester and Prut Rivers, later spreading to the Don region (Stanko and Kiosak, 2010). Typical tools included endscrapers and microliths, almost exclusively trapezes, which were found at sites such as Mirnoe and Girzhevo (Dolukhanov, 2008).

4. Subsistence economy

The subsistence economy hinges of Paleolithic hunter-gatherers on the distribution, availability and predictability of exploitable resources on the landscape. While some assumed a direct correlation with tool types and hunted species, usewear studies document growing evidence of diverse economic activities (Alexandrova, 2012; Sapozhnikova, 2003). For instance, tools from Amvrosievka showed traces of hunting and processing of meat and bones, which correspond with the abundant bison remains on site (Sapozhnikova, 2003). Furthermore, the patterns of the butchering and processing behaviors of foragers remain elusive and detailed analyses of anthropogenic and post-depositional modifications from some sites are in order, although the nature of zooarchaeological study is changing with greater emphasis on taphonomic research (Julien, 2009; Leonova et al., 2006). The zooarchaeological record from the steppe region has been studied largely on the basis of the faunal spectrum, which is reviewed here.

Data that are relevant to the location, cultural industry and dates for each site are included in Table 1. All sites have been dated using radiocarbon dating and charcoal as well as burnt/unmodified faunal remains comprise the majority of the dated material listed in this paper. At sites where there are a number of similar results from the same cultural context (such as Kamennaya Balka II), certain samples were selected for the table based on the dating method (i.e. AMS dates over conventional radiocarbon dating) or the reliability of the sampled material (i.e. shell is not included due to the reservoir effect, see Lillie et al. (2009)), but the comprehensive list of dates is published in the respective references, which are included in the table.

The site description includes the general location, nearby river system, research history (i.e. name of excavators and years) excavated surface area (m^2), a brief summary of the cultural assemblages, presence of features, which is followed by a summary of the faunal data. The faunal list and NISP data are used to for inter-site comparison and generalized view of resource exploitation (Table 2), and when available, the MNI data are included in the text as well.

4.1. Epigravettian

4.1.1. Amvrosievka complex

Located at the southern periphery of the Donetsk Ridge in southeastern Ukraine, the site complex of Amvrosievka is composed of two deposits interpreted as a camp and a bone bed (kill site) (Krotova and Belan, 1993). Dated to ca. 19-18,000 uncal ^{14}C BP, the site culturally belongs to the Early Epigravettian. Roughly 500 m^2 of surface area from two deposits was excavated by L. Pidoplichko and P. Boriskovskii from 1940's and 50's and O. Krotova from 1980's. The cultural remains of the camp comprise of a large lithic assemblage amounting to 100,000 pieces with roughly 3% of the assemblage consisting of burins, endscrapers and backed bladelets (Fig. 2). In addition, the cultural assemblage has yielded bone points, stone anvils, worked antlers as well as ornaments made from stone, fossils and shell and ochre (Krotova, 2013). The lithic assemblage from the bone bed was smaller with ~2500 pieces, and many consisted of similar tool types as the camp site including backed bladelets (~5% of the assemblage), burins and endscrapers. As mentioned above, the usewear traces indicate that many of the tools served for hunting and processing of meat (Sapozhnikova, 2003).

Faunal remains are largely dominated by bison, with a limited occurrence of other mammals (Table 2). The assemblage of the bone bed consists solely of bison remains (Table 2), with the exception of worked cervid antler fragments in forms of projectile points, two horse remains and one hare. Genetic investigations have shown that Amvrosievka's bison were likely not steppe bison (*Bison priscus*) but direct ancestors of the modern European bison (*Bison bonasus*) (Soubrier et al., 2016). The MNI of bison for bone bed and camp site is 246 and 28 respectively. The fauna are well preserved, despite a high level of fragmentation resulting from post-depositional processes (Julien, 2009, 2013; Krotova, 2013). The age structure reflects a pattern of semi-catastrophic mortality and all age groups were equally represented. Further, seasonality analysis indicates that bison commonly were hunted over winter - spring, a result based on multiple methods, which differ from previous interpretations (Julien, 2009; Julien and Krotova, 2008; Krotova, 2013; Krotova and Belan, 1993; Krotova and Snizhko, 1993; Pidoplichko, 1953; Todd, 2013).

Filleting for removing meat was the most common form of anthropogenic modification reflected in the abundance of cut marks on the ribs, vertebra as well as long bones such as the femur, humerus and tibia. The evidence of skinning and dismemberment is far less common although some intentional bone breakage may have supplemented additional butchering activities (Julien, 2009; Julien and Krotova, 2008; Krotova and Snizhko, 1993). The data indicate primary butchery in earlier phases of carcass processing and demonstrate targeted exploitation of meat on site with a clear choice for the optimal portions, in particular, the removal of meat from the hump (Julien, 2009). The faunal assemblage from the bone bed is a clear example of repetitive mass killing, which is represented by over 600 individuals of bison (Julien, 2009; Krotova and Belan, 1993). In contrary to the common assumption that such hunting events took place during large distance migrations, stable isotopic studies suggest that the bison population represented at Amvrosievka occupied the local area year round without any major seasonal displacement (Julien et al., 2012; Julien, 2009).

4.1.2. Anetovka II

The site of Anetovka II, which is one of the sites in a site complex with 25 deposits, is situated on the bank of the Bakshala River in western Ukraine. Stanko led excavations between 1978 and 2007, sharing similar traits as that of Amvrosievka (Stanko et al., 1989). The site extends over 1500 m^2, with a butchery area that is separated from the habitation area. A spatial analysis of the cultural material demonstrates that despite some displacement, many artifacts were close to their original *in situ* position (Glavenchuk, 2012). The lithic industry is characterized by typical Epigravettian tools characterized by the abundance of microliths including “Sagaydak” points and backed pieces (Stanko et al., 1989).

The site yielded one of the most diverse faunal assemblages, represented by 12 medium to large sized mammalian species among Epigravettian sites in Eastern Europe. The bone remains are globally very well preserved, despite fragmentation largely due to post-depositional processes (Julien, 2009). The species composition is relatively low in diversity and bison make up more than 97% of the identified bone remains (NISP = 25017, MNI = 160). In addition, reindeer and horses were occasionally hunted. Few saiga antelopes, which are rare in the faunal record from the steppe, were also recovered. Non-ungulate animals include marmots and arctic foxes but are also rare compared to bovids and cervids. The bison are the

Table 1
Sites, Geographical coordinate, culture and the C^{14} dates referred in the text.

Site	Country	N (lat)	E (long)	Culture	Dated Layer/ Context	Date (^{14}C BP)	SD	Lab number	Dated material	References
Govoruha	Ukraine	48°34′	39°05′	Epigravettian		20190	180	Ki-10357	mammal, bone	Krotova, 2003
Amvrosievka	Ukraine	47°47′	38°29′	Epigravettian	bone bed	18700	240	OxA-4890	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18860	220	OxA-4891	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18700	220	OxA-4892	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18620	220	OxA-4893	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18220	200	OxA-4894	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18660	220	OxA-4895	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	15900	200	Ki-10307	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	17800	200	Ki-9709	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18040	200	Ki-9704	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18240	200	Ki-9706	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	bone bed	18350	200	Ki-9705	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	Camp	18450	200	Ki-9707	bison, bone	Krotova and Belan, 1993
Amvrosievka	Ukraine			Epigravettian	Camp	18700	200	Ki-9708	bison, bone	Krotova and Belan, 1993
Anetovka 2	Ukraine	47°28′	31°25′	Epigravettian	Layer 1	18040	150	LE-2424	bison, bone	Stanko et al., 1989
Anetovka 2	Ukraine			Epigravettian	Layer 1	19710	120	LE-2947	bison, bone	Stanko et al., 1989
Anetovka 2	Ukraine			Epigravettian	Layer 1	19090	980	LE-4610	burned bone	Stanko et al., 1989
Muralovka/Mouralovka	Russia	47°16′	38°41	Epiaurignacian		19630	200	LE-1601	mammal, bone	Krotova, 1995
Muralovka/Mouralovka	Russia			Epiaurignacian		18780	300	LE-1438	mammal, bone	Krotova, 1995
Zolotovka	Russia	47°38′	40°59′	Epiaurignacian		17400	700	GIN-1968	burned bone	Sinitsyn and Praslov, 1997
Fedorovka/Fedorivka	Ukraine	47°17′	37°10′	Epigravettian	lower layer	15200	110	Ki-10354	mammal, bone	Neprina et al., 1986
Fedorovka/Fedorivka	Ukraine			Epigravettian	upper layer	14600	110	Ki-10355	mammal, bone	Neprina et al., 1986
Kamennaya Balka II	Russia	47°25′	38°40′	Epigravettian	Layer 2	10900	400	OxA-699	burnt bone	Leonova et al., 2006
Kamennaya Balka II	Russia			Epigravettian	Layer 2	13660	180	OxA-778	burnt bone	Leonova et al., 2006
Kamennaya Balka II	Russia			Epigravettian	Layer 2	14850	80	GrA-964	unspecified	Leonova et al., 2006
Kamennaya Balka II	Russia			Epigravettian	Layer 2	15610	80	GrA-17349	unspecified	Leonova et al., 2006
Kamennaya Balka II	Russia			Epigravettian	Layer 2	15590	80	GrA-17937	Unspecified	Leonova et al., 2006
Kamennaya Balka III/Tretii Mys	Russia	47°25′	38°40′	Epigravettian	Layer 2	13100	200	SPb-521	burnt bone	Simonenko and Aleksandrova, 2014
Rogalik VII	Ukraine	48° 47′	39° 17′	Epigravettian		11400	140	Ki-8476	charcoal	Gorelik, 2001
Divnogorye 9	Russia	50°57′	39°18′	Epigravettian	Layer 2	13430	130	AA-90650	mammal, bone	Bessudnov et al., 2012
Divnogorye 9	Russia			Epigravettian	Layer 3	13870	140	AA-90652	horse, bone	Bessudnov et al., 2012
Divnogorye 9	Russia			Epigravettian	Layer 4	13830	150	AA-90653	horse, bone	Bessudnov et al., 2012
Divnogorye 9	Russia			Epigravettian	Layer 6	14430	160	AA-90655	horse, bone	Bessudnov et al., 2012
Divnogorye 1	Russia	50° 56′	39°16′	Epigravettian	Layer 1	12050	170	Le-8649	horse, bone	Bessudnov et al., 2012
Divnogorye 1	Russia			Epigravettian	Layer 1	13380	220	Le-8648	horse, bone	Bessudnov et al., 2012
Divnogorye 1	Russia			Epigravettian	Layer 1	13430	130	AA-90651	horse, bone	Bessudnov, 2013
Beloles'e/Bilolisja	Ukraine	45° 56	29° 41′	Mesolithic		8900	190	Ki-10886	mammal, bone	Stanko, 2009
Girzhevo/Gyrzheve	Ukraine	47° 5′	29° 49′	Mesolithic		7050	60	LeI703	mammal, bone	Stanko, 1966 in Biagi and Kiosak, 2010
Girzhevo/Gyrzheve	Ukraine			Mesolithic		7390	100	Ki-11240	mammal, bone	Stanko, 1966 in Biagi and Kiosak, 2010
Igren 8	Ukraine	48°29′	35°12′	Mesolithic	pit dwelling 4, lowermost	8695	45	GrA-33112	mammal, bone	Biagi and Kiosak, 2010
Igren 8	Ukraine			Mesolithic	pit dwelling 8, lowermost	8880	45	GrA-33113	mammal, bone	Biagi and Kiosak, 2010
Igren 8	Ukraine			Mesolithic	pit dwelling 8	7640	90	OxA-17491	fish bone	Lillie et al., 2009
Igren 8	Ukraine			Mesolithic	pit dwelling 8	8885	40	OxA-17489	red deer, bone	Lillie et al., 2009
Mirnoe/Myrne	Ukraine	46°28′	30°22′	Mesolithic	PI 24/G24	8280	45	GrA-37336	aurochs, bone	Biagi and Kiosak, 2010
Mirnoe/Myrne	Ukraine			Mesolithic	PIII B1/V1	8350	45	GrA-37335	mammal, long bone	Biagi and Kiosak, 2010
Mirnoe/Myrne	Ukraine			Mesolithic	PII 5/B5	8385	45	GrA-37337	horse, long bone	Biagi and Kiosak, 2010
Mirnoe/Myrne	Ukraine			Mesolithic	PI 22/D22	8475	45	GrA-37312	horse, long bone	Biagi and Kiosak, 2010
Soroca/Soroki II	Moldova	48° 8′	28° 18′	Mesolithic	Layer 2	7420	80	Bln-587	Charcoal	Markevich, 1974
Soroca/Soroki II	Moldova			Mesolithic	Layer 3	7515	120	Bln-588	Charcoal	Markevich, 1974

Table 2
The faunal list and NISP/MNE from Epigravettian sites. All values in NISP. '+' denotes presence without the exact NISP counts.

		Govoruha	Amvrosievka: bone bed	Amvrosievka camp	Anetovka II	Muralovka /Mouralovka	Zolotovka	Fedorovka /Fedorivka	Kamennaya Balka II	Kamennaya Balka III/ Tretii Mys	Rogalik II	Rogalik III	Rogalik VII	Rogalik XII	Divnogor'ye 9	Divnogor'ye 1
Horse	*Equus ferus*	14		2	120	+		46	1116	298	57	61	39	89	7885	789
European wild ass	*Equus hydruntinus*									1						
Bison	*Bison priscus/bonasus*		14562	37500	25017	36	46	48	1189	83			5	5		
saiga antelope	*Saiga tatarica*				5	+				1						
Reindeer (w/o antlers)	*Rangifer tarandus*				590				6	9				2		24
red deer	*Cervus elaphus*				1	+				3						
brown bear	*Ursus arctos*				4				1							
Fox	*Vulpes/Alopex*									1					1	
polar fox	*Alopex lagopus*				11	+	+								1	
Wolf	*Canis lupus*				3					4						
wolverine	*Gulo gulo*				1										1	
European badger	*Meles meles*				1											
European hare	*Lepus europaeus*			1	4		1	1?	1	1						
marmot	*Marmota bobac*				31				1	2						
Dominant species		horse	bison	bison	bison	bison	bison	bison/horse	bison/horse	bison/horse	horse	horse	horse	horse	horse	horse
References		Julien this study	Julien, 2009; Krotova, 1986, 2013 (old collection excluded)	Krotova, 2013	Starkin, 2006	Min'kov in Plohenko, 2015	Plohenko, 2015	Julien this study	Leonova et al., 2006	Min'kov in Plohenko 2015	Kitagawa this study			Gorelik, 2001	Bessudnov et al., 2012	

most preferred prey and their abundance suggests that hunting was the one of the most common activities on the site. The faunal accumulation represents several mass killing events and as the site is contemporaneous to Amvrosievka, it appears that the occupations represent similar activities (Stanko, 1999; Starkin, 2006). In addition, researchers recovered a feature consisting of bison mandibles and scapulae covered with red ochre, which has been interpreted as evidence for symbolic or ritual practices. The significance of these remains is obscure, but its symbolic/non-functional meaning is worth exploring in future studies (Bibikova and Starkin, 1989; Glavenchuk, 2012; Starkin, 2006).

4.1.3. Divnogor'ye 1 and 9 (Divnogorie 1 and 9)

Divnogor'ye 1 and 9 are located near the Tikhaya Sosna River, a tributary to the Don River, which cuts into the southern margin of the Central Russian Upland (Bessudnov et al., 2012; Sycheva et al., 2016). Both occupations have been excavated by A. N. Bessudnov and A. A. Bessudnov since 2000's until the present. Divnogor'ye 1 is situated on a low river terrace while Divnogor'ye 9 is topographically located in an old ravine cutting through the slope of the watershed at a higher elevation. The lithic assemblages of roughly 100 and 1500 artifacts from Divnogor'ye 9 and 1 respectively have been classified as Late Epigravettian, characterized by truncated blades, double-truncated blades, backed bladelets, burins on truncations and endscrapers (Fig. 3). The high proportion of tools, comprising 25% of the entire lithic assemblage at Divnogor'ye 9, is typical of kill and butchery sites (Hoffecker et al., 2010). This is in contrast to Divnogor'ye 1 where the artifact assemblage is typical for short-term hunting camp including smaller faunal assemblages, low proportion of articulated bones, lithics, ochre and charcoal remains. Divnogor'ye 9 comprises of seven layers, all yielding faunal remains and represents continuous hunting activities of the Epigravettian occupants.

Wild horses are the dominant prey at both sites. At Divnogor'ye 9, many remains were articulated in some of the layers. Layer 5 from Divnogor'ye 9 is the richest bone bed yielding NISP of 3583 and MNI of 31 (Bessudnov et al., 2012). The skeletal representation is even and while some elements are more abundant than others, there is no strong bias against fragile elements. The anthropogenic modification on the fauna is rare, which mostly occurred on ribs and cartilages, but the accumulation of prey remains attests to mass killing of the horses. Divnogor'ye 1 is characterized by a smaller assemblage and greater attrition, which is documented by the lack of fragile elements. The surfaces of the fauna showed root etching and there were only a few signs of observable anthropogenic modification. Further, the latter yielded additional evidence of reindeer exploitation. The two sites are comparable to other mass kill sites, which are described above, where the bone bed (Divnogor'ye 9) and the camping site (Divnogor'ye 1) were close to one another and were likely occupied by the same groups of hunter-gatherers.

4.1.4. Govoruha

The site is located on the bank of the Lugan' River, a tributary of the Seversky Donets River in the Lugansk of eastern Ukraine. About 60 m^2 of the cultural level was investigated since its discovery in 1975 and has been investigated by O. Krotova (2013). The paleoenvironmental reconstruction based on palynological data indicates that the site was occupied in a forest-steppe landscape with a strong steppe element, which corresponded to the warmer phase of the Late Glacial around 18-17,000 uncal ^{14}C BP (Krotova and Pashkevich, 2004), which does not correspond to the date recovered from the site (Krotova, 2003). The cultural remains include lithics produced from flint, *Chione gallina* shell, mollusk ornament, red ochre with a small combustion feature. The lithic industry

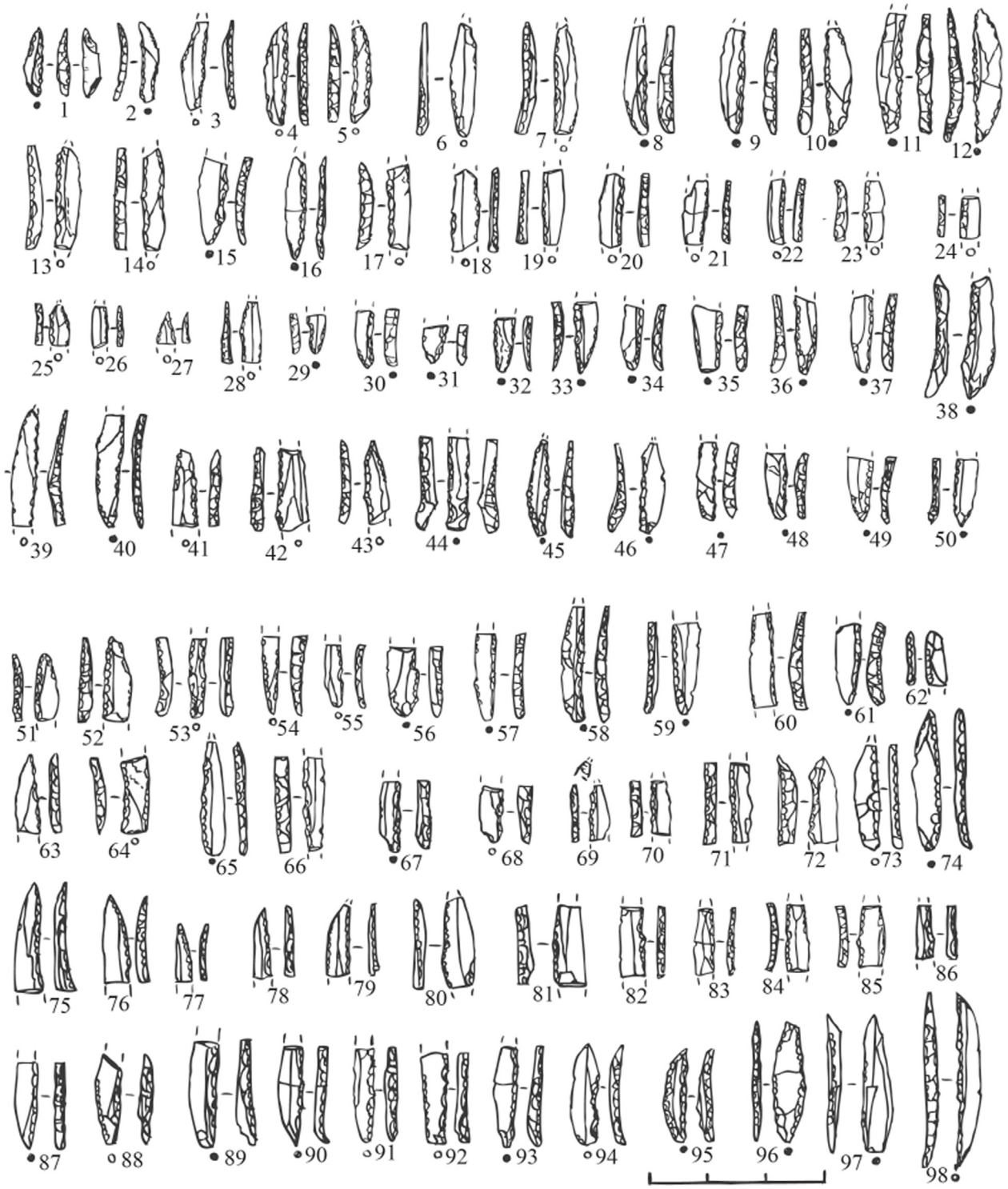

Fig. 2. Lithic assemblage from Amvrosievka camp, Lithics from the western section (excavation IV): microliths (excavation of 2000, 2005 [1–50] and 2007 [51–98]) (Krotova, 2013).

includes blades, flakes, cores, backed bladelets, burins and scraper. The overall assemblage has produced 1059 pieces and roughly 5% of which were retouched. Some artifacts bear microwear suggesting their use for working flint, wood, bone and meat (Krotova and Pashkevich, 2004).

The faunal material is highly fragmented and reducing the number of fully identified remains. From the identified specimens, horse is so far the solely represented species (Table 2). The site has been interpreted as a short-term base camp of hunter-gatherers (Krotova, 2013).

4.1.5. Fedorovka (Fedorivka)

The site is situated at the southern part of the Donetsk Ridge in Ukraine near the river channel of the Karatysh River, which drains into the Azov Sea. About 170 m^2 of cultural occupation was investigated since its discovery in 1972 and excavation between 1980

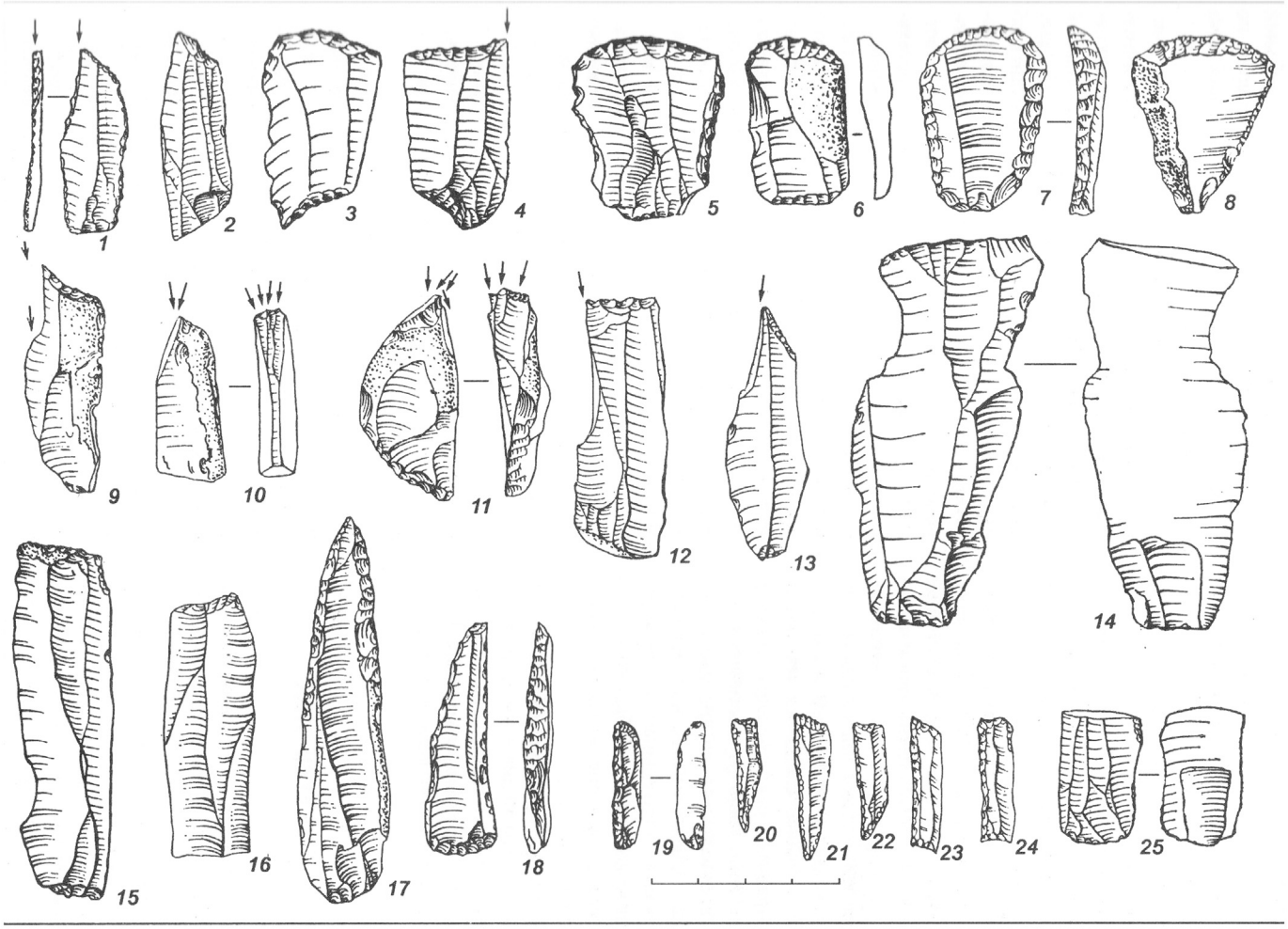

Fig. 3. Lithic assemblages from Divnogor'ye 9 (1–12; 12 – layer 2; 1,5,7 – layer 4; 2–4,6,8–10 – layer 6; 11 – surface find) and Divnogor'ye 1 (13–30). 1 – unifacial tool; 2,3,8–10 – truncated blades; 4,13–16,18,19 – backed implements; 5,20,23–27 – end-scrapers; 6 – retouched flake; 7,12,28,29 – burins on truncations; 11 – retouched bladelet; 17 – micropoint fragment; 21,22 – points; 30 – double-platform core (Bessudnov et al., 2012).

and 5. The lithic assemblages from two cultural horizons are relatively large amounting to ~3753 pieces, out of which 274 were identified as tools. It is comparable to the industry of Kamennaya Balka that is characterized by a large number of scrapers, burins, backed bladelets, atypical gravette points, truncated blades and bladelets (Krotova, 1986; Leonova, 1994). While some have identified Kamennaya Balka industry as unique, it is classified here under Epigravettian.

Compared to the stone assemblages, the studied faunal remains remain modest, with only 95 remains fully identified (Table 2). The remains are highly fragmentary and are represented mostly by dental fragments. A minimum individual of 1 horse, 1 bison and possibly 1 hare are present. However, the identified specimens indicate that equids and bison were equally represented. This is one of the few cases where two species are similarly targeted while the previous sites are dominated by one species.

4.1.6. Kamennaya Balka II

Kamennaya Balka II is located on the bank of the past ravine, which runs into the Don valley and represents one of the occupational areas in the site complex. 1700 m^2 of the site has been excavated by since the discovery by M. D. Gvozdover in 1957 with N. B. Leonova. Three cultural layers have been identified and the richest layer (second layer) is dated to 16,400–15,000 uncal ^{14}C BP. Excavations have produced ample evidence that the site was repeatedly occupied, partially documented by a high concentration of artifacts. Several hearths associated with high density of lithic artifacts show that the living surfaces were well preserved (Leonova, 2003; Leonova et al., 2015). The raw material of many lithic tools was exotic, and microliths dominate the lithic inventory (amounting to >300,000 pieces) with relatively few cores. The tools include pointed and backed bladelets showing some similarity to the Caucasus lithic assemblages (Fig. 4) (Leonova et al., 2006). The artifact distribution helps discern areas of lithic production/workshop and domestic activities (Leonova et al., 2006, 2015).

The assemblage shows that hunters preferred two types of prey: horses and bison (Leonova and Min'kov, 1988). While the bison slightly outnumber horses, the difference is insignificant and the MNI of horses and bison are 35 and 40 respectively. The site represents one of the few sites where two species were exploited by hunters. The skeletal representation of horse and bison is similar with dampened representation of axial elements including vertebra and rib while the long bones such as radius were overrepresented. There is no temporal trend in the exploitation of the two species although this should be tested through the comparison of taphonomic patterns. Other animals in the assemblage include

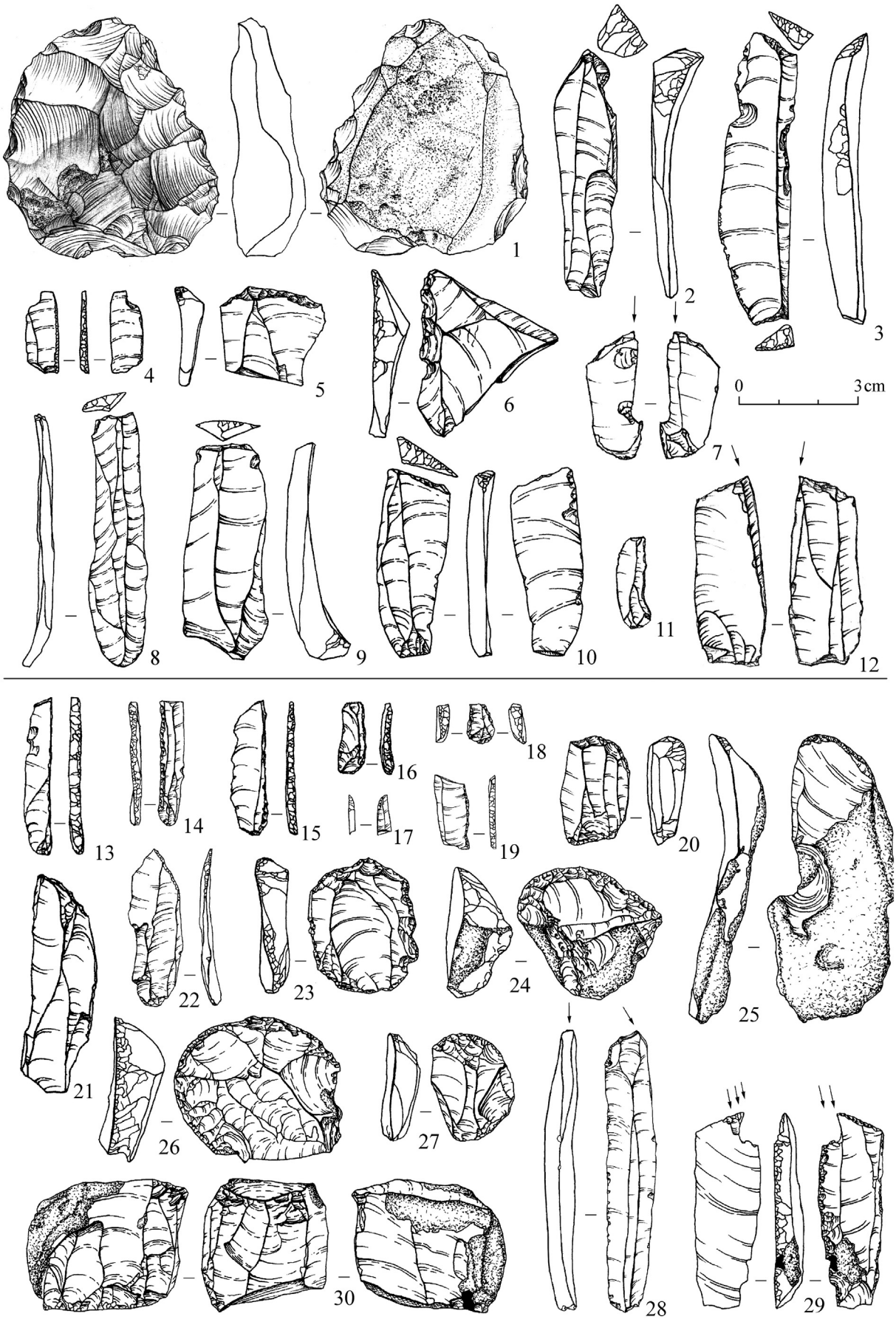

Fig. 4. Lithic assemblage from Kamennaya Balka II. 1–4 combined tools; 5–8 - scrapers; 9–13 - burins; 14, 25 - splintered pieces; 15,16 - truncated blades; 17,18 - points; 19–24 - backed bladelets.

elk, reindeer, brown bear and marmot.

4.1.7. Tretii Mys (Tretiy Mys)/Kamennaya Balka III

The site is 500 m away from Kamennaya Balka II and contains three cultural layers (Haykunova, 2011). Currently, ~450 m^2 of the surface has been uncovered by work from M. D. Gvozdover for a few years in the 1960s and later by N. A. Haykunova from 1990 onwards. The second layer with the main concentration of faunal remains is contemporaneous with Kamennaya Balka II (Simonenko and Aleksandrova, 2014). The lithic assemblage from this neighboring sites is similar to that of II and is characterized by the dominance of microliths. Recent usewear study confirms the use of endscrapers for hide working, which was spatially concentrated in the proximity of the hearth with red ochre (Simonenko and Aleksandrova, 2014). Additionally, the spatial distribution and concentration of microdebitage show that an area was dedicated for reworking scrapers.

The assemblage from Tretii Mys is considerably smaller compared to that of Kamennaya Balka II, but the prey composition remains similar, with the majority of the animals represented by horses and bison (Plohenko, 2015). The general trend in the equal proportion of horses and bison indicates a focus on hunting and the population of bison and horses that were equally abundant on the landscape and opportunistically exploited. Other rare species include saiga antelope, reindeer, fox and rabbit.

4.1.8. Muralovka (Mouralovka)

Muralovka is located near the Mius River in the Rostov region. The surface area of 127 m^2 revealed remains of a dwelling complex with some combustion features characterized by concentrations of ash. Flaked stone and animal remains are associated with the combustion features and artificial concentration of pebbles has been interpreted as part of a dwelling structure (Praslov and Filippov, 1967). Microliths have some unique features, including on oval scaled pieces (Leonova, 1994). The fauna have been studied by Min'kov, but the assemblage is small and the most common species is bison. Horse, saiga antelope, red deer and polar fox also have been identified.

4.1.9. Rogalik

Rogalik-Peredelskoye complex represents one of the largest concentrations of sites dating to the late Upper Paleolithic in southeastern Ukraine. It is represented by a lithic industry that is contemporaneous with Late Epigravettian cultures. The sites are located on the border between the Donets plateau and the terrace, which formed as a result of the fluvial activities of the Donets River, a tributary of the Don River. The survey and excavation from roughly 22 deposits have resulted from fieldwork led by A. F. Gorelik between 1989 and 1995 (Gorelik, 2001).

In addition to lithic artifacts, the sites of Rogalik have produced a number of mobile artwork, including personal ornaments made from shell, likely transported from the Black Sea, retoucher engraved with a female figure and engraved slabs (Gorelik, 2001). The site concentration and distribution are typical of mobile hunter-gatherers' home range. Relative low artifact density and stratigraphic profiles suggest that the sites were opportunistic camps that were specifically functioned as a logistical camp for acquiring raw material (Turonian flint and quartzite), despite the presence of some exotic flint nodules such as obsidian from the Caucasus region (Gorelik, 2005). In the region, two lithic traditions appeared to have coexisted, raising questions about possible differences in function or occupation of hunter-gatherers from different cultural traditions. One tradition has a lower proportion of microliths (3–8% of the lithic inventory depending on the site), but microliths are in forms of trapezes, backed points and 'microburins'. In contrast, the other tradition is characterized by the abundance of microliths (25% of retouched artifacts) but often lacked geometric microliths (Gorelik, 2001).

It has been argued that the sites are located strategically along the possible migration route of horses, which are the main prey. The condition of the faunal remains did not permit detailed taphonomic study and only few fracture marks were identified in the sampled collection housed in the Zoological Institute, St. Petersburg. The assemblages derive from four separate deposits in the Rogalik-Peredelskoye complex including Rogalik II, III, VI and XII. In terms of species abundance, there is a clear dominance of horses and the diversity of the assemblages is low. There is one specimen of onager (*Equus hemionus*), but the majority derives from horses. The MNI values based on the teeth remains show that there are at least 5–6 individuals of horse represented at the site of II and XII. Bison were rare compared to horses although present. The occupation of the site is closer to Divnogor'ye 1 and 9 where horses are the main prey and it is possible that the bison population peaked around 19-18,000 uncal ^{14}C BP and steadily declined while the horse population increased after the Last Glacial Maximum.

4.1.10. Zolotovka I/Zolotivka I

The site is located on the Lower Don in the Rostov region. The topographical condition is similar to that of Kamennaya Balka site complex. The excavations of 1976 and 1978 revealed concentrations of artifacts as well as hearths (Praslov et al., 1980). The lithics, defined as Epiaurignacian, are predominantly characterized by microliths and bladelets. 80 m^2 of cultural settlement revealed traces of hearths surrounded by concentrations of lithics and faunal remains (Plohenko, 2015). The faunal material is characterized by bison and the assemblage resembles that of Muralovka, which is contemporaneous and has an Epiaurignacian affinity. While small game such as rabbit and polar fox were identified, they remain rare overall and likely was only exploited opportunistically.

Additional sites have not been discussed in detail due to lack of C^{14} data or details of the faunal data. These assemblages include Bolshaya Akkardja, Dmitrivka, Min'evskiy Yar, Osokorovka, Yamburg and Yami (Krasnokutsky, 1999; Krotova, 1995; Starkin, 2006).

4.1.11. Summary

In all, the faunal spectrum is characterized by a low diversity and often dominated by one game animal. The two most common species are bison and horses. This is evident across most Epiaurignacian and Epigravettian sites of the southern steppes in Eastern Europe. Other ungulates including reindeer and smaller bovids, such as saiga antelopes were occasionally exploited as secondary prey.

Bison dominate at sites of Amvrosievka, Anetovka II, Muralovka and Zolotovka I, which all date to ~20-17,000 uncal ^{14}C BP (Boriskovskii, 1993; Julien, 2009; Krasnokutsky, 1996; Krotova, 2013; Praslov et al., 1980, 1989; Sapozhnikova, 2003). The chronology of the sites (~20-17,000 uncal ^{14}C BP) corresponded to the cold maximum of the Late Glacial period and steppic landscape, which was a favorable environment for the large bovids, prevailed. Bison constitutes the most prominent prey for the hunters of the steppe. The mass killing of these gregarious animals has been interpreted as a subsistence strategy adapted by the highly mobile hunters (Praslov et al., 1989; Stanko, 2009). However, because of the richness of the cultural assemblages as well as the abundance of fauna, this model of mobile adaptation has been questioned (Krotova, 2013). It is possible that the large site complexes reflect aggregation sites for hunger-gatherer groups, which occurred annually or on a seasonal basis, and may not be a simple reflection of daily mobile strategy. On the other hand, the evidence of horse exploitation remains sparse.

Table 3
The faunal list and NISP/MNE from Mesolithic sites. . All values in NISP. '+' denotes presence without the exact NISP counts.

		Beloles'e/Bilolissya	Girzevo/Gyrzheve	Igren' 8	Mirnoe/Myrne	Soroki I/II
		Early Mesolithic	Late Mesolithic	Late Mesolithic	Late Mesolithic	Late Mesolithic
Equus ferus	horse	67	48		1369	
Equus hydruntinus	European wild ass		2		112	
Bos primigenius	aurochs	+	12	+	8101	
Bison priscus	bison					
Saiga tatarica	saiga antelope	+			61	
Rangifer tarandus	reindeer					
Cervus elaphus	red deer			+	29	+
Capreolus capreolus	roe deer					+
Sus scrofa	wild boar			+	69	+
Ursus arctos	brown bear					
Alopex/Vulpes	fox	+				
Vulpes vulpes	red fox				4	
Alopex lagopus	polar fox					
Canis lupus	wolf				36	
Gulo gulo	wolverine					
Meles meles	European badger				6	
Lepus europaeus	European hare				13	
Marmota bobac	marmot					
Coturnix coturnix	common quail					+
Sander lucioperca	sander			+		
Silurus glanis	catfish			+		+
Helix vulgaris/pomatia	snail					+
Total Number of bones		89	35	~1000	~10000	~1400
		horse	horse	–	aurochs	–
		Bibikova, 1978/1982	Bibikova, 1978	Benecke, 1997, Telegin 82 in Anthony 07	Bibikova in Stanko 82	Benecke, 1997, Markevich, 1974 in Dergachev and Dolukhanov, 2007

Kamennaya Balka II, Kamennaya Balka III/Tretii Mys and Fedorovka show an even representation of bison and horses. Horses were preferentially and repeatedly sought after at Divnogor'ye 1, Divnogor'ye 9 and Rogalik, which were occupied around 17-13,000 uncal ^{14}C BP. These sites are identified as Late Epigravettian and postdate many sites with bison-dominated assemblages (Djindjian et al., 2005). This pattern is indicative of possible changes in the abundance or biogeographical range of steppe bison. The temporal phase coincided with the late glacial epoch with extreme climatic conditions resulting in considerable shifts in the faunal composition (Krotova, 2013). Bison often inhabited ecosystems with a relatively lower diversity of plants and were able to digest low-quality forage with longer digestive interval (Reynolds et al., 2003). Thus, it is likely that their dietary adaptation was advantageous in occupying an ecological niche in the steppic environment and coexist with other large Quaternary herbivores (Hoeffecker, 2002). The increase of horses may be linked to the contraction of bison population, which occurred at the Pleistocene-Holocene boundary (Benecke, 2005; Bocherens et al., 2015; Marsolier-Kergoat et al., 2015). The sfhit of the prey choice from bison to horses is a reflection of changing environment and there is no clear indication that hunting strategies altered.

We need more detailed fauna data (such as those pertaining to taphonomic patterns) to test if mobility strategies and settlement patterns were affected by the resource availability of prey animals. The assessment of sampling and taphonomic studies is vital for future research, as some published faunal data do not provide details of the post-depositional history. Nonetheless, the results suggest consistency in the exploitation of large game animals during the Late Upper Paleolithic in the southern steppe of Eastern Europe. The notion of economic specialization is often used to describe assemblages such as of Amvrosievka with evidence of mass hunting events, but the dominance of one or two species does not necessarily equate to specialization per se. Instead, the pattern likely reflects the abundance and density of the game on the landscape, as well as the specialized function of sites. Without any consistent assessment of the hunting and butchery patterns, we are currently limited to the comparison of a faunal spectrum, but future taphonomic analyses will permit us to explore the hypothesis of economic specialization in greater details. The prey choice of Epi-aurignacian and Epigravettian hunters demonstrates a clear regional and temporal pattern with little variability.

4.2. Mesolithic

As with the Late Upper Paleolithic, all the sites are open-air in the steppe region and many are situated close to a current or past river system. The sites in this study are limited due to sites with published faunal data. The Mesolithic occupations are characterized by a change in targeted large mammalian prey, reflecting post-glacial climatic shifts and documenting evidence of diet diversification at some localities (see Table 3).

4.2.1. Bilolissja (Beloles'e/Bilolissya)

It is a dwelling site located on the river terrace found in the lower Dnestr region. It has been studied by V. N. Stanko from 1960's and 1970's. Based on the spatial analysis of artifacts, the researchers identified several concentrations of artifacts, one of which is associated with a hearth, and the presence of dwelling structures. Due to the density and the nature of the stratigraphy, it was interpreted as a seasonally occupied site (Stanko, 1985). The lithic industry is marked by the production of bladelets from prismatic and sub-prismatic cores, and most geometric microliths are dominated by lunates with some trapezes and backed points, a characteristic that is shared among multiple sites. The faunal data are small but the horses were the most common animal, followed by the aurochs and saiga antelopes. The exact proportion remains unclear, but horses account for more than half of the identified specimens (Bibikova, 1978).

4.2.2. Girzhevo (Gyrzheve)

It is located on a hill close to the Kuchurgan River that is the tributary of the Dniester River in Odessa, Ukraine. The site contains a Late Mesolithic and Early Neolithic component, the presence of

the latter demonstrated by ceramics. In the lithic assemblage, endscrapers are the most common tool, followed by trapezes obtained with a retouch from bladelets. The majority of the faunal spectrum consisted of horses, followed by aurochs and European wild ass. It appears that horses continued to be dominant while the European wild ass, which become more prominent during the Mesolithic, remains scarce (Benecke, 1997; Bibikova, 1978).

4.2.3. Igren' 8

It represents a settlement on the western bank of the lower Dnieper, excavated by D. J. Telegin 1973–1990 (Telegin, 1982). The site is located in the Dneiper Rapids region and close to other occupations such as Vasilyevka III, which consisted of cemeteries dating to the Mesolithic (Jacobs, 1993; Lillie and Jacobs, 2006). The occupation is dated to the Late Mesolithic and the Early Neolithic. The lithic industry has been attributed to the Kukrek culture. The excavation identified pit dwellings with four to nine meter in depth and as well as a shell midden. The faunal data consisted of an array of species including aurochs, red deer and wild pig. Unlike other sites, the equids remain absent in the assemblage. Further, fish such as zander and catfish were also recovered (Telegin, 1982).

4.2.4. Mirnoe (Myrne)

It is one of the largest Mesolithic sites in Odessa area, a single layered settlement in the southern region of the Danube-Dniester interfluve in the lowlands of the terrace that is connected to the Danube Valley (Stanko, 1982). V. N. Stanko led the excavations from 1969 to 1976 which have yielded 18 household complexes with permanent structures, although it likely did not serve as a settlement year round. The excavation has revealed the largest Mesolithic site of Ukraine, yielded surface area of 1800 m^2. 2759 retouched tools out of 2,0593 pieces of lithics comprise one of the largest assemblages in the region. Further, many tools yielded usewear that shows indication of plant processing, and show that the use of organic material increased and becomes common in the Mesolithic (Korobkova, 1993). The site was occupied during the 9500–9000 uncal ^{14}C BP in the second half of the Boreal period. Common features include hearths, cooking pits and artifact scatters. Around 7500–7000 uncal ^{14}C BP, the area was dominated by meadow steppe, which consisted of plant species of Chenopodiaceae, Compositae and Graminae (Smyntyna, 2007). The woodland element is mainly represented by pine and birch (Pashkevich, 1982). The source of flint is likely from the alluvial deposits of the Prut and Dniester River (Petrun unpublished in Stanko and Kiosak, 2010). The blades are more abundant than flakes and the endscrapers are the most common tool (Stanko and Kiosak, 2010).

The fauna have been analyzed by Bibikova (1982). It is one of the largest and well-studied faunal assemblages from the Mesolithic in the region. Aurochs are the main prey followed by horses and European wild ass. Some of the curated collection was reanalyzed later, but there is a clear signal of aurochs, which dominated the assemblage (Benecke, 1997). The horse population represented in the assemblage shows that the majority of aged teeth derive from prime adults.

4.2.5. Soroki II (Soroca II)

The site was occupied from Late Mesolithic to the Neolithic (characterized as Bug-Dniestr culture). It is located in the floodplain of the Dniester River in Moldova. The site, along with Soroki I, was excavated by Markevich in the 1950's to 1960's (Markevich, 1974). Two pit-dwellings have been recovered. The tool assemblage consists of endscrapers, trapezes, triangles and retouched blades. Some argue that due to the lack of permanent dwelling structures, the site was occupied seasonally by foragers (Dolukhanov, 1979). The site has called into question the nature of the transition between the Late Mesolithic and the Neolithic.

The identified species include red deer, roe deer and wild boar. Further, there is evidence of fishing evidenced by cyprinids and catfish remains (Markevich, 1974). Further, snails and mussels have been identified at the sites, which point to diversified subsistence strategy. Specifically, gathering becomes a clear signal in the economic activities of the Mesolithic forager of this site. The diverse use of multiple resources demonstrates diversification of dietary practices, which is often argued as the hallmark of the Mesolithic diet.

4.2.6. Summary

The Mesolithic faunal record shows a spectrum of diet with a relatively unchanged preference for game prey, such as horses or aurochs, on the one hand, and the diversified diet based on terrestrial and aquatic resources, on the other. The overview, although far from comprehensive due to a small dataset, suggests a mixed signal of changes with increased diversity of exploited resources as well as continuity from the Late Glacial to the Holocene period, where medium to large ungulates remained the common prey.

With the zooarchaeological data at hand, mammalian remains were the most common source of diet among the hunters. On the one hand, horses continued to prevail among certain settlements and regions, which is one of the shared traits of the Late Upper Paleolithic and the Mesolithic record (Praslov et al., 1989; Stanko, 2009). For instance, the faunal assemblages of Beloles'e/Bilolissya and Girzevo/Gyrzheve share the similarity, namely, in the abundance of equids. Horses continue to be a staple species in Eastern Europe despite the gradual disappearance of the steppic landscape starting ~10,000 uncal ^{14}C BP.

On the other hand, the Holocene warming triggered an increase in forested environments, which led to changes in the faunal communities and the targeted prey species (Bibikova, 1975; Stanko, 2007). In particular, it is widely thought that aurochs replaced bison in the Holocene as the latter went extinct regionally in most areas of Europe by the end of the Pleistocene (Bibikova, 1974, 1975; Stanko, 1999). Increased tree cover led to the rise of herbivores with relatively small group size compared to gregarious Pleistocene animals such as bison. Therefore, aurochs became more common in the Mesolithic faunal record, despite their continued presence in Pleistocene Europe. For example, the substantial proportion of the assemblage from Mirnoe is dominated by aurochs (Bibikova, 1982). Saiga antelopes, wild boars, red deer and roe deer were also pursued during the Mesolithic, all of which lived in a semi-closed forest environment (Benecke, 1997; Bibikova, 1978). The evidence suggests that environmental changes were a major catalyst that triggered a diachronic trend in species composition of the hunted fauna. Game animals with different herd structures and migration patterns arguably forced hunters to readapt their strategies for tracking and the pursuit of prey (Bibikov, 1975; Dolukhanov, 2008; Smyntyna, 2014; Stanko, 2007).

This faunal record is far from complete and requires further investigation. Furthermore, the reconstruction of past ungulate behavior, including herd structures, is not straightforward and we cannot deduce the behavioral traits of ancient prey based on their present counterparts. The notion that bison all practiced long distance migration has been refuted in a recent study from Amvrosievka (Julien et al., 2012). Herd composition is fluid depending on the season and is heavily influenced by the available resources and environment. Horses in faunal records also contradict a common assumption that solitary preys were the main target of Mesolithic hunters.

It is also hard to demonstrate the degree to which shifts in target preys and their herd structure affected the strategies of hunters.

With regards to hunting technology, bows and arrows are often linked to technology adapted in forested environments, but microliths persisted from the Epigravettian to the Mesolithic. There is no clear difference in the strategies of hunters from both cultural phases, given that the composite tools were common in the lithic repertoire of the Epigravettian hunters. Hunting of large game may have involved some technological and behavioral shifts, but it is not clearly evident from the current lithic data that such changes occurred concurrently with the global climatic forcing and what the nature of the trend entails.

Furthermore, the question often posed for the Mesolithic diet is the possibility of resource diversification (Bicho et al., 2010; Starkovich and Stiner, 2009; Stiner, 2001). The Mesolithic coincided with trend in the diversification of environment, leading to the forest-steppe in the Holocene. Moreover, wetlands and riverine with aquatic resources increased (Dolukhanov et al., 2009b). Despite the limited dataset, the diverse diet is more apparent in the Late Mesolithic and some sites show continuity into the Neolithic. Researchers documented the evidence of freshwater resources and the construction of a shell midden at Igren' 8 and Soroki II. Areas such as the Dneistr and Dnieper River, where Soroki II and Igren' 8 are located, saw higher biological productivity sustained by freshwater sources including shellfish and fish (Smyntyna, 2004, 2014). Furthermore, sites with shell middens are associated with dwelling pits, and the diversified diet may be linked to the increase in sedentary settlement patterns of the foragers in riverine areas.

The dietary difference between the Late Upper Paleolithic and Mesolithic lies primarily in the diversity of faunal species. The number of ungulate species identified in the Mesolithic is greater than in the Late Upper Paleolithic, where some of the sites yielded assemblages, which were dominated by one species. The Epiaurignacian and Epigravettian assemblages share common traits including the dominance of ungulate, namely bison and horses. There are few outliers to this pattern, with the exception of few sites where equids and bison are equally abundant, but the prey choice among Epigravettian hunters is a regional signal of the steppe region. On the other hand, Mesolithic faunal remains, despite the limited sample size, suggest that there are a greater inter-site variability and faunal record with local signals. This is a possible reflection of increased diversity of the available resources or shifts in the settlement patterns on a seasonal basis and by the end of Mesolithic, likely triggered by greater sedentism. One of the continuities observed between the Epigravettian and Mesolithic is the exploitation of equids. It is the only species that is found in 'critical mass' in both the Epigravettian and Mesolithic regardless of an increase in forest elements. The possible existence of several equid (sub)species in the Pleistocene and Holocene remains to be clarified, but the persistence of equid attests to their adaptive flexibility and reflects their consistent presence on the landscape. Equids remain an important prey despite drastic climatic fluctuations and have interesting implication for the later domestication of horses in the steppe region.

5. Discussions

Despite limitations in the datasets due to differences in sampling and curational methods, the faunal record informs us of the adaptive shifts of hunters from glacial to post-glacial periods in the southern steppe of Eastern Europe. The Epigravettian technocomplex appeared before the height of LGM and persisted through multiple climatic oscillations until the end of the Pleistocene. Bone beds dominated by one species (bison/horse) demonstrate that mass hunting was a subsistence strategy that was practiced by some Epigravettian hunters and the abundance of the faunal material demonstrates reoccurring occupations over time (Hoffecker, 2009; Julien, 2009; Krasnokutsky, 1999). The dietary practice does not alter until 15,000 uncal ^{14}C BP when there is a significant decrease in bison and a greater focus on horses, which remained a stable prey throughout most of the Paleolithic in other regions of the East European steppe. Changes in the faunal composition occurred during the Bølling-Allerød Interstadial, marking the beginning of the regional extirpation of bison in Europe. This shift can be linked to climatic forcing, but future paleoenvironmental studies will provide insight into past vegetation and its relationship to the disappearance of bison.

The faunal record of the Mesolithic differs from the Epigravettian on two accounts. First, the assemblages characterized by monospecific selection of prey in the Epigravettian became more diverse with a greater number of prey, which preferred forested biomes. In particular, aurochs increased considerably, followed by red deer, roe deer as well as wild boars. Second, there was a diversification of resource base with an increase in non-mammalian animals. Specifically, sites inhabited close to rivers dated to the Middle to Late Mesolithic and documented greater incorporation of fish and shellfish. In short, a greater proportion of non-mammalian species is represented in certain faunal assemblages.

Studies other than zooarchaeological analyses provide a different insight into dietary practice. The stable isotopic analyses of human fossils from the Dnieper foragers indicate regular consumption of plant resources (Lillie et al., 2011). This result corresponds to the archaeological evidence such as usewear study, which has yielded lithic tools with traces of plant processing (Korobkova, 1993). Future archaeobotanical studies will complement our understanding of the full breadth of the Epigravettian and Mesolithic diet, which goes beyond the zooarchaeological record. The diversification and regionalization of Mesolithic subsistence can be explained by either regional or temporal variability. The dietary response of hunter-gatherers varied due to local environmental conditions and species representation shifted with the vegetational changes. The diversity of subsistence practices reflects increased biological productivity and perhaps increased seasonality of resource availability, which can be tested using future investigations into seasonality of sites.

The patterns in zooarchaeological assemblages can largely be explained as hunter-gatherers' response to the fluctuations in the floral and faunal community in the steppe region during the Late Pleistocene and the beginning of the Holocene. The climatic fluctuations corresponded roughly to shifts in the dominant ungulate species in the faunal record, an economic choice made by foragers based on resource availability and abundance. The Epigravettian sites may have been tied to locales that facilitated mass hunting of bison, which may have influenced the settlement patterns of hunter-gatherers. Furthermore, the nature of shifts in the fauna is linked to the general environmental conditions, but the dietary shift from bison to horses do not necessarily correspond to any observable differences in technological strategies or artifact assemblages and may reflect environmental shifts. Factors such as differences in the season of occupations, the demographic population history as well as hunting traditions also need to be considered.

The Mesolithic industries appear to reflect some continuity from the Epigravettian technological tradition and thus far, we have not documented any significant clear technological break to demonstrate that later Mesolithic hunters adapted technological innovation in response to changing resources. Interpretations that regard close link of technology and hunting strategies may need reconsideration based on the current regional data (Praslov et al., 1989). However, the dearth of Early Mesolithic sites as well as little data with continuous occupation from the Late Upper Paleolithic to the

Mesolithic on a local scale leave this interpretation inconclusive and future research is needed to complement our understanding of the cultural and economic shifts over time. Thus, we have yet to assess regional and temporal factors to test these hypotheses and conduct a systematic comparison of Upper Paleolithic and Mesolithic record in combination with local paleoenvironmental data to better address the previous questions.

6. Conclusion

Environmental changes from the end of the Pleistocene to the Holocene equate to the cultural transition from the Upper Paleolithic to Mesolithic. As with other cultural transitions in prehistory, geographical variation underlies the emergence of the Mesolithic period, including in Eastern Europe, which had largely been dominated by steppe biomes. The diet of glacial and post-glacial hunter-gatherers in these two cultural periods in the southern steppe of Eastern Europe shows consistencies as well as differences. Environmental fluctuations resulted in changes in the targeted species, bison followed by equids in the Late Upper Paleolithic. The Mesolithic diet demonstrates greater temporal and spatial variability in the faunal spectrum of large game and aquatic resources, and this pattern is partially attributed to differences between the Early/Middle Mesolithic and Late Mesolithic. In the future, dietary diversity within the Mesolithic period should be explored both in terms of greater geographic and temporal scale.

This preliminary review study of hunter-gatherers in the southern steppe of Eastern Europe should not be interpreted as a final statement. Our objective was to highlight key questions and conjure hypotheses available for future study to elucidate hunter-gatherers' adaptations during glacial and post-glacial conditions. Many questions remain to be answered about the transition from the Late Upper Paleolithic to the Mesolithic and its link to the Pleistocene-Holocene climatic shifts. The Mesolithic often remains secondary to researchers in the Upper Paleolithic and Neolithic, making it harder to characterize this transitional period, and having consequences for our interpretation of cultural evolution at large in this critical region. Additional faunal record from the East European steppe will be necessary. Finally, future research can greatly benefit from interdisciplinary approaches in order to complement traditional understanding of prehistoric societies, which is largely based on research of lithic industries. The current state of our knowledge in hunter-gatherer adaptation during the Late Glacial and Interstadial periods in the steppe region of Eastern Europe highlights the importance of and the potential obstacles to documenting and characterizing the cultural transition accompanied by climatic forcing.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2017.01.005.

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