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1 **Middle Pleistocene fauna and palaeoenvironment in the south of Eastern Europe: A case**
2 **study of the Medzhybizh 1 locality (MIS 11, Ukraine)**

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22 **Abstract**

23 The Middle Pleistocene was a period of dynamic changes in Europe. During MIS 11, a number
24 of modern mammal taxa appeared and environmental conditions remained warm and favourable
25 for a relatively long time. The Medzhybizh 1 locality of Ukraine dated to this very period
26 comprises alluvial deposits with rich animal remains, which allow not only to reconstruct the
27 fauna composition, but also to highlight the environmental conditions that dominated at this
28 locality. A revision of the fauna of Medzhybizh 1 locality based on remains of all vertebrate
29 groups revealed a taxonomically diverse fish community (16 species of 11 genera) dominated by
30 cyprinids common for lacustrine or riverine assemblages. Amphibians are represented by 11
31 species, while the number of reptile and bird remains are less significant. Mammals are the most
32 represented group at the locality, including small mammals (30 species), carnivorans (2 species),
33 and ungulates (5 taxa), the latter dominated by *C. elaphus*. The taxonomic composition of
34 terrestrial groups indicates temperate climate with boreal-type forests and meadows similar to
35 cold steppe, as well as low wet areas and riparian habitats inhabited by amphibians, reptiles,
36 insectivores, beavers, and various voles. The fish assemblage indicates a partially overgrown but
37 well-aerated water body (lake or slow-flowing river) with sandy-silty bottom. Lithic artefacts
38 found at the Medzhybizh 1 locality contribute to a better understanding of relationships between
39 ancient hominins and faunas during the Middle Pleistocene of Eastern Europe.

40

41 *Key words:* Vertebrates; Diversity; Environment; Archaeological site; Pleistocene; Europe

42 **1. Introduction**

43 The Middle Pleistocene was the time when forms of Early Pleistocene origin were still
44 present in the European fauna. They slowly retreated or vanished, but many of them survived
45 one of the most extensive and strongest glacials during MIS 12 (Hughes and Gibbard, 2018;
46 Hughes et al., 2020). Environmental conditions were much more favourable during a particularly
47 long (ca. 40 kya) warm period following MIS 12 – the MIS 11 interglacial, which is correlated
48 with the Likhvinian of Eastern Europe, the Holsteinian of the British Isles, and the Hoxnian of
49 Northern Europe. Despite numerous palaeontological studies, this time interval is weakly
50 documented in Eastern Europe (in particular, in Ukraine), contrary to that in Central and Western
51 Europe. The number of sites known from Austria, the Czech Republic, France, Great Britain,
52 Germany, and Spain allow reconstructing this interval in detail.

53 The period between 400 ka and 500 ka BP is of high interest because of the appearance of
54 a number of modern mammal taxa during that time (van Kolfschoten and Turner, 1996; Caloi
55 and Palombo, 1997; Kahlke, 1999; Von Koenigswald and Heinrich, 1999; van Kolfschoten,
56 2000; Kahlke and Lacomat, 2008; Markova and van Kolfschoten, 2012; Rzebik-Kowalska and
57 Rekovets, 2015; Markova and Puzachenko, 2016, 2017; Ridush et al., 2020; Stefaniak et al.,
58 2021b). Therefore, any new or complete study of sites in Eastern Europe dated to MIS 11 is
59 especially important. Although Medzhybizh 1 (= Medzhybozh 1) is a single site documenting
60 only a temporal fragment, this manuscript includes a revision of the entire fauna of this locality.
61 The collection from Medzhybizh 1 had been studied earlier in both palaeontological and
62 archaeological aspects (Rekovets, 2001a, 2001b; Rekovets et al., 2007; Stepanchuk et al., 2014;
63 Stepanchuk and Moigne, 2016). Here we present results of the revision of fauna of this locality,
64 and an attempt to correlate it with data from other sites of Europe of the same age. Based mostly
65 on numerous vertebrate remains, we try to reconstruct the environmental conditions that
66 characterised that territory during MIS 11, and with the addition of the scarcer material on other
67 animal groups, to present as much as complete picture of the surrounding environment.

68

69 **2. Stratigraphy and age**

70 The studied site (coordinates 49.427731, 27.378464; Fig. 1) is located on the left bank of
71 the Southern Bug River, ca. 1 km west of the town Medzhybizh, Letychivskyi Raion,
72 Khmelnytskyi Oblast, Ukraine. The profile (Stepanchuk and Moigne, 2016: fig. 3) is composed
73 of a subaerial sequence of Upper Pleistocene loess and palaeosols, as well as a double Middle
74 Pleistocene alluvial member overlying the basal Archean granites (Fig. 2). Alluvial deposits of
75 the Medzhybizh 1 locality comprise rich pollen assemblages (with the predominance of pine and
76 oak pollen, and a smaller portion of linden, elm and hornbeam pollen), as well as micro- and
77 macrofaunal remains (Rekovets et al., 2007). The lowermost alluvial cycle includes a few layers
78 (nos. 12-16 according to Rekovets et al., 2007; see Fig. 2), some of which (in particular, layers
79 15 and 16) comprise stone tools and other signs of ancient human activity at the site, and are
80 equal to the so-called layer 16a (i.e. cultural horizon) sensu Stepanchuk and Moigne (2016) or
81 layer III sensu Stepanchuk et al. (2021). A pedological study (Matviishina et al., 2013) revealed
82 the presence of Middle and Upper Pleistocene loess and soil sediments (Stepanchuk and Moigne,
83 2016: fig. 4). Lower Palaeolithic artefacts and faunal remains are associated with pedosediments,
84 loamy soils, and sandy sediments dated to the Zavadivka stage (equal to MIS 11-9). The results
85 of a pilot ESR dating (ca. 400 kya) are corroborated with biostratigraphic data for the layer 16a
86 (Qi et al., 2018). At the same time, geomorphological data allow suggesting an MIS 15-13 age
87 for sediments containing artefacts of layer III (Stepanchuk et al., 2021).

88 The Medzhybizh 1 fauna is almost exclusively associated with the Zavadivka sediments,
89 mainly with its early period (zv 1, equal to MIS 11). It was found that the presence or absence of
90 faunal remains is directly related to the water content of the site in ancient times: in other words,
91 bones were preserved in the aquatic environment in which they found themselves immediately or
92 shortly after accumulation, and then were conserved by alluvial deposits. On the contrary, faunal
93 remains are almost completely absent in areas not flooded with water. Palaeoecological

94 reconstructions (Rekovets et al., 2014b; Stepanchuk and Moigne, 2016) indicate that the fauna
95 existed in a warm and humid climate of the temperate zone (MIS 11).

96

97 **3. Lithic industry**

98 The lithic industry of Medzhybizh 1 revealed in the lower alluvial member includes
99 artifacts made of flint, quartzite, quartz, granite, and other rocks (Stepanchuk and Moigne, 2016:
100 figs. 6-8). Fauna remains are principally associated with the younger layer III (former layer 16a),
101 while layer IV (former 16b) contains predominantly lithic artifacts and yields only few poorly
102 preserved undiagnostic eroded bone splinters. The entire collection from the layer III comprises
103 more than 80 flint artefacts and about 70 such items from other rock types. The assemblage is
104 characterised by bipolar cores, artificial fragments of various rocks, sometimes with signs of use,
105 simple choppers, and flake products including isolated retouched flakes. The available materials
106 show practically no signs of freehand knapping, bilaterally processed products and any signs of
107 their manufacture are totally absent. The industry of layer III can be compared with the “core-
108 and-flake” industries and has nothing in common with Acheulean.

109 Bone fragments from Medzhybizh 1 show numerous signs of intentional fragmentation in
110 fresh state, cut marks and isolated chop marks are also common (Stepanchuk and Moigne, 2016:
111 figs. 11-12). Some bones were exposed to high temperatures (over 700 °C) that is consistent with
112 fireplace evidence recognized at the level of layer III. The age and sex composition of animals is
113 an evidence of intentional hunting (Stepanchuk and Moigne, 2016).

114

115 **4. Material and methods**

116 The studied sample consists of complete and fragmentary bones of all major vertebrate
117 groups (fishes, amphibians, reptiles, birds, and mammals). These materials were obtained during
118 excavations of the site in 2000, 2002, 2004-2006, 2008-2009, 2011-2012, and 2016. These
119 fossils are deposited in the Department of Palaeontology (NMNHU-P) of the National Museum

120 of Natural History, National Academy of Sciences (NAS) of Ukraine, as well as in the
121 Department of Stone Age Archaeology of the Institute of Archaeology, NAS of Ukraine (Kyiv).

122 Remains of fishes, amphibians, reptiles, birds, and small mammals were taxonomically
123 classified using the osteological collections of NMNHU-P. The morphological identification of
124 specimens follows Lepiksaar (1994) for fishes, Böhme (1977) and Ratnikov (2002a) for
125 amphibians, Szyndlar (1984) for reptiles, Baumel et al. (1993) for birds, and Rekovets (1994) for
126 small mammals. Bear teeth morphology and the scheme of measurements follow Baryshnikov
127 (2007). The remains of even-toed ungulates were identified and measured according to von den
128 Driesch (1976), Van der Made and Tong (2008), Van der Made (2010), and Stefaniak (2015).

129 Osteometrical analyses allowed verifying most of the previous taxonomic identifications
130 and placing the ungulate fauna in a wider biochronological context (Van der Made et al., 2014;
131 Stefaniak, 2015). The material used for comparison are stored in the collections of the following
132 institutions: Musée national de Préhistoire (Les Eyzies, France), Medical University (Baku,
133 Azerbaijan), Forschungsstelle Bilzingsleben, Friedrich Schiller Universität (Jena, Germany),
134 Historisches Museum (Verden, Germany), Landesmuseum für Vorgeschichte (Halle, Germany),
135 Aristotle University of Thessaloniki (Greece), Hebrew University (Jerusalem, Israel), Centro
136 Nacional de Investigación sobre la Evolución Humana (Burgos, Spain), Museo de Arqueología
137 de Cartagena (Spain), Museo Nacional de Ciencias Naturales (Madrid, Spain), and Institut Català
138 de Paleoeologia Humana i Evolució Social (Tarragona, Spain). Rhinoceros remains from
139 Medzhybizh 1 were measured according to Van der Made (2010). All measurements are given in
140 millimetres. Rhinoceros teeth were compared with those of different species of the genus
141 *Stephanorhinus* stored in the Senckenberg Research Station of Quaternary Palaeontology
142 (Weimar, Germany), University of Ferrara (Italy), Museum of Geology and Palaeontology,
143 University of Florence (Italy), NMNHU-P, and Natural History Museum (London, UK).

144 In cases where identification to species was impossible, specimens were classified to
145 higher taxonomical levels. Bones that could not be classified were categorised as indeterminate.

146 The taphonomic interpretation is referred to special papers (Ericson, 1987; Bocheński, 2005;
147 Fernández-Jalvo et al., 2016). The ecological analysis was based on habitat preferences of the
148 identified taxa. The number of identifiable specimens (NISP) refers to all recovered specimens.

149

150 **5. Results**

151 *5.1. Fishes*

152 Fish remains were obtained from the layers 11–16 of Medzhybizh 1 (Table 1). The
153 majority of the identified specimens (n=179) belong to pikes (Esocidae), fewer bones (NISP
154 104) represent carp fishes (Cyprinidae), while bones of perches (Percidae) were of minor
155 importance (NISP 9). At the same time, cyprinids are taxonomically the most diverse represented
156 by nine genera and eleven species, including five taxa described in open nomenclature. Among
157 them, bones of the roach (*Rutilus rutilus*, *Rutilus* sp.) and dace *Leuciscus* sp. were recovered
158 from all (or almost all) layers, and together with the bream *Abramis* sp. and tench *Tinca tinca* are
159 the most numerous among the studied carp fish remains. The rudd *Scardinius erythrophthalmus*
160 and the Pontic roach *Rutilus frisii* were quite common components of the studied fish
161 community, contrary to the nase *Chondrostoma* sp., asp *Aspius aspius*, barbel *Barbus* sp. and the
162 crucian carp *Carassius carassius*, each represented only by two isolated pharyngeal teeth. Pike
163 remains from Medzhybizh 1 are composed predominantly of jaw teeth and dentaries, with some
164 axial skeleton elements (vomer, parasphenoid), various viscerocranial bones (i.e. maxilla,
165 palatine, articular, ceratohyal, subopercle) and, to a lesser extent, abdominal vertebrae and a
166 single cleithrum. The anatomical spectrum of percid remains includes two dentaries, as well as
167 quadrate, preopercle, vertebra centrum and four complete scale plates.

168

169 *5.2. Amphibians*

170 Amphibian remains are quite numerous among vertebrate fossils from Medzhybizh 1
171 (Table 2). They represent eleven species of six genera of four families (Pelobatidae, Hylidae,

172 Bufonidae, and Ranidae). The most numerous remains recovered from the studied locality
173 belong to the common spadefoot toad *Pelobates fuscus* (Laurenti, 1768), European toad *Bufo*
174 *bufo* (Linnaeus, 1758), and common frog *Rana temporaria* Linnaeus, 1758 (NISP 52, 29 and 26,
175 respectively). At the same time, the European tree frog *Hyla arborea* (Linnaeus, 1758) and *Hyla*
176 sp. are each represented by a single bone. Only forelimb (radius-ulna, humerus, scapula,
177 coracoideum) and hindlimb elements (tibiofibula and ilium) as well as isolated vertebrae were
178 recognised among amphibian remains in the studied sample.

179

180 5.3. Reptiles

181 Reptile remains obtained from Medzhybizh 1 are scarce compared to those of other
182 vertebrates (Table 2). Only four trunk vertebrae of snakes were found in lower (14th and 15-
183 16th) layers. Of them, two specimens with distally obtuse hypapophyses and strongly built
184 parapophyseal processes were assigned to the grass snake *Natrix natrix* (Linnaeus, 1758), while
185 the two other vertebrae with distally pointed hypapophyses and slender parapophyseal processes
186 are identical to those in the dace snake *Natrix tessellata* (Laurenti, 1768).

187

188 5.4. Birds

189 Only two bird bones were found in materials from Medzhybizh 1. A complete ungual
190 phalanx of the middle (third) toe of the left leg found in the layer 15-16 belongs to the white-
191 tailed eagle *Haliaeetus albicilla* (Linnaeus, 1758). It is identical in morphology and equal in size
192 to that of extant representatives of this species. The other specimen is a diaphysis of a tubular
193 bone that could not be identified precisely. It comes from the layer 16a. The eagle bone has
194 obvious artificial damage (scraping marks) indicating that it was processed by stone tool.

195

196 5.5. Mammals

197 5.5.1. Insectivores, lagomorphs, and rodents

198 The list of small mammals from Medzhybizh 1 includes about 28 species, the vast
199 majority of which belong to rodents (Table 3). The most numerous remains among Eulipotyphla
200 (nine mandibles with teeth) belong to *Sorex praeearaneus praetetragonurus* Mezhzherin and
201 Svistun, 1966, which is morphologically close to *S. runtonensis* Hinton, 1911, and was
202 characteristic for the Calabrian and Chibanian age of Central Europe. Members of the genus
203 *Talpa* (*Talpa* cf. *praeglacialis* Kormos, 1930) are represented by humeri and teeth. *Erinaceus* sp.
204 from Medzhybizh 1 is represented by a single P3 and a broken molar. Two mandible fragments
205 were assigned to *Neomys newtoni* Hinton, 1911 (see Rzebik-Kowalska and Rekovets, 2016).

206 Lagomorphs from Medzhybizh 1 are represented by two species – *Lepus* cf. *europaeus*
207 Pallas, 1778 (one fragment of tibia morphologically similar to that in extant species), and
208 *Ochotona* sp. (one molar and two fragments of upper incisors with a characteristic groove on
209 external tooth side). The latter is metrically close to *Ochotona pusilla* Pallas, 1768.

210 Rodents from Medzhybizh 1 are represented by six families (Sciuridae, Spalacidae,
211 Castoridae, Muridae, Cricetidae, and Arvicolidae). Ground squirrels were one of the dominant
212 groups of small mammals in the Pleistocene of Ukraine (Rekovets, 1994), however only a single
213 fragment of tibia belonging to *Marmota* sp. was found in Medzhybizh 1. Remains of
214 *Spermophilus* from this locality are also quite rare being represented by one p4 (tooth height 5.5
215 mm, crown height 1.6 mm, crown width 2.0 mm, crown length 1.95 mm) and two molars
216 assigned to *Spermophilus* cf. *suslicus* Gueldenstaedt, 1770. The hypoconid on p4 is strongly
217 developed. These characters are inherent to those in extant *Spermophilus suslicus*. Two
218 additional m1 of *Spermophilus* sp. were found in the layer 14 in 2018 (Nezdolii, 2019).

219 Among mole-rats (Spalacidae) from Medzhybizh 1, a single mandible and two isolated
220 molars of *Spalax* cf. *zemni* Erxleben, 1777 were found in the transitional layer 10-11. In addition,
221 a single m1 of *Spalax* sp. comes from the layer 14 of the studied locality (Nezdolii, 2019).

222 Beavers (Castoridae) are represented by three genera and three species – *Euroxenomys*
223 *minus* Newton, 1890, *T. cuvieri* Fischer von Waldheim, 1809, and *Castor fiber* Linnaeus, 1758.

224 The bones of the latter are morphologically identical to the extant species (Rekovets, 2017).
225 Remains of the two other castorid species were probably re-deposited from older sediments.

226 Mice (Muridae) from Medzhybizh 1 are represented by the genus *Apodemus*. Isolated
227 molars and mandible fragments resembling those in *Apodemus agrarius* (Pallas, 1771) were
228 obtained during the excavations. Nezdolii (2019) also reported the finding of two m1 assigned to
229 *Sylvaemus* cf. *flavicollis* (Melchior, 1834) in the layers 14 and 15 of Medzhybizh 1.

230 A small number of remains from Medzhybizh 1 belong to cricetids, namely to *Cricetus*
231 *cricetus* Linnaeus, 1758. It is morphologically identical to the extant species and represented by
232 two mandibles with teeth (m1-2 length is 8.8 mm, compared to 8.0 mm in extant *C. cricetus*).

233 The presence of eight genera and about 13 species of voles (Arvicolidae) is recognised in
234 the material from Medzhybizh 1 (Rekovets, 1994, 2001a, 2001b; Povodyrenko and Rekovets,
235 2006; Rekovets et al., 2007; Krokmal' and Rekovets, 2010; Rekovets, 2017; Nezdolii, 2019;
236 Krokmal' et al., 2021). Among them, the genus *Microtus* s.l. is represented by the largest
237 number of species (*M. (Terricola) arvaldens*, *M. (Agricola) agrestis*, *M. (Microtus) nivaloides*,
238 *M. (M.) ex gr. arvalis*, and *Microtus* sp.), while *Arvicola* (namely, *A. mosbachensis* Schmidtgen,
239 1911) prevails by the number of remains (Table 3). The remains of *Allophaiomys deucalion* and
240 *Mimomys* ex gr. *intermedius-savini* were probably re-deposited from much older sediments since
241 these species were not typical for the Pleistocene faunas of this age (Rekovets, 2017; Nezdolii,
242 2019; Krokmal' et al., 2021). A significant number of remains from this locality (NISP 27)
243 belong to *Lasiopodomys (Stenocranius) gregalis* (Pallas, 1779) which is a marker for cooling
244 climate. The material from Medzhybizh 1 documents the first appearance of *Microtus (Agricola)*
245 *agrestis* Linnaeus, 1761 in the Pleistocene of Ukraine (Rekovets, 2017).

246

247 5.5.2. Carnivorans

248 Carnivoran remains from Medzhybizh 1 are scarce (Table 4) and represented by isolated
249 teeth and postcranial elements. Stepanchuk and Moigne (2016) mentioned the presence of *Ursus*

250 *deningeri* Reichenau, 1904 and *Ursus thibetanus* Cuvier, 1823. The majority of their remains
251 (calvarium fragment, two mandibles, two ribs, and baculum fragment) are too damaged for
252 species identification. Only the isolated m1 (L=29.2 mm, Bp=13.0 mm) with developed talonid,
253 and the distal tibia fragment (L=64.8 mm, B=40.0 mm) can be classified as *U. deningeri*.

254 The right m2, due to its small size and simple morphology, could be identified as *U.*
255 *thibetanus*. Stepanchuk and Moigne (2016: 5) noted that “the tooth is closed, forming a sinuous
256 groove because the cusps are tightened”. Tooth dimensions (Table 5) fit well into the size range
257 of *U. thibetanus* (M=18.7 mm, 17.4-21.3 mm) (Fistani and Crégut-Bonnoure, 1993).

258 The m2 is rectangular in occlusal view, with straight lingual margin and convex buccal
259 margin in mesial and distal parts, while the middle part is concave. The trigonid is longer than
260 the talonid, but almost the same in breadth. The metaconid and lower protoconid are well
261 developed, but not very expanded, and connected by a thick, well defined transverse crest, which
262 is divided in its middle part by a thin V-shaped valley. The mesial part is collared with a thick
263 sharp wall, on which a few small low cuspids are visible. The entire metalophid complex is
264 simple, with a proportionally small and flat trigonid surface; two larger cusps are located on the
265 lingual margin near the metaconid. The metastylid has a complicated morphology, with three
266 mesial and five parietal metastylids arranged in a line. On the lingual margin, a minute and low
267 mesostylid is also placed behind them. The mesolophid forms a thick ridge running from the
268 middle part of the buccal margin in posterior-lingual direction and ends at the boundary between
269 the trigonid and talonid. The enthyppoconid is poorly differentiated from the hypoconid, which is
270 a low but well-developed cusp. The talonid surface is smooth and flat, only slightly complicated
271 by a few lines. The entire crown is compact in occlusal view, with the cusps directed internally.

272 The m2 from Medzhybizh 1 can be misidentified only as *Ursus arctos* Linnaeus, 1758
273 (Erdbrink, 1953; Baryshnikov, 2007). However, it can be distinguished from that of *U. arctos* by
274 smaller size, narrower talonid, smaller and lower main cusps and crests, and less complicated
275 occlusal surface (Rode, 1935; Kurtén, 1959, 1968a, 1968b, 1977; Baryshnikov, 2007).

276 A few additional bear remains were found in Medzhybizh 1: a canine fragment of a
277 young individual, a right I2, a right P4, a right calcaneus, and a distal end of a metapodium.
278 Although the material is scarce, these remains can be identified as *Ursus deningeri*.

279 The intact P4 (L=21.4 mm, Bp=14.7 mm) is a triangular and tricuspid (metacone,
280 paracone, and protocone) tooth with a simple morphology representing morphotype A (Fig. 3).
281 The mesial, distal, and lingual margins of the P4 are much rounded, while the buccal margin is
282 almost straight. The elongated and oval protocon is low and well developed, sharply delineated
283 from the crown. The paracone is large, round and high, the metacon is almost equal in size, but
284 lower and more oval, the difference between the paracone and metacone is significant. Its mesial
285 margin forms a wide-open angle with the distal margin. The weak cingulum is more developed
286 only in the disto-buccal part of the crown. There is at least one additional cuspid. The protoloph
287 forms a cone extending from the protocone and connecting with this cusp toward the paracone,
288 which crosses the V-shaped valley between the two cusps. The tooth differs from the P4 of *U.*
289 *thibetanus* by larger size (Fig. 4), lower paracone, and higher metacone. The P4 of *U. arctos* is
290 broader and rounded in occlusal view, with a larger and broader protocone, lower and smaller
291 metacone (Rode, 1935; Erdbrink, 1953; Kurtén, 1959, 1968a, 1968b, 1977; Baryshnikov, 2007).

292 The right I2 has a short root and a large and bulging crown that appears very massive
293 compared to the root. Despite its massiveness, the I2 shows a primitive morphology, with the
294 lingual cingulum divided into two thin corrugations. There is no sign of a lingual edge or fossa
295 lunaris, and the tooth was assigned to the morphotype d0 sensu Baryshnikov (2007).

296 The calcaneus is comparable in size to a large cave bear. The bone has proportionally
297 long and laterally broadened tuber calcanei. The medial process is also large and broad, situated
298 vertically to the corpus, but square rather than triangular. The facies articularis astragali medialis
299 is oval, rather flat, and its margin forms a thin but pointed ridge. Facies articularis astragali
300 medialis is oriented in parallel to the corpus. The lateral process is more pronounced; the flat

301 facies articularis astragali medialis is longer and runs more obliquely. The facies articularis
 302 cuboidea is shallower and does not contact with the facies articularis astragali medialis.

303

304 *5.5.3. Even-toed ungulates*

305 *Capreolus* sp.

306 There are a few teeth and bones with the morphology and approximate size of *Capreolus*
 307 (Fig. 5A-C). Stepanchuk and Moigne (2016) assigned the fossils from Medzhybizh 1 to *C.*
 308 *suessenbornensis* because it is larger than the *Capreolus* fossils from the end of the Middle
 309 Pleistocene. These authors neither cited Pfeiffer (1998) nor mentioned *C. priscus*. According to
 310 Pfeiffer (1998), the Middle Pleistocene to Recent European roe deer are *Capreolus*
 311 *suessenbornensis*, *C. priscus*, and *C. capreolus*, which decrease in size from the first to the last
 312 species and differ by the proportions of the limb bones, the first species having relatively longer
 313 forelimbs. *Capreolus capreolus* inhabits Europe as far east as the Caucasus, while the geographic
 314 range of a larger species, *C. pygargus*, extends from China to the Caucasus (Wilson and
 315 Mittermeier, 2011). Recent specimens in the Georgian State Museum, which are labelled as *C.*
 316 *capreolus*, are as large as *C. pygargus*, but have relatively small antlers similar to those in *C.*
 317 *capreolus*. This suggests geographic size differences in this species. Our data on m3 (Van der
 318 Made et al., 2014: fig. 6) and m2 (Fig. 6) show that there is a small decrease in size in Western
 319 Europe and the teeth of *C. suessenbornensis*, *C. priscus*, *C. pygargus*, and East European *C.*
 320 *capreolus* have overlapping sizes. The size of specimens from Medzhybizh 1 fall into the range
 321 of variation of all three species and we cannot assign them to any of these species. However,
 322 based on age and context, the material could be assigned to *Capreolus* cf. *priscus* Soergel, 1914.

323

324 Cervidae indet. of the size of *Dama*

325 Stepanchuk and Moigne (2016) reported on fallow deer fossils from Medzhybizh 1 and
 326 assigned them to *Dama dama clactoniana*. These authors regarded *D. clactoniana* as a

327 subspecies of *Dama dama* and did not consider other fallow deer species. In support of the
328 identification, they mentioned the features of straight crests of the upper teeth, the cheek teeth
329 being long as in *D. d. clactoniana* but wider as in *D. d. geiselana*, and the postcranials having
330 sizes in the upper ranges of *D. d. clactoniana*. We are not aware of other authors having used
331 straight molar crests and the relative width of the cheek teeth as features to distinguish fallow
332 deer species or subspecies (Fig. 5D-E). These authors mentioned the collection number of a
333 single specimen, a metatarsal (Mez.23L.119.16A), and gave its distal width. This specimen is
334 larger than any *D. d. geiselana* and fits well into the range of *D. clactoniana*. However, its size is
335 also similar to that in a small *Cervus elaphus*, and the specimen shows a large oval foramen in
336 the lower part of the posterior side, which is common for *Cervus* (feature 4 in Lister, 1996).

337 The evolution of the Middle Pleistocene *Dama* is becoming a little better known and
338 appears to be more complex than it was believed earlier (Fig. 6). The earliest Middle Pleistocene
339 fallow deer are assigned to *Dama vallonnetensis* and *Dama roberti* (Breda and Lister, 2013; Van
340 der Made et al., 2017). They do not have a palmation, though the latter has two distal tines with a
341 bony plate between them close to their separation. The palmate *Dama clactoniana*, *Dama dama*
342 *geiselana*, and *D. dama dama* seem to form a single lineage, which first acquired more perfect
343 palmation and then decreased in size (Pfeiffer, 1997, 1999). These forms had a low separation
344 between the brow tine and main beam. The lineage leading to *Dama mesopotamica* is considered
345 to be another descendant of *Dama clactoniana* (Di Stefano, 1995a, 1996; Di Stefano and
346 Petronio, 2002). It lowered the brow tine and then reduced it, lowered the next tine and also
347 decreased in overall size. The Mesopotamian fallow deer currently has a largely restricted
348 geographic range, but during the Late Pleistocene and Holocene it was much wider distributed
349 (Di Stefano, 1996). Another lineage is known from only a few localities. These forms retained a
350 relatively high bifurcation between the brow tine and main beam and acquired a very wide
351 palmation. The first is known from Megalopolis (Sickenberg, 1976) of unknown precise age
352 within the range of about 900 and 370 ka (Van Vugt et al., 2001) and the second one, which is a

353 little larger, from Azokh V (Van der Made et al., 2016). These sites are also in the east, but older
354 than those of *D. mesopotamica*, which seems to have replaced this lineage. Another deer of
355 similar size is *Haplodoiceros mediterraneus*, which is known from only few localities and of
356 which the affinities are not clear (Croitor et al., 2008; Sanz et al., 2014; Van der Made and Mazo,
357 2014). It differs from *Dama* by antler, dental, and postcranial features. Apart from size- and
358 antler-related differences, few or no other dissimilarities have been published to discriminate
359 between these *Dama* species. The fossils we studied are insufficient for classification.

360 During our research, we did not find remains of *Megaloceros* in Medzhybizh 1.

361

362 *Cervus elaphus* Linnaeus, 1758

363 There are many teeth and bones with morphology and size similar to that in *Cervus*
364 *elaphus* (Fig. 5F-J). These include elements with very clear and diagnostic morphology such as
365 the p2 with flat and high crowns and short and straight parastylid (Lister, 1996; Di Stefano,
366 1995b). These teeth and bones are larger than their homologues in *Dama* and *Capreolus* and
367 smaller than in *Megaloceros giganteus* and *Megaceroides*. The sizes could be closer to
368 *Megaloceros savini* and *M. matritensis*, but these have a morphology more similar to *Dama*.

369 The earliest *C. elaphus* had antlers without crown and all tines, including the distal ones,
370 were situated in one plane as is still the case in *C. e. canadiensis*. In Europe, a crown evolved,
371 the distal part has three tines that go in different directions and which do not lie in one plane. The
372 older *Cervus* is usually placed in *C. e. acoronatus* (for some *C. acoronatus*). There are no distal
373 parts of antlers from Medzhybizh 1. *Cervus elaphus* is known to have fluctuations in size (Van
374 der Made et al., 2014; Niedziałkowska et al., 2021). The temporal distribution of different sizes
375 is indicated in Fig. 6. These differences in size are not the result of comparing fossils from
376 different latitudes, or cold and warm stages, and thus are not a result of Bergmann's rule.

377 The large deer from MIS 16 and earlier and those from MIS 7 and later have a large
378 overlap in size with the smaller deer from MIS 15/13 to MIS 8. For the comparisons which we

379 made, most bones and teeth from Medzhybizh 1 are in the overlap of the small and large forms,
380 while some specimens are definitely small and others definitely large. As a result, we assign the
381 fossils from Medzhybizh 1 to the species *Cervus elaphus*, but not to a particular subspecies.

382

383 *Sus* sp.

384 A few specimens can easily be identified as *Sus*, including a very high crowned incisor
385 (Fig. 5K). The material is insufficient to discriminate from the many other species of this genus,
386 but *Sus scrofa* is the only Middle Pleistocene species of Suidae in Europe (Van der Made et al.,
387 2017) and in the north of Eurasia. There are size changes in this species (Gómez Olivencia et al.,
388 2020), but the fossils from Medzhybizh 1 are insufficient to estimate the size.

389

390 5.5.4. *Odd-toed ungulates*

391 Remains of odd-toed ungulates obtained from Medzhybizh 1 are quite scarce and
392 represented by a few teeth (both complete and fragmented) identical in morphology to those in
393 representatives of the genus *Stephanorhinus* (Fig. 5L-M). Among them, only three lower molars
394 (m1, m2, and m3) are preserved in a state suitable to measure the length and width of the crown.
395 The following measurements were used: DAP (anteroposterior dimension), DTa (transverse
396 dimension of the anterior lobe), and DTp (transverse dimension of the posterior lobe of a crown).

397 The values of DAP and DTa of the m1 (Fig. 7) from Medzhybizh 1 allow locating it near
398 the specimens of *S. etruscus* from Infermuzzo and Upper Valdarno, *S. hundsheimensis* from
399 Süssenborn and a single tooth of *S. hemitoechus* from Grays. In general, species taken into
400 consideration are divided into two groups. The first mostly consists of species that are considered
401 older: *S. etruscus* and *S. hundsheimensis*. The second group, in which both DAP and DTa reach
402 higher values, mostly consists of representatives of *S. kirchbergensis*. Based on the analysis of
403 DTp and DTa of m1, the specimen from Medzhybizh 1 is again located closely to *S.*
404 *hundsheimensis* from Süssenborn and *S. etruscus* from Upper Valdarno.

405 In the case of m2 (Fig. 7), the specimen from Medzhybizh 1 has a rather wide anterior
406 lobe, but its length places it closely to *S. etruscus* from Shutnivtsi (located in western Ukraine),
407 some specimens of *S. etruscus* from Upper Valdarno and Olivola, the second biggest tooth of *S.*
408 *hundsheimensis* from Süssenborn and the widest tooth of *S. hemitoechus* from Isernia la Pineta.

409 Seen from the lingual side of m3, the posterior valley is very wide with a U-shaped
410 bottom. This is clearly unlike *S. hemitoechus*, but is very common in *S. kirchbergensis*. The
411 others are in between. Comparison of this tooth (Fig. 7) with others gives the clear division
412 between the specimens assigned to *S. etruscus* and *S. hundsheimensis* from one side and *S.*
413 *kirchbergensis* from the other. The main difference compared to the previous analyses is the
414 rather wide range of DAP and DTp of *S. hemitoechus*, which intermingles with those of *S.*
415 *kirchbergensis* with the small DTa values. In both analyses, the specimen from Medzhybizh 1 is
416 located closely to the smallest specimens of *S. hundsheimensis* from Süssenborn, *S. hemitoechus*
417 from Isernia la Pineta and a single tooth of *S. etruscus* from Trimmingham.

418 The comparison of the dimensions of the lower molars of the specimen from Medzhybizh
419 1 does not enable classifying it more precisely than *Stephanorhinus* sp. Based on the size only, it
420 seems to be justified to rule out *S. kirchbergensis*, however the posterior valley of m3 has a wide
421 and U-shaped bottom, which is commonly observed in this species. The other teeth do not
422 express features that would point out whether this is, in fact, an exceptionally small tooth of *S.*
423 *kirchbergensis*. A wide range of the metric diversity of *S. hemitoechus* makes it impossible to
424 rule it out as well. All dimensions of the teeth of *Stephanorhinus* from Medzhybizh 1 are close to
425 those in primal species of the genus, i.e. *S. etruscus* or *S. hundsheimensis*. Taking into account an
426 MIS 11 age, it seems to be reasonable to expect this specimen to be *S. hundsheimensis*, but due
427 to lack of proper scientific evidence, the only justified assignment is *Stephanorhinus* sp.

428

429 **6. Discussion**

430 *6.1. Taxonomic diversity*

431 Taxonomic composition of the fish community of Medzhybizh 1 resembles those of Lysa
432 Gora 1 (Rekovets et al., 2014a), Protopopovka 1 and 2, Bilshovyk, Cherevychno 1 and some
433 other palaeocommunities in Ukraine (Kovalchuk, 2017; Kovalchuk et al., 2017) and Russia
434 (Zastrozhnov et al., 2021). The species list of fishes from the studied locality shares a number of
435 taxa, which remains are common in Chibanian deposits of Poland, including somewhat older
436 palaeocommunities (MIS 15-13: Łuków 3a, Ferdynandów 2011 (Stefaniak et al., 2021a),
437 Belchatów (Jerzmańska and Raczyński, 1991), Podgórze near Wyśmierzyce (Skompski, 2004)),
438 equal in age (MIS 11: Szelaż near Poznań (Lubicz-Niezabitowski, 1929), Barkowice Mokre
439 (Pawłowska, 1963), Koczarki near Mrągowo (Skompski, 2002)), as well as slightly younger
440 ones (MIS 5-3): Nędzerzów near Kalisz (Hebig, 1978), Imbramowice and Gorzów Wielkopolski
441 (Stefaniak et al., 2020). In a wider geographic scope, the studied fish palaeocommunity is similar
442 in its composition to those recovered from the Middle Pleistocene of England (Schreve et al.,
443 2002; Böhme, 2010) and Germany (Böttcher, 1994; Böhme and Ilg, 2003). Anatomical
444 distribution of fish remains from Medzhybizh 1 indicates a natural character of their
445 accumulation in the alluvium (Casteel, 1976). Fish fossils recovered from similar archaeological
446 sites do not usually reflect a direct human activity (Zohar et al., 2008; Stefaniak et al., 2021a).

447 Numerous Chibanian localities comprising amphibian and reptile remains similar in
448 taxonomic aspect to that of Medzhybizh 1 are known from the entire territory of Europe. Some
449 of these palaeocommunities include almost the same set of species, while others lack some taxa
450 present in Medzhybizh 1 instead comprising other forms. Those localities are Beeches Pit,
451 Boxgrove, Cudmore Grove, East Farm, Greenlands Pit, Hoxne, Little Oakley, West Runton in
452 England (Holman et al., 1990; Holman, 1991, 1998; Schreve et al., 2002; Preece et al., 2007;
453 Böhme, 2010), Abimes de la Fage, Lazaret C, Montousse 3 in France (Rage, 1972; Bailon and
454 Rage, 1992; Böhme and Ilg, 2003), Bilzingsleben, Gossweinstein, Miesenheim I, Muelhausen,
455 Stuttgart quarry Schmid, Stuttgart-Sulzerrain, Weimar-Ehringsdorf in Germany (Brunner, 1957;
456 Młynarski and Ullrich, 1975; Böhme, 1989; Böttcher, 1994; Böhme, 1998, 2000), Tourkobounia

457 2 in Greece (Böhme and Ilg, 2003), Tar-kő in Hungary (Jánossy, 1986), Kozi Grzbiet in Poland
458 (Młynarski, 1977; Szyndlar, 1981, 1984; Sanchiz and Szyndlar, 1984), Chernyi Yar, Koziy
459 Ovrage, Kuznetsovka, Volnaya Vershina 3, Zmeevka 1 in Russia (Ratnikov, 1996, 2001, 2002a,
460 2002b, 2009), Gran Dolina TD 8-10, Atapuerca in Spain (Blain et al., 2008, 2009; Lobo et al.,
461 2016), as well as Nagirne 1 and Ozerne 1 in Ukraine (Ratnikov and Krochmal', 2003, 2005).

462 In addition, remains of *Bufo viridis* and *Natrix* cf. *natrix* were reported from the
463 Middle Pleistocene locality Emirkaya 2 in Turkey (Venczel and Şen, 1994). The Pleistocene
464 fossil record of the grass snake is much more extensive compared to that of *Natrix tessellata*.
465 The latter is known only from a few European localities, where it usually occurred together with
466 *Natrix natrix* (Venczel, 2000; Böhme and Ilg, 2003; Ratnikov and Mebert, 2011).

467 Pleistocene remains of the white-tailed eagle are not known from the territory of Ukraine
468 and Poland (Bocheński et al., 2012). This species is recorded in the Late Pleistocene of Binagadi
469 in Azerbaijan (Serebrovsky, 1948; Gorobets and Yanenko, 2018), as well as Artazu VII (Suárez-
470 Bilbao et al., 2020) and Cueva de Santa Catalina (Sánchez-Marco, 2018) in Spain.

471 Small mammals from Medzhybizh 1 are similar in systematic aspect to those of
472 Bilzingleben 2, Chigirin, Gun'ki, Hoxne, Kärlich H, Neede, Petersbuch 1, Raigorod, Schöningen
473 13 DB and 13 I, Swanscombe, and Vierkhniaya Emancha (Heinrich, 1990; Von Koenigswald
474 and Heinrich, 1999; Markova, 2006, 2007; Markova and Van Kolfschoten, 2012; Markova and
475 Puzachenko, 2016, 2017). Faunal lists from these localities comprise *Arvicola mosbachensis* (vel
476 *cantiana*), *Lagurus transiens/lagurus*, *Microtus nivaloides*, and *M. arvalis*. Some modern
477 species (*Microtus arvalis*, *Clethrionomys glareolus*) appeared at that time, while *Microtus*
478 *agrestis* and members of *Alexandromys* and *Lasiopodomys* have become common in
479 palaeocommunities of Eastern Europe. The beginnings of their formation belong to the earlier
480 stages of the Likhvinian interglacial (Ozerne, Morozivka 2, Nagirne 2), which characterizes this
481 stage as the period of formation of the modern micromammal fauna at the level of genera and

482 species. The general composition of the small mammal community confirms the age of the
483 Medzhybizh 1 locality as MIS 11, Likhvinian Interglacial (Krokhmal' et al., 2021).

484 The new bear material from Medzhybizh 1 is assigned to the spelaeoid lineage.
485 Unambiguous representatives of the black or brown bears were not recorded unlike in the
486 previous studies (Stepanchuk and Moigne, 2016). The ursid palaeoguild from Medzhybizh 1
487 includes two bear species, *Ursus deningeri* and *Ursus thibetanus*, widely distributed across
488 Eurasia during MIS 11 (Kurtén, 1968a). Since then the black bear has become a rare faunal
489 component of European assemblages and slowly disappeared from the continent (Crégut-
490 Bonnoure, 1997; Baryshnikov, 2010). The remains of *Ursus deningeri* are the most common and
491 abundant among large carnivorans (Schütt, 1968; Wagner, 2014). From a metric and
492 morphological viewpoint, they represent classical spelaeoid bears of earlier evolutionary stages,
493 classified as *Ursus deningeri*. The Late Pleistocene cave bear *Ursus ex gr. spelaeus* is
494 characterised by an advanced molarisation correlated with an increase in total crown length
495 (Rabeder, 1983, 1989; Wagner, 2014). However, there are no substantial meristic changes in this
496 respect in the material of *Ursus deningeri* from MIS 12-9.

497 The value for a single P4 from Medzhybizh 1 is within the variation range of the late
498 Middle Pleistocene populations across Europe. Since two ursid lineages, arctoid and spelaeoid,
499 separated in the middle Early Pleistocene, ca. 1.4-1.2 Ma (Rabeder et al., 2009), it is clear that
500 the teeth of *Ursus deningeri* and *U. arctos* were already different during MIS 11. The interglacial
501 ursid community comprised the large and massive *Ursus deningeri*, arctoid bear *Ursus arctos*
502 *taubachensis*, accompanied by *Ursus thibetanus* in few sites (Kurtén, 1968a).

503 The ungulate fauna of Medzhybizh 1 is not highly diverse and consists mostly of cervids
504 represented by *Capreolus* sp. (? *C. cf. priscus*), *Cervus elaphus*, and Cervidae indet. of the size
505 of *Dama*. These three forms are present in Bilzingsleben, Atapuerca TD10, Atapuerca TG11,
506 Heppenloch, Plaidter Hummerich A, and probably many others. Although *Megaloceros* was

507 present at this time, it is not found in many localities and these three species, usually without
508 *Alces*, *Megaloceros*, or *Megaceroides* appear to be common in MIS 11-9 localities.

509 A few fragments of teeth belong to the wild boar. A similar situation is in the Early and
510 early Middle Pleistocene sites of Poland, among which interglacial (Żabia Cave, Kozi Grzbiet)
511 prevail, and the ungulate fauna is dominated by cervids, with almost no equids and bovids. More
512 numerous remains of these groups appeared no earlier than 400 ka BP in Biśnik Cave (Stefaniak,
513 2015). The faunal composition may suggest similarities with the Middle Pleistocene Kozi
514 Grzbiet site in Poland, which is also dated to an interglacial and lacks equid and bovid remains.
515 The lack of reindeer remains is noteworthy. In Poland, the occurrences of the genera
516 *Stephanorhinus* and *Dama* were recorded only for the Upper Pleistocene (Badura et al., 2017).

517 Faunal assemblages similar in species composition were dated as MIS 13 (Mosbach,
518 Hundsheim, Miesenheim 1, Mundelsey, Vértesszőlős, Romagnano, Soave), MIS 12 (Arago Sol
519 G), MIS 11 (Bilzingsleben, Clacton, Hoxne, Jaywick, Petralona, Terra Amata, Vergranne), MIS
520 10 (Riano), MIS 11-9 (Schöningen, Swanscombe), and MIS 9 (Heppenloch, Lunel Viel, Orgnac
521 3, Steinheim). Mammal assemblages of that period represent the so-called Middle Pleistocene
522 transition (see Maslin and Ridgwell, 2005; Clarck et al., 2006 for details).

523

524 6.2. Palaeoenvironmental implications

525 Fishes of Medzhybizh 1 inhabited a lake or a slow-flowing river with quite well aerated
526 water, sandy-silty or silty bottom and well-developed aquatic vegetation (Fig. 8). Most of the
527 identified species are phytophilous, laying eggs on the underwater parts of plants. Some fishes
528 (pike and perch) are ambush predators requiring the presence of shelters. The dace, roach,
529 bream, and perch fed on invertebrates, while aquatic vegetation predominates in the diet of the
530 rudd. The presence of the tench and crucian carp indicates overgrowth of some parts of the
531 reservoir and an increase of its trophism. However, there were also open areas with gravel or
532 pebbly bottom suitable for the spawning of lithophilous fishes (e.g. nase, barbel). *Chondrostoma*,

533 *Aspius* and *Barbus* are rheophylic fishes inhabiting moderately flowing waters. All identified fish
534 species prefer the coastal and/or near-bottom areas. White-tailed eagles usually occur near large
535 water bodies, where they hunt large fish and waterfowl. These birds can also consume dead fish.

536 Representatives of temperate climate and mesophilic habitats dominate among small
537 mammals of Medzhybizh 1. A few taxa can be considered as indicators since their existence is
538 closely related to particular habitat types. A thorough analysis of the list of species revealed in
539 this locality implies the presence of a quite high diversity of habitats in this area, which could be
540 related to the climatic changes taking place during that time (Rekovets et al., 2014b). In
541 particular, relatively recent deglaciation as well as cyclic changes in the duration of the cold
542 period of the year, in the amount of precipitation, and in fluctuations of temperature amplitudes
543 have clearly affected the formation of various types of habitats and of ecotone communities of
544 forest-, shrub- and meadow-dwelling species (Fig. 8). The presence of boreal-type forests is
545 indicated by the relatively large amount of remains belonging to the genera *Clethrionomys*,
546 *Alexandromys* and some *Microtus*. Meadow habitats had rather resembled cold steppe as it can
547 be suggested by the number of typical steppe taxa (*Ochotona*, *Spermophilus*, *Spalax*, *Cricetus*,
548 and *Lagurus*). In addition, many species indicate the occurrence of lower wet areas and riparian
549 habitats (insectivores, beavers, *Arvicola*, *Microtus*). The large number of revealed amphibian
550 taxa also supports the idea of existence of extensive forested (*Hyla*, *Rana*, *Bufo*, and *Pelobates*)
551 and aquatic habitats (*Pelophylax*) around Medzhybizh 1. Representatives of the genus
552 *Stephanorhinus* preferred forest habitats and shrubs close to water bodies (Stefaniak et al., 2020),
553 which is also an optimal habitat for cervids and suids (Fig. 8). The absence of large and dry open
554 areas may explain the absence of equids and the small number of bovid remains.

555

556 **7. Conclusions**

557 The revision of vertebrate remains of the Medzhybizh 1 locality allowed to correlate this
558 palaeocommunity with data from Middle Pleistocene sites of Europe and to reconstruct the
559 environment surrounding the site in more detail.

560 The fish community of Medzhybizh 1 is quite diverse. It includes 16 taxa representing 11
561 genera of three families (Cyprinidae, Esocidae, and Percidae). Carp fishes are represented by a
562 wide range species, while the majority of the identified specimens belong to pikes. The
563 taxonomic composition of the studied palaeocommunity is typical for lacustrine or riverine
564 assemblages and very similar to those known from the Middle and Late Pleistocene of Europe.

565 Amphibians are represented in materials from Medzhybizh 1 by 11 species of six genera.
566 Among them, the most numerous remains belong to *Pelobates fuscus*, *Bufo bufo*, and *Rana*
567 *temporaria*, while the presence of some other taxa (*Hyla arborea*, *Hyla* sp.) is documented by
568 findings of single bones. Reptiles were also not numerous since only four trunk vertebrae of
569 grass snakes (*Natrix natrix*, *N. tessellata*) were recovered from the studied site.

570 Birds represent the least numerous group among vertebrates from Medzhybizh 1. They
571 were directly used by ancient men as evidenced by the presence of scraping marks made by
572 stone tools on the surface of the ungual phalanx of the white-tailed eagle *Haliaeetus albicilla*.

573 The list of small mammals of Medzhybizh 1 includes 30 taxa that represent three orders
574 (Eulipotyphla, Lagomorpha, and Rodentia). The most represented genera are *Microtus*, *Arvicola*,
575 and *Clethrionomys* of the family Arvicolidae. *Microtus agrestis* appeared at this site for the first
576 time in Eastern Europe. Non-typical representatives in the Medzhybizh 1 fauna are
577 *Trogontherium*, *Allophaiomys*, and *Mimomys*, which presence might be explained by the alluvial
578 nature of the site and possible re-deposition of remains from older layers. Some other taxa
579 (*Erinaceus* sp., *Neomys newtoni*, *Lepus* cf. *europaeus*, *Marmota* sp., *Sylvaemus* cf. *flavicollis*,
580 *Cricetus cricetus*, and *Lagurus lagurus*) are quite rare. According to the level of evolutionary
581 progressiveness, in particular of species of the genera *Microtus* and *Arvicola*, the fauna of
582 Medzhybizh 1 generally corresponds to the MIS 11 age and is similar in taxonomic aspect to

583 those from Bilzingsleben 2, Chigirin, Gun'ki, Hoxne, Kärlich H, Neede, Petersbuch 1, Raigorod,
584 Schöningen 13 DB and 13 I, Swanscombe, and Vierkhniaya Emancha. At this time, the
585 formation of Zavadivka soils had begun in Eastern Europe, which is compared with the
586 Likhvinian and Holsteinian climatic stages. Although the alluvial type of burial suggests some
587 mixture of taxa and their remains, it is still a reproduction of the real state of continental
588 biocoenoses that were subject to successions. This is evidenced by slightly different data from
589 the first and second alluvial cycles in which the stage of cooling on the verge of their
590 manifestation is recorded both faunistically and palynologically.

591 Carnivorans of Medzhybizh 1 are represented by two species of bears – *Ursus deningeri*
592 and *U. thibetanus*, both of which were widely distributed in Eurasia during MIS 11. The
593 ungulate fauna of Medzhybizh 1 consists mostly of cervids represented by *Capreolus* sp., *Cervus*
594 *elaphus*, and Cervidae indet. of the size of *Dama*, as well as includes a rhino of the genus
595 *Stephanorhinus*. *Cervus elaphus* was the dominant ungulate species in this palaeocommunity,
596 while the others were found in smaller numbers. Bones of cervids often display signs of
597 intentional fragmentation, cut marks and chop marks. It is a typical group of species common for
598 the Middle Pleistocene of Europe. The taxa occurring in the site confirm the interglacial nature
599 of the fauna because of the absence of typical cold-loving forms (e.g. reindeer, musk ox).

600 The qualitative and quantitative composition of the terrestrial fauna of Medzhybizh 1
601 indicates its existence in temperate climate conditions. *Clethrionomys*, *Alexandromys* and some
602 *Microtus* inhabited the boreal-type forest, while *Ochotona*, *Spermophilus*, *Spalax*, *Cricetus*, and
603 *Lagurus* are indicators of meadow habitats resembling cold steppe. Forest habitats and shrubs
604 were optimal habitats for cervids, suids, and rhinos. The presence of low wet areas and riparian
605 habitats around the studied site is suggested due to the occurrence of insectivores, beavers, and
606 representatives of the genera *Arvicola* and *Microtus*. Fishes of Medzhybizh 1 inhabited the near-
607 bank and/or near-bottom areas of a lake or, more likely, a slow-flowing river with quite well
608 aerated water. Some parts of this water body were overgrown, while there were also open areas

609 with gravel or pebbly bottom suitable for spawning of the nase and barbel. The amphibians
610 (*Pelophylax*) and reptiles (*Natrix tessellata*) found at the locality also preferred aquatic habitats.

611 The study of localities of this or similar age and bearing faunal remains is an important
612 direction of further research because it allows tracing changes in palaeocommunities,
613 reconstructing past environment in Eastern Europe more precisely, and a better understanding of
614 relationships between ancient humans and faunas during the Middle Pleistocene.

615

616 **Author contributions**

617 KS and OK conceptualised and led the study. VS presented the results of stratigraphic
618 studies and provided data on lithic industry. OK identified and described remains of fishes, VY –
619 amphibians and reptiles, AT – birds, LR – small mammals, AM – carnivorans, JvdM and KS –
620 even-toed ungulates, and AK – odd-toed ungulates. KS, OK, AM, LR, and ZB analysed
621 taxonomic diversity and carried out palaeoenvironmental reconstructions. URS prepared the map
622 (Fig. 1), the outcrop model (Fig. 2), and Fig. 5. AM prepared Figs. 2 and 3, JvdM – Fig. 6, AK –
623 Fig. 7, and WG – Fig. 8. OK, AM, and ZB wrote the original draft of the manuscript. All authors
624 participated in the editing and revision of the manuscript.

625

626 **Declaration of competing interests**

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

629

630 **Data availability**

631 The authors declare that all data supporting the finding of this research are available
632 within the paper. The palaeontological collections are kept at the Institute of Archaeology,
633 National Academy of Sciences of Ukraine (large mammals) and the National Museum of Natural
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1023 **Figure captions**

1024

1025 **Figure 1.** Location map of Medzhybizh 1 (A) and relief of the surrounding area (B).

1026

1027 **Figure 2.** Complete geological profile (A), panorama of the excavation site (B) and its position
1028 within the Southern Bug River valley (C).

1029

1030 **Figure 3.** Various ursid teeth from sites dated at MIS 11. A-D – comparison of morphology of
1031 P4: *Ursus deningeri* from Medzhybizh 1 (A), *Ursus deningeri* from Draby 5 (B), *Ursus arctos*
1032 *taubachensis* from Draby 8 (C) and *Ursus thibetanus* (D) from Kudaro 1 cave (Baryshnikov,
1033 2010: 70, fig. 2D). E – right I2 of *Ursus deningeri* from Medzhybizh 1, F – right m2 of *Ursus*
1034 *thibetanus* from Medzhybizh 1. All tooth showed to the same scale, scale bar 10 mm.

1035

1036 **Figure 4.** Posterior breadth plotted against total length of P4 in ursids (*Ursus deningeri*, *U.*
1037 *arctos taubachensis*, and *U. thibetanus*) from MIS 11 sites (Kurtén, 1968b, 1977; Crégut-
1038 Bonnoure, 1997; Baryshnikov, 2001, 2007, 2010; Wagner, 2014, and own measurements).

1039

1040 **Figure 5.** Remains of ungulates from Medzhybizh 1: A-C – *Capreolus* sp., fragment of the right
1041 DP4 (A) and right m2 (B) in occlusal view, right centrotarsal (C) in dorsal view; D-E – Cervidae
1042 indet. of the size of *Dama*, fragment of the right m1 or m2 (D) in occlusal view, distal epiphysis
1043 of the left radius in proximal view (E1) and dorsal view (E2); F-J – *Cervus elaphus*, right P4 (F)
1044 and left P4 (G) in occlusal view, skull fragment with antler (H) and fragment of antler (I),
1045 proximal shaft of the right metacarpus in proximal (J1) and dorsal view (J2); K – *Sus* sp., lower
1046 incisor (i1 or i2) in lateral view; L-M – *Stephanorhinus* sp., incomplete left p4 in occlusal (L1)
1047 and lateral view (L2), broken right M3 in occlusal view (M).

1048

1049 **Figure 6.** Size changes in *Capreolus* shown as changes in the width of the first lobe (DTa) of the
1050 m2 (mm) (only specimens with known position in tooth row included). Provenance of data as in
1051 Van der Made et al. (2014). Phylogeny and temporal distribution of *Capreolus*, *Dama*,
1052 *Haploidoceros* and the different sizes of *Cervus elaphus*. Palaeotemperature curve for the
1053 Northern Hemisphere after Van de Wal et al. (2011).

1054

1055 **Figure 7.** Bivariate diagrams of the transverse dimension of the posterior lobe (DTp) to the
1056 transverse dimension of the anterior lobe (DTa), and the anteroposterior dimension (DAP) to the
1057 transverse dimension of the anterior lobe (DTa) of the crowns of m1, m2 and m3 of
1058 *Stephanorhinus* from various localities.

1059

1060 **Figure 8.** Landscape reconstruction of the Middle Pleistocene locality Medzhybizh 1, with
1061 general view of the reconstructed biotope and fauna. Drawings by W. Gornig.

1062

1063 ***Table captions***

1064

1065 **Table 1.** The list of fishes from Medzhybizh 1.

1066

1067 **Table 2.** The list of amphibians and reptiles from Medzhybizh 1.

1068

1069 **Table 3.** The list of small mammals from Medzhybizh 1.

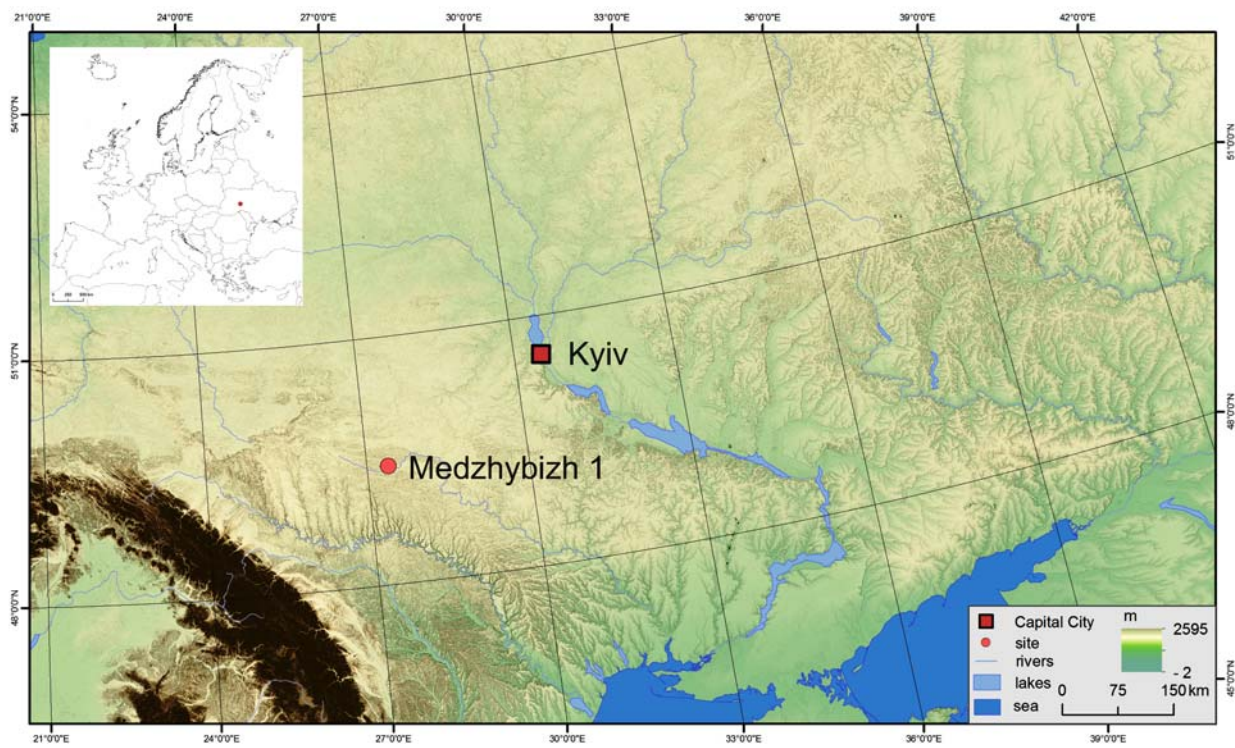
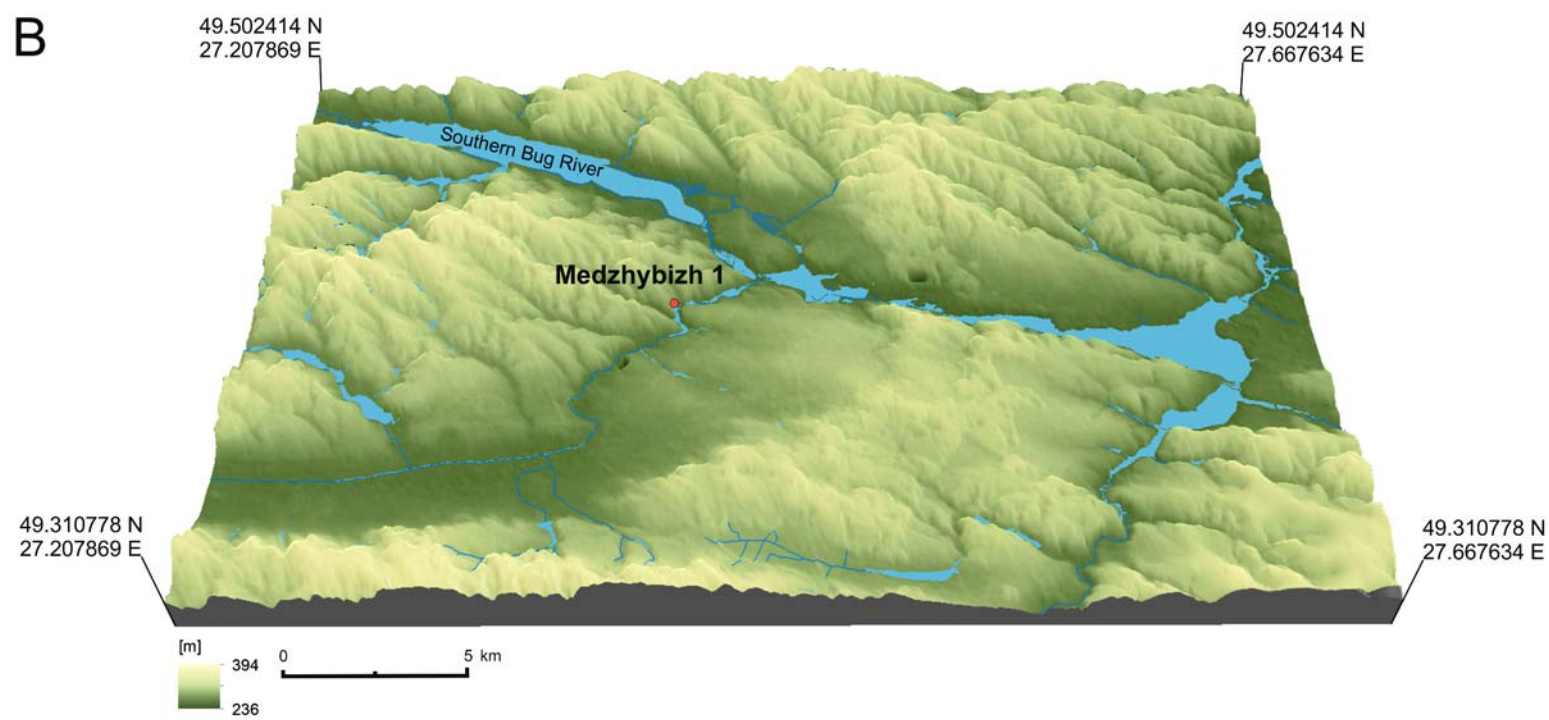
1070

1071 **Table 4.** The list of large mammals from Medzhybizh 1.

1072

1073 **Table 5.** Measurements (in mm) of m2 of the Middle Pleistocene brown bear and black bear
1074 from various Eurasian sites (according to Fistani and Crégut-Bonnoure, 1993; Baryshnikov,

1075 2007).

A**B**

A



B



C





A



B



E



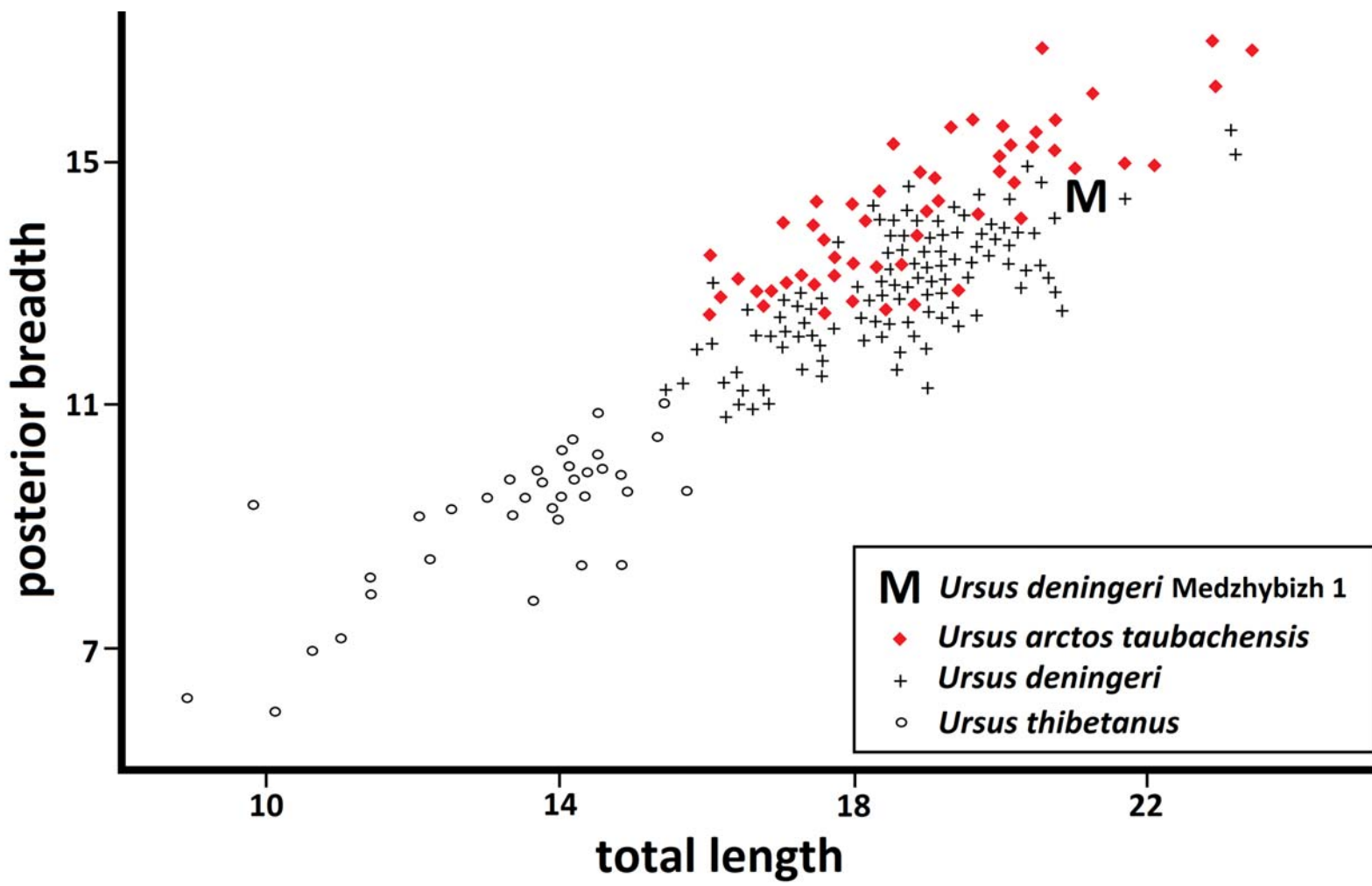
C

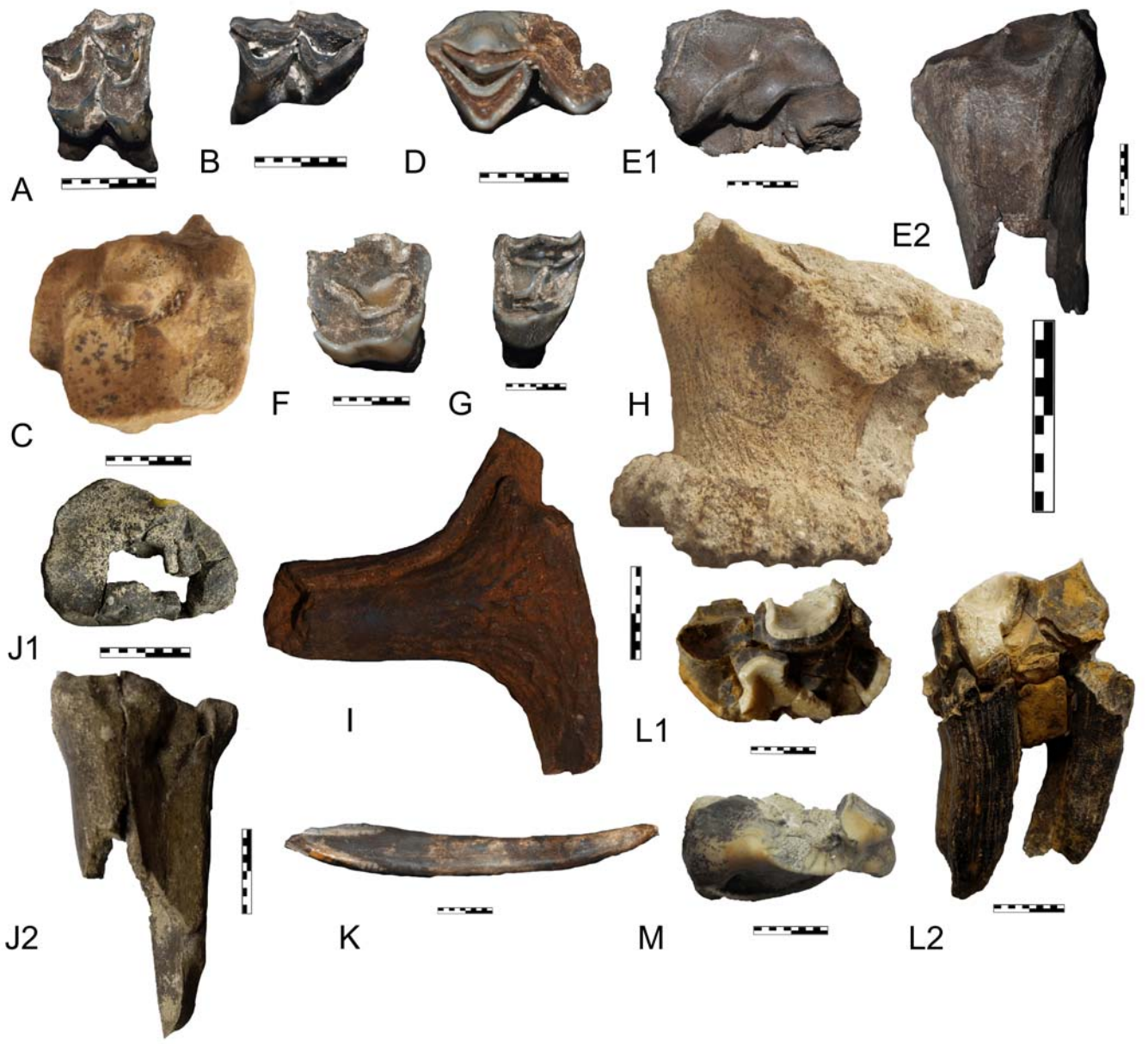


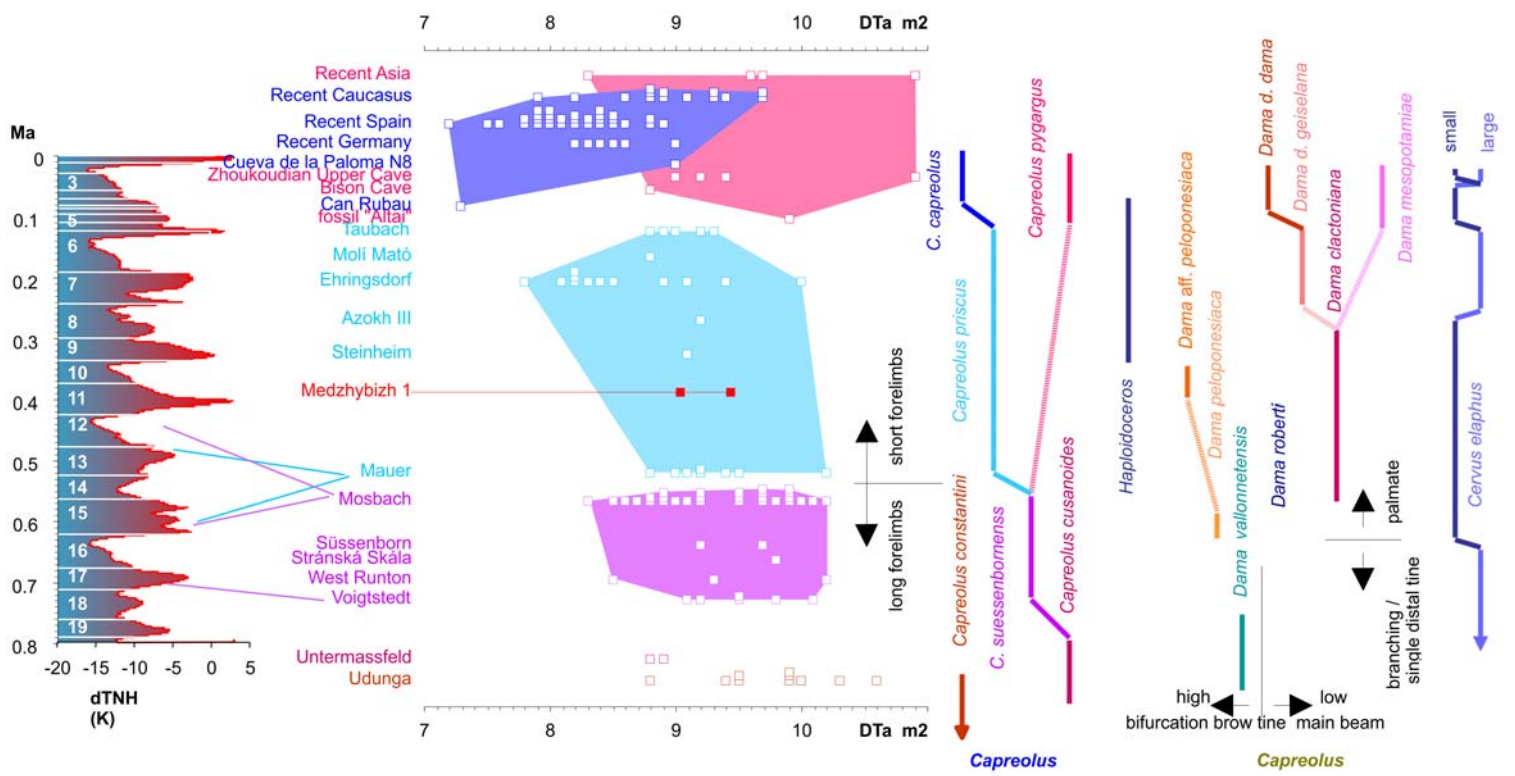
D



F







Ma

0

0.1

0.2

0.3

0.4

0.5

0.6

0.7

0.8

7 8 9 10 DTa m²

dTNH (K)

-20 -15 -10 -5 0 5

7 8 9 10 DTa m²

Capreolus

Capreolus

short forelimbs

long forelimbs

high

low

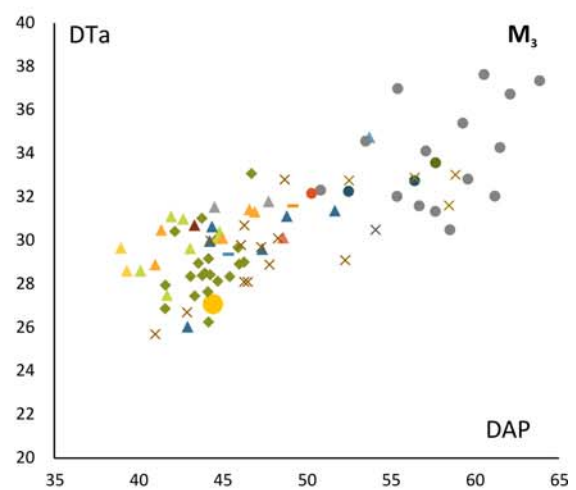
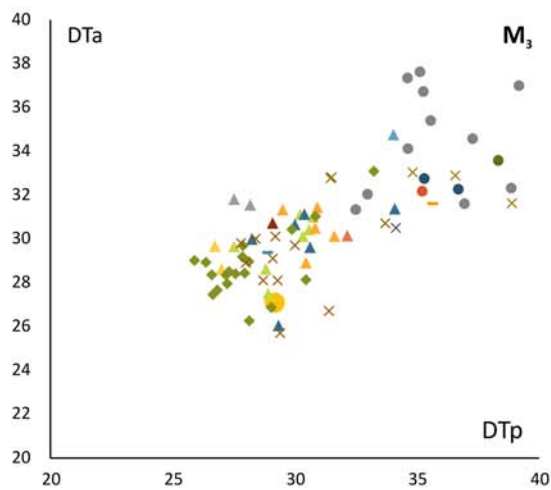
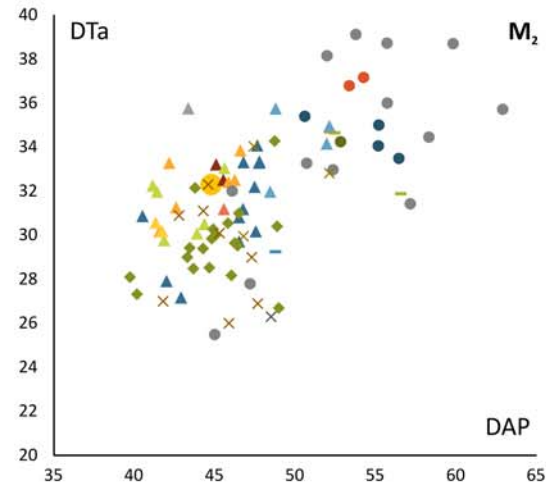
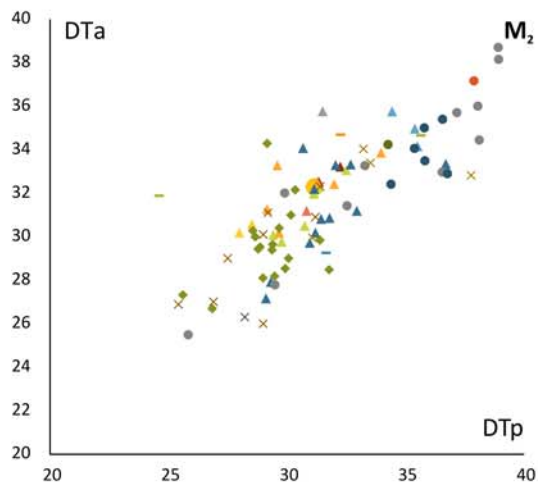
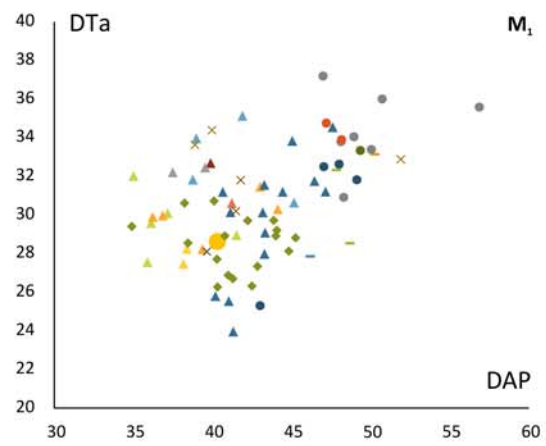
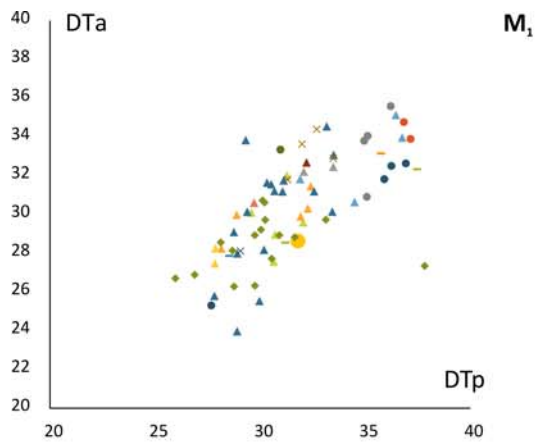
bifurcation brow tine main beam

branching / single distal tine

small

large

Cervus elaphus



- Medzhybizh 1 (Ukraine)
- *Stephanorhinus* sp. Grays (UK)
- ▲ *S. etruscus* Shutnivtzi (Ukraine)
- ▲ *S. etruscus* Upper Valdarno (Italy)
- ▲ *S. etruscus* Il Tasso (Italy)
- ▲ *S. etruscus* Pakefield (UK)
- ◆ *S. hundsheimensis* Sussenborn (Germany)
- *S. kirchbergensis* Clacton-on-Sea (UK)
- *S. kirchbergensis* Ilford (UK)
- × *S. hemitoechus* Grays (UK)

- *Stephanorhinus* sp. Clacton-on-Sea (UK)
- *Stephanorhinus* sp. West Thurrock (UK)
- ▲ *S. etruscus* Kuchurgan (Ukraine)
- ▲ *S. etruscus* Olivola (Italy)
- ▲ *S. etruscus* Infermuzzo (Italy)
- ▲ *S. etruscus* Trimmingham (UK)
- *S. kirchbergensis* Taubach (Germany)
- *S. kirchbergensis* Grays (UK)
- × *S. hemitoechus* Isernia la pineta (Italy)
- × *S. hemitoechus* Ilford (UK)



Taxon	Layer / NISP						Σ
	11	12	13	14	15	16	
Carp fishes (Cyprinidae)							
<i>Leuciscus</i> sp.	4	–	1	6	3	1	15
<i>Rutilus rutilus</i>	3	2	1	8	–	5	19
<i>Rutilus frisii</i>	–	–	1	1	1	1	4
<i>Rutilus</i> sp.	4	1	2	6	5	2	20
<i>Scardinius erythrophthalmus</i>	1	–	–	2	2	1	6
<i>Chondrostoma</i> sp.	–	1	–	1	–	–	2
<i>Abramis</i> sp.	3	2	1	–	4	–	10
<i>Aspius aspius</i>	1	–	–	1	–	–	2
<i>Barbus</i> sp.	–	–	–	–	2	–	2
<i>Carassius carassius</i>	1	–	1	–	–	–	2
<i>Tinca tinca</i>	3	–	–	3	2	–	8
Cyprinidae gen. et sp. indet.	2	–	–	6	3	3	14
Pikes (Esocidae)							
<i>Esox lucius</i>	–	1	–	11	11	10	33
<i>Esox</i> sp.	107	3	7	6	–	23	146
Perches (Percidae)							
<i>Perca fluviatilis</i>	2	2	–	1	3	–	8
Percidae gen. et sp. indet.	–	–	–	–	–	1	1
TOTAL	129	11	14	52	36	47	289

Taxon	Layer / NISP							Σ
	10-11*	11-12*	12	13	13-14*	14	15-16*	
Amphibia								
<i>Pelobates fuscus</i>	34	–	3	4	2	4	5	52
<i>Hyla arborea</i>	1	–	–	–	–	–	–	1
<i>Hyla</i> sp.	–	–	–	–	–	–	1	1
<i>Bufo bufo</i>	1	–	6	4	3	7	8	29
<i>Bufo</i> sp.	–	1	4	–	–	6	2	13
<i>Bufotes viridis</i>	–	–	–	–	–	3	1	4
<i>Rana temporaria</i>	–	2	4	1	1	14	4	26
<i>Rana</i> sp.	2	2	–	2	–	3	–	9
<i>Pelophylax ridibundus</i>	–	5	2	–	2	–	2	11
<i>Pelophylax lessonae</i>	2	1	–	1	–	3	–	7
<i>Pelophylax</i> sp.	1	–	4	–	1	2	–	8
Anura indet.	4	–	3	1	3	3	3	17
Reptilia								
<i>Natrix natrix</i>	–	–	–	–	–	–	2	2
<i>Natrix tessellata</i>	–	–	–	–	–	2	–	2
TOTAL	45	11	26	13	12	47	28	182

* Material from transitional layers (i.e. collected in between two successive layers)

Taxon	Layer / NISP									Σ
	8	9	10	11	12	13	14	15	16	
Eulipotyphla										
<i>Erinaceus</i> sp.	–	–	2	–	–	–	–	–	–	2
<i>Talpa</i> cf. <i>praeglacialis</i>	–	–	–	5	1	–	3	–	–	9
<i>Sorex praeearaneus praetetragonurus</i>	–	–	2	3	1	–	1	2	–	9
<i>Neomys newtoni</i>	–	–	–	–	–	–	–	2	–	2
Lagomorpha										
<i>Lepus</i> cf. <i>europaeus</i>	–	–	–	–	–	–	1	–	–	1
<i>Ochotona</i> sp.	–	–	3	–	–	–	–	–	–	3
Rodentia										
<i>Marmota</i> sp.	–	–	–	–	–	–	–	–	1	1
<i>Spermophilus</i> cf. <i>suslicus</i>	–	–	3	–	–	–	–	–	–	3
<i>Spermophilus</i> sp.	–	–	–	–	–	–	2 ^b	–	–	2
<i>Spalax</i> cf. <i>zemni</i>	–	–	–	3	–	–	–	–	–	3
<i>Spalax</i> sp.	–	–	–	–	–	–	1 ^b	–	–	1
<i>Euroxenomys minus</i> ^a	–	–	–	–	1	–	1	–	–	2
<i>Trogontherium cuvieri</i> ^a	–	–	–	–	–	–	–	1	–	1
<i>Castor fiber</i>	–	–	2	2	–	–	–	–	9 ^c	13
<i>Apodemus agrarius</i>	–	–	–	5	1	–	–	–	–	6
<i>Sylvaemus</i> cf. <i>flavicollis</i>	–	–	–	–	–	–	1 ^b	1 ^b	–	2
<i>Cricetus cricetus</i>	–	–	1	1	–	–	–	–	–	2
<i>Allophaiomys deucalion</i> ^a	–	–	–	–	–	–	3 ^b	–	–	3
<i>Lagurus lagurus</i>	–	–	–	2	–	–	–	–	–	2
<i>Clethrionomys glareolus</i>	–	–	5	3	–	–	–	7	–	15
<i>Clethrionomys</i> sp.	–	–	–	–	–	–	4 ^b	–	–	4
<i>Mimomys</i> ex gr. <i>intermedius-savini</i> ^a	–	–	–	–	–	–	–	2	–	2
<i>Arvicola mosbachensis</i>	–	1	22	27	1	–	10	24	–	85
<i>Alexandromys</i> (<i>Pallasinus</i>) <i>oeconomus</i>	–	–	3	–	–	–	1 ^b	–	–	4
<i>Lasiopodomys</i> (<i>Stenocranius</i>) <i>gregalis</i>	4	1	2	6	–	–	14	–	–	27
<i>Microtus</i> (<i>Terricola</i>) <i>arvalidens</i>	–	–	–	7	–	–	4	6 ^d	–	17
<i>Microtus</i> (<i>Agricola</i>) <i>agrestis</i>	–	–	–	1	1	–	–	7 ^d	–	9
<i>Microtus</i> (<i>M.</i>) <i>nivaloides</i>	1	–	2	12	–	–	5	9 ^d	–	9
<i>Microtus</i> (<i>M.</i>) ex gr. <i>arvalis</i>	3	2	3	3	1	2	4	2	–	20
<i>Microtus</i> sp.	–	–	–	–	–	–	–	–	3	3
TOTAL	8	4	50	80	7	2	55	63	13	282

^a Probably re-deposited from older sediments

^b Data presented after Nezdolii (2019)

^c Data presented after Stepanchuk and Moigne (2016)

^d Including two additional specimens after Nezdolii (2019)

Taxon	Layer / NISP			Σ
	15	15-16	16	
Carnivora				
<i>Ursus deningeri</i>	–	–	6	6
<i>Ursus thibetanus</i>	–	–	1	1
<i>Ursus</i> sp.	–	–	2	2
Perissodactyla				
<i>Stephanorhinus</i> sp.	2	6	4	12
Artiodactyla				
<i>Capreolus</i> sp.	3	1	5	9
<i>Cervus elaphus</i>	30	12	22	64
Cervidae indet. of the size of <i>Dama</i>	2	–	8	10
<i>Sus</i> sp.	1	2	2	5
TOTAL	38	21	50	109

	<i>Ursus arctos taubachensis</i> /ssp.				Medzhybizh 1	<i>Ursus thibetanus</i> Pleistocene				<i>Ursus thibetanus</i> recent			
	M	min-max	SD	n		M	min-max	SD	n	M	min-max	SD	n
1	28.7	26.0-32.7	1.3	104	21.3	20.9	19.3-23.1	1.1	8	18.7	17.4-21.3	1.4	9
2	16.8	13.2-18.8	1.4	55	13.8	-	-	-	-	-	-	-	-
3	16.2	10.9-21.4	1.4	55	15.1	-	-	-	-	-	-	-	-
4	14.2	10.1-16.1	1.5	55	7.6	-	-	-	-	-	-	-	-
5	12.3	9.4-14.5	1.6	55	5.9	-	-	-	-	-	-	-	-
6	17.9	14.8-20.6	1.4	96	12.6	-	-	-	-	10.9	10.2-11.9	0.6	9
7	18.1	15.8-21.8	1.5	103	12.8	12.7	11.0-14.2	1.1	8	10.9	10.1-11.6	0.7	9