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1 **Exploring the landscape and climatic conditions of Neanderthals and**
2 **anatomically modern humans in the Middle East: the rodent assemblage**
3 **from the late Pleistocene of Kaldar Cave (Khorramabad Valley, Iran)**

4
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21
22 **Abstract**

23 The Middle East, specially the Zagros region, lies in a strategic position as a
24 crossroads between Africa, Europe and eastern Asia. The landscape of this
25 region that prevailed around the Neanderthal and anatomically modern human
26 occupations is not well known. Only a few sites have been studied in detail in
27 this area, often providing only a faunal list. These reveal that Neanderthals and
28 anatomically modern humans lived in a landscape mainly composed of dry
29 steppes.

30 Here we extend the data obtained from Kaldar Cave through a systematic
31 study of the rodent assemblage. The site provided evidence of a Pleistocene
32 occupation attested by lithic tools associated with the Middle and Upper
33 Palaeolithic, but it was also occupied during the Holocene, as evidenced by
34 Neolithic artefacts. First excavations have revealed small vertebrates in Layer 4
35 (sub-layer 5 and 5II), belonging to the Upper Palaeolithic, and Layer 5 (sub-
36 layers 7 and 7II), belonging to the Middle Palaeolithic.

37 The rodent assemblage of Kaldar Cave is mainly composed of six arvicoline,
38 two cricetine, one glirid, one dipodid, one gerbilline and two murine species.

39 This assemblage shows that during the Late Pleistocene the environment
40 around the site was mainly composed of open dry steppes, as indicated by the
41 most abundant taxa, *Microtus*, *Ellobius* and *Meriones*. However, murine species
42 indicate the presence of a vegetation cover. The palaeoclimatic conditions are
43 characterised by lower temperatures and also less precipitation than at present.

44 The results obtained with the rodent assemblages show that there is no
45 major palaeoenvironmental or palaeoclimatic change that would explain the

46 cultural shift between Layer 5 (Middle Palaeolithic) and Layer 4 (Upper
47 Palaeolithic).

48

49 **Keywords:** *Rodentia, Middle East, taxonomy, palaeoecology, human*
50 *occupations*

51

52

53 1. Introduction

54

55 Small vertebrates are recognized to be good palaeoecological indicators due
56 to their rapid evolution, the limited geographic range of a species and unique
57 niche requirements, as well as their frequent preservation in archaeological and
58 palaeontological sites. They might be excellent indicators of palaeovegetation
59 type and provide a high-resolution proxy for palaeoenvironmental changes (e.g.
60 Belmaker and Hovers, 2011). Studies of small vertebrates from archaeological
61 sites in the Middle East are still scarce (Belmaker and Hovers, 2011; Belmaker
62 et al., 2016; Demirel et al., 2011; Fernández-Jalvo, 2016a; Kandel et al., 2017;
63 Maul et al., 2015a, 2015b; Smith et al., 2015; Weissbrod and Zaidner, 2014),
64 and they mainly propose preliminary lists of taxa. On the other hand, some
65 studies of extant owl pellet assemblages have been performed in the Middle
66 East (Abi-said et al., 2014; Darvish et al., 2000; Haddadian Shad et al., 2014;
67 Kopij and Liven-schulman, 2013; Obuch and Khaleghizadeh, 2012; Rey-
68 Rodríguez et al., 2019; Shehab et al., 2013), providing taxonomic and some
69 taphonomic reference data in Iran, Lebanon, Israel, Turkey and Syria.

70 The main palaeoecological and palaeoclimatic reconstructions based on
71 faunal assemblages relate to the unique niche requirements of a particular
72 species. Belmaker *et al.* (2011) pointed out that their interpretations, in contrast,
73 are based on analyses of community composition. Analyses of persistence
74 *versus* change over time should take into account species presence-absence,
75 rank abundance and proportional abundance (Belmaker and Hovers, 2011).

76 The Middle East is a prime location to study Neanderthal and anatomically
77 modern human (AMH) interactions during the Middle to Upper Palaeolithic
78 transition (Belmaker et al., 2016). However, sites yielding evidence of both
79 Neanderthal and AMH occupations in the same sequence are rare, only five
80 sites were well excavated (Bazgir et al., 2014; Bazgir et al., 2017). In this
81 framework, Kaldar Cave is a key archaeological site for evaluating the influence
82 of environment on cultural changes in both human species because of its
83 location and the faunal and lithic remains. The main objective of this paper is to
84 infer the landscape composition and the climatic conditions in which
85 Neanderthal and AMH populations pursued their activities through the study of
86 small mammals. We identify and describe the rodent fossils recovered from
87 Kaldar Cave in order to establish the main criteria for further identifications in
88 this region and provide a preliminary basis for future systematic studies.

89

90

91 **2. Kaldar Cave**

92

93 Kaldar Cave is located in the northern part of the Khorramabad valley,
94 Lorestan Province, western Iran (48°17'35" E, 33°33'25" N) at 1290 m a.s.l.
95 (Fig. 1a,b). The cave was discovered in 2007, and the first archaeological
96 intervention was undertaken by an Iranian-Spanish team in 2011-2012,
97 revealing the great potential of the cave (Bazgir et al., 2014). A second
98 excavation was performed in 2014-2015. The trench exposed an approximately
99 2m-thick section of sedimentary deposits, characterized by 5 main layers,
100 themselves divided into several sub-layers (Fig. 1c).

101 Layer 5 (including sub-layers 7 and 7II) consists of an extremely cemented
102 reddish-brown sediment with some small angular limestone blocks and Middle
103 Palaeolithic artefacts with Levallois elements. So far, no chronometric data are
104 available for this layer (Bazgir et al., 2017).

105 Layer 4 (including sub-layers 5, 5II, 6 and 6II) consists of a silty but compact
106 dark-brown sediment with cultural remains attributed to the Upper and early
107 Upper Palaeolithic. In the uppermost parts of this layer, two fireplaces made of
108 clay were recovered and dated through thermoluminescence, yielding ages that
109 ranged from 23,100 ± 3 300 to 29,400 ± 2 300 BP (Bazgir et al., 2017). The
110 dates obtained show that these fireplaces were made or re-used from existing
111 older sediment from the upper part of this layer in the later stages of the Upper
112 Palaeolithic. AMS radiocarbon dates of 38,650–36,750 cal BP, 44,200–42,350
113 cal BP, and 54,400–46,050 cal BP have been obtained from charcoal material
114 located below this layer (Bazgir et al., 2017; Becerra-Valdivia et al., 2017).

115 Layers 1 to 3 (including sub-layers 4 and 4II) consist of ashy sediments of a
116 blackish-green colour containing both thick and thin angular limestone clasts.
117 These layers varied in thickness from 60 to 90 cm and contained many phases
118 dating to the Holocene: Islamic and historical eras, Iron Age, Bronze Age,
119 Chalcolithic and Neolithic. However, due to the presence in these layers of
120 bioturbation mainly by burrowing animals, the phases were recognized only by
121 a preliminary study of the potsherds, metal artefacts and some diagnostic lithic
122 artefacts from the lower layers.

123 This site provides evidence for the Middle to Upper Palaeolithic transition in
124 the Middle East (Bazgir et al., 2017). Moreover, Kaldar Cave has yielded the
125 oldest evidence of *Prunus* spp. in the area, through the study of thirty charcoal
126 remains (Allué et al., 2018), that helps us to reconstruct the environmental
127 conditions, evidencing a wooded vegetation.

128

129 **3. Material and methods**

130

131 The rodent fossil remains used in this study, 1112 molars, come from the
132 archaeological excavation campaigns carried out in Kaldar Cave in 2011-2012
133 and 2014-2015.

134 The samples comprise disarticulated bones and isolated teeth that were
135 collected in the field by water screening using superimposed 5 and 0.5 -mm
136 mesh screens.

137

138 **3.1. Taxonomy**

139

140 In this article we only focus on rodents, because these are one of the most
141 useful tools for palaeoenvironmental and palaeoclimatic reconstructions of
142 archaeological sites, and the other material, as amphibians, squamates, birds,
143 shrews and bats, will be studied later. The taxonomic identification of the rodent
144 remains is based mainly on molar morphology and measurements of the lower
145 m1, the taxonomically most diagnostic tooth.

146 The remains were identified at a specific level whenever possible, thanks to
147 comparisons with reference collections from the Natural History Museum of
148 London (NHM) and comparative morphological and biometric data from the
149 literature, notably for *Microtus* (Coşkun, 2016; Kryštufek and Shenbrot, 2016;
150 Kryštufek and Vohralík, 2009; López-García, 2011; Rusin, 2017; Shenbrot,
151 Kryštufek et al. 2016; Tesakov, 2016), *Cricetulus* (Bogicevic et al., 2011;
152 Kryštufek et al., 2017; Sándor, 2018), *Mesocricetus* (Kryštufek and Vohralík,
153 2009), *Meriones* (Coşkun, 1999; Darvish, 2011; Dianat et al., 2017; Kryštufek
154 and Vohralík, 2009; Souttou and Denys, 2012; Stoetzel et al., 2017), *Allactaga*
155 (Karami et al., 2008; Shenbrot, 2009), *Myomimus* (Gerrie and Kennerley, 2017;
156 Karami et al., 2008; Kennerley and Kryštufek, 2019), *Apodemus* (Amori et al.,
157 2016; Bogicevic et al., 2011; Knitlová and Horáček, 2017; Kryštufek and
158 Vohralík, 2009; López-García, 2008) and *Mus* (Darviche et al., 2006; Kryštufek
159 and Vohralík, 2009; Siahsarvie and Darvish, 2008).

160 Quantification of taxonomic frequencies was based on standard measures in
161 zooarchaeological analyses, including the number of identified specimens
162 (NISP) and minimum number of individuals (MNI) (Weissbrod and Zaidner,
163 2014). This latter was estimated using the most abundant skeletal element
164 present in the assemblage (molars in our case).

165

166 **3.2. Taphonomic remarks**

167

168 A preliminary study was performed on the Kaldar Cave micromammal
169 remains. This was based on the systematic descriptive method that examines
170 the modifications of prey bones induced by predation, focusing on the degree of
171 digestion observed in teeth during the identification (Andrews, 1990;
172 Fernández-Jalvo et al., 2016). This study showed a significant number of
173 digested teeth (Bazgir et al., 2017), indicating that predation activity was the
174 origin of at least part of the accumulation. According to the different degrees of
175 digestion (mostly light, moderate and, heavy in a few cases) observed in the
176 molars, the predator responsible for this accumulation could be a category 3
177 predator such as the tawny owl (*Strix aluco*) or the Eurasian eagle owl (*Bubo*

178 *bubo*). Both species are currently present in the area, have opportunistic
179 hunting habits, and are sedentary, so their prey spectrum is assumed to be a
180 good representation of the ecosystem in which they live.

181

182 **3.3. Palaeoenvironmental and palaeoclimatic reconstructions**

183

184 *3.3.1. Habitat weighting method*

185

186 Palaeoecological interpretations derived from faunal data are based on
187 analyses of community composition (Belmaker and Hovers, 2011). The method
188 used for the palaeoenvironmental reconstruction is the *habitat weighting*
189 *method*, also named the *taxonomic habitat index* (Evans et al., 1981; Andrews,
190 2006; modified by Blain et al., 2008; López-García et al., 2011), which is based
191 on the current distribution of each taxon in the habitat(s) where it can be found
192 nowadays. We assume that the Kaldar Cave species had equivalent ecological
193 requirements to their present-day relatives, because the Late Pleistocene
194 species are the same as those today and no extinct fossil species are found in
195 the assemblage. We adapt the method to our studied area, differentiating the
196 following types of habitats: Forest (Fo), a large area covered with trees;
197 Shrubland (Sh), vegetation dominated by shrubs; Grassland (Gr), an open area
198 covered with grass; Desert (De), an area with little precipitation and no
199 vegetation cover; Wetland (We), an area where water covers the soil; Steppe
200 (St), a dry grassy plain; and Rocky (Ro), a rocky or stony substrate. Each
201 species has a score of 1.00, which is divided between the habitats where the
202 species can be found at present (Table 1), all the species ranges were taken
203 from the IUCN Red List of Threatened Species
204 (<https://www.iucnredlist.org/resources/spatial-data-download>).

205

206 *3.3.2. Bioclimatic Model*

207

208 In order to reconstruct the climate at Kaldar Cave, we applied the *bioclimatic*
209 *model (BM)*, which was developed by Hernández-Fernández (2001) on the
210 basis of the faunal spectrum, assuming that small- and large-mammal species
211 can be ascribed to ten different climates (Hernández-Fernández, 2001;
212 Hernández-Fernández and Peláez-Campomanes, 2003; Hernández-Fernández
213 et al., 2007). It was first necessary to calculate the climatic restriction index
214 ($CRI_i = 1/n$, where i is the climatic zone where the species appear and n is the
215 number of zones where the species is present) and the bioclimatic component
216 ($BC_i = (\sum CRI_i) 100/S$, where i is the climatic zone and S is the number of
217 species). To BC a mathematical model is applied as a regression that allows us
218 to calculate climatic parameters (see Appendix 1).

219

220 The different climatic groups defined by Hernández-Fernández (2001) and
221 Hernández-Fernández et al. (2007) are: I *equatorial*; II *tropical with summer*
rains; II/III *transition tropical semiarid*; III *sub-tropical arid*; IV, *subtropical with*

222 winter rains and summer droughts; V, *warm temperate* with not very severe
223 winters but high humidity; VI, *typical temperate* with winters that are cold but not
224 very long, but summers that are cool; VII, *arid-temperate* with large temperature
225 contrasts between winter and summer; VIII, *cold-temperate* with cool summers
226 and long cold winters (boreal) and IX, *artic* (Table 2).

227 By means of the *BM* we were able to estimate the mean annual temperature
228 (MAT), the mean temperature of the coldest month (MTC), the mean
229 temperature of the warmest month (MTW) and the mean annual precipitation
230 (MAP). This method also allowed us to assess whether there were changes in
231 the temperature and precipitation regimes during the Middle to Upper
232 Palaeolithic transition at Kaldar Cave.

233

234 **4. Results and discussion**

235

236 **4.1. Taxonomic identifications**

237

238 In total 264 minimum number of individuals (MNI) were identified (Table 3
239 and Fig. 2). Some differences were found with respect to the preliminary list
240 previously published by Bazgir et al. (2017). We notably found some new
241 specimens and reconsidered the identifications for *Ellobius talpinus*,
242 *Calomyscus* sp. and *Dryomys* cf. *nitedula*.

243

244 **Order Rodentia Bowdich, 1821**

245

Rodentia indet.

246

247 There are 14 teeth (11 in Layer 4 and 3 in Layer 5) that have not been identified
248 to the family or genus level because they were broken.

249

250 **Family Cricetidae Fisher, 1817**

251

Subfamily Arvicolinae Gray, 1821

252

Genus *Microtus* Schrank, 1798

253

***Microtus* spp.**

254

255 **Material:** 554 isolated teeth. **Layer 1-3:** four isolated teeth; three left lower
256 m1 and one right lower m1. **Layer 4:** 258 isolated teeth; 81 m2; 101 m3, 13
257 right upper M1, 31 right lower m1; four left upper M1 and 28 left lower m1.
258 **Layer 5:** 292 isolated teeth; 119 m2; 53 m3; nine left upper M1, 51 left lower
259 m1; 10 right upper M1; 50 right lower m1.

260

261 ***Microtus socialis* Pallas, 1773**

262

263 **Material:** 74 isolated teeth. **Layer 1-3:** three isolated teeth, three right lower
264 m1. **Layer 4:** 36 isolated teeth; 20 right lower m1 and 16 left lower m1. **Layer 5:**
265 35 isolated teeth; 20 right lower m1 and 15 left lower m1.

266

267

Microtus irani Thomas, 1921

268

269 **Material:** 15 isolated teeth. **Layer 1-3:** one isolated tooth, one right lower m1.

270

Layer 5: 14 isolated teeth; nine right lower m1 and five left lower m1.

271

272

Microtus guentheri Danford & Alston, 1880

273

274 **Material:** 17 isolated teeth. **Layer 1-3:** one isolated tooth, one left lower m1.

275

Layer 4: 16 isolated teeth; nine right lower m1 and seven left lower m1.

276

277

Description and discussion: all the molars are hypsodont and arhizodont with crown cementum in the re-entrant angles. The enamel differentiation is *Microtus*-like. Six extant species of *Microtus* have been identified in Iran: *Microtus arvalis*, *Microtus irani*, *Microtus kermanensis*, *Microtus socialis*, *Microtus transcaspicus* and *Microtus guentheri* (Aşan Baydemir and Duman, 2009; Golenishchev et al., 2019; Firouz, 2005).

282

283

Microtus m1 are characterized by four buccal and five lingual re-entrant angles (Kryštufek and Vohralík, 2009; Tsytsulina et al., 2017) with a posterior lobe (PL), seven triangles (T) and an anterior cap (AC). We identified the Kaldar specimens on the basis of their measurements (Table 4), the arrangement and morphology of the triangles, and the AC (which may or may not be connected with the other elements).

288

In our sample we identified *Microtus* spp., *Microtus socialis*, *Microtus guentheri* and *Microtus irani*.

290

291

In *Microtus socialis*, the triangles from T1-T5 are closed, but T6-T7 are parallel and broadly confluent with the AC. *Microtus guentheri* is distinguishable from *Microtus socialis* by the rounded shape of the AC, which is of an arhombomorph type (Aşan Baydemir and Duman, 2009), and also by T6-T7, which are separated from the AC. In accordance with the measurements given in Aşan Baydemir et al. (2009), the size of *Microtus guentheri* and *Microtus socialis* is similar. In *Microtus irani*, triangles T1-T5 are closed, but T6-T7 are open and not parallel with one another; moreover, *Microtus irani* is clearly larger than the other species considered in our reference collection and also in our sample. Finally, we include in *Microtus* spp. all the elements that we cannot attribute to one species or another, in particular because of their bad state of preservation (due to digestion, breakage).

302

Habitat and distribution: *Microtus irani* occupies grasslands in Iran, Turkey and the Caucasus (Kryštufek and Kefelioğlu, 2001).

304

305

Microtus socialis is found in Russia, Ukraine, the Caucasus, Transcaucasia, Turkestan, Iran and Afghanistan (Tsytsulina et al., 2017), although the range is fragmented. It is a highly colonial species, found in steppe habitats and also in agricultural lands, but extending also to bushy scrubs and uncultivated mountain valleys, as well as to open oak forests on dry hillsides (Tsytsulina et al., 2017).

309

310 *Microtus guentheri* occurs from the southeastern Balkans and Turkey through
311 Syria, Lebanon and Israel, with an isolated range segment in northern Libya,
312 Iran and some parts of Europe (Aşan Baydemir and Duman, 2009). This
313 species is present in dry grasslands with sparse vegetation (Amr, 2015).

314

315

Genus *Chionomys* Miller, 1908

316

***Chionomys nivalis* Martins, 1842**

317

318 **Material:** 25 isolated teeth. **Layer 1-3:** two isolated teeth; one left lower m1
319 and one right lower m1. **Layer 4:** 17 isolated teeth; 12 right lower m1; five left
320 lower m1. **Layer 5:** six isolated teeth; three left lower m1; three right lower m1.

321

322 **Description and discussion:** in our specimens it can be observed that the
323 first lower molars display five triangles and that the morphology of the
324 anteroconid complex (AC) is characteristic of the *nivalis* morphotype, where
325 triangles T6 and T7 are absent and the anterior cap is of an arrowhead or oval
326 shape, inclined towards the labial part. The enamel is of the *Microtus* type with
327 cement (Krystufek, 2017; Kryštufek and Vohralík, 2009; López-García, 2011).
328 These specimens differ from *Microtus* in that they only have five triangles, and
329 the morphology of the AC is the other main characteristic of this species that
330 helps us to differentiate it from *Microtus*.

330

331 **Habitat and distribution:** *Chionomys nivalis* has a global distribution
332 extending from southwestern Europe through southeastern Europe to the
333 Caucasus, Turkey, Israel, Lebanon, Syria and Iran. In Iran it is distributed in the
334 north and also in the west (Shenbrot and Krasnov, 2005; Krystufek, 2017). This
335 is the only *Chionomys* species occurring today in Iran, but two other species (*C.*
336 *gud*, *C. roberti*) are represented a little further north (northeastern Turkey,
337 southern Georgia).

338 Regarding its habitat, it is present in open rocky areas, typically above the tree
339 line and with scarce vegetation cover (Amori, 1999).

339

340

Genus *Ellobius* Fischer, 1814

341

***Ellobius* spp.**

342

343 **Material:** 173 isolated teeth. **Layer 1-3:** two isolated teeth; two left lower m1.
344 **Layer 4:** 91 isolated teeth; seven indet.; eight right lower m1; five left lower m1;
345 11 upper M1; 43 m2; 17 m3. **Layer 5:** 80 isolated teeth; seven left lower m1;
346 three upper M1; 45 m2; 25 m3.

347

348

***Ellobius fuscocapillus* Blyth, 1843**

349

350 **Material:** 11 isolated teeth. **Layer 1-3:** one isolated tooth; one right lower m1.
351 **Layer 4:** five isolated teeth; two right lower m1; three left lower m1. **Layer 5:**
352 five isolated teeth; four left lower m1 and one right lower m1.

353

Ellobius lutescens Thomas, 1897

354
355

356 **Material:** 20 isolated teeth. **Layer 4:** 10 isolated teeth; seven right lower m1
357 and three left lower m1. **Layer 5:** 10 isolated teeth; four left lower m1 and six
358 right lower m1.

359 **Description and discussion:** 204 isolated teeth show the typical traits of the
360 genus *Ellobius* (Miller, 1896; Hinton, 1962, Kretzoi, 1969; Coşkun, 2016;
361 Kryštufek & Shenbrot, 2016; Kryštufek and Vohralík, 2009; Rusin, 2017;
362 Shenbrot et al., 2016; Tesakov, 2016). *Ellobius* molars are notably
363 characterized by the presence of roots that are well visible in adults and old
364 individuals, but not always apparent in young specimens (Coşkun, 2016).
365 Moreover, *Ellobius* molars lack cement in the re-entrant angles. The *Ellobius*
366 m1 is composed of the anterior cap (AC), five triangles (T) with three buccal and
367 four lingual salient angles, and one posterior lobe (PL). Both M3 and m3 are
368 reduced and smaller than the other molars, with three triangles on the labial
369 side and two triangles on the lingual side. M1 has three inner and outer folds,
370 and M2 and M3 have two inner and two outer re-entrant folds. The first and
371 second upper molars have three triangles on the lingual and labial sides.
372 However, the re-entrant angle between the first and the second triangles on the
373 lingual side is more superficial (Gharkheloo and Kivanç, 2003).

374 In Iran, the genus *Ellobius* is currently represented by three species: *Ellobius*
375 *fuscocapillus*, *Ellobius lutescens* and *Ellobius talpinus* (Firouz, 2005; Kryštufek
376 & Shenbrot, 2016; Kryštufek and Vohralík, 2009; Moradi Gharkheloo, 2003;
377 Rusin, 2017; Shenbrot et al., 2016). The m1 is quite similar among these
378 species, but there are some differences that can help us to differentiate them.

379 The AC is broad in *Ellobius lutescens*, narrow in *Ellobius talpinus* and elongated
380 in *Ellobius fuscocapillus* (Maul et al., 2015b). The distance between T4 and T5
381 (W) and the total length (L) differ among the species (Table 5). We have
382 observed in modern specimens from the Natural History Museum of London
383 that *Ellobius fuscocapillus* is the largest and *Ellobius talpinus* the smallest.

384 In our sample we identify as *Ellobius* spp. those m1s that are too broken or
385 digested to distinguish, as well as all the m2, m3, M1, M2 and M3 because of
386 the lack of discriminant characters. The identification of *Ellobius lutescens* and
387 *Ellobius fuscocapillus* in the Kaldar material is based on the morphology of the
388 AC and the measurements (L and W). We do not identify *Ellobius talpinus* in our
389 sample, as no specimen displays morphological features characteristic of this
390 species, such as the narrow AC, and because the measured specimens are
391 larger than *E. talpinus*.

392 **Habitat and distribution:** *Ellobius* species frequent steppes, grasslands and
393 semi-deserts in eastern Europe and central Asia; these fossorial species are
394 specialised in subterranean life (Coşkun, 2016; Kryštufek and Vohralík, 2009).
395 *Ellobius lutescens* is a Palaearctic species distributed across Iran, Iraq,
396 Azerbaijan, Armenia, Transcaucasia and East Anatolia (Thomas, 1905;
397 Ellerman and Morrison-Scott, 1951; Darlington, 1957; Osborn, 1962; Walker,

398 1964; Lay, 1967; Hassinger, 1973; Roberts, 1977; Corbet, 1978; Corbet and
399 Hill, 1991; Wilson and Reeder, 2005; Coşkun, 1997, 2016; Nowak, 1999;
400 Kryštufek & Shenbrot, 2016). In Iran, this species is found in mountain
401 grasslands, sandy semi-deserts and steppe areas (Kryštufek & Shenbrot, 2016;
402 Tesakov, 2016). *Ellobius fuscocapillus* shows a wide range across eastern Iran,
403 Turkmenistan, Afghanistan and Pakistan. In Iran it is found in open steppes with
404 loose soil (Shenbrot, Kryštufek & Molur, 2016).

405

406 **Subfamily Cricetinae Fischer, 1817**

407

407 **Genus *Cricetulus* Milne-Edwards, 1867**

408

408 ***Cricetulus migratorius* Pallas, 1773**

409

410 **Material:** 19 isolated teeth. **Layer 1-3:** one isolated tooth; one right lower m3.
411 **Layer 4:** 13 isolated teeth; three left lower m1, two left upper M2; three right
412 lower m1, three right upper M1 and two right upper M2. **Layer 5:** five isolated
413 teeth; three left lower m1 and two right lower m1.

414

415 **Description and discussion:** the first molars (m1 and M1) are brachyodont
416 and cuspidate, with two longitudinal series of cusps. Each series of cusps
417 consists of three pairs. The m1 and M1 are the largest and the m3/M3 the
418 smallest. The lower m3 only has two pairs of cusps (Kryštufek and Vohralík,
419 2009). We identify *Cricetulus migratorius* in all the layers of Kaldar Cave in
420 accordance with the measurements and identification keys for molars based on
421 the morphology and arrangement of the tubercles and cusps provided by
422 Kryštufek and Vohralík (2009). We also draw comparisons with the reference
423 collection from Iran, Afghanistan and Azerbaijan housed in the Natural History
424 Museum of London. The grey hamster, or migratory hamster, is the smallest
425 hamster species (Bogicevic et al., 2011; Sándor, 2018).

426

427 **Habitat and distribution:** *Cricetulus migratorius* extends from eastern
428 Europe through Russia and central Asia to Mongolia and western China
429 (Kryštufek et al., 2017; Kryštufek and Vohralík, 2009). In Iran, this species is
430 found all over the country. The habitats of this species are mostly dry
431 grasslands, steppes and semi-deserts. Arid areas with relatively sparse
432 vegetation are preferred (Kryštufek et al., 2017; Maul et al., 2015a).

431

432 **Genus *Mesocricetus* Nehring, 1898**

433

433 ***Mesocricetus brandti* Nehring, 1898**

434

435 **Material:** 10 isolated teeth. **Layer 4:** three isolated teeth; one left upper M1,
436 one right lower m1 and one right upper M1. **Layer 5:** seven isolated teeth; four
437 left upper M1, one right upper M2 and two right upper M1.

438

439 **Description and discussion:** the specimens from Kaldar Cave are
440 attributed to *Mesocricetus brandti* on the basis of the size and morphology of
441 the teeth. The molars present a similar morphological pattern to *Cricetulus*
442 *migratorius*, but are significantly larger in size. The first molars have six

442 tubercles, the second and third molars only four. The largest molars are m1 and
443 M1, whereas m2/M2 and m3/M3 are reduced (Kryštufek and Vohralík, 2009). In
444 Iran we also find *Mesocricetus raddei*, which presents a similar morphology of
445 the teeth to *Mesocricetus brandti*, but compared with the NHM reference
446 collection of the latter, *Mesocricetus raddei* is bigger

447 **Habitat and distribution:** *Mesocricetus brandti* has the largest distributional
448 area of the species belonging to the genus *Mesocricetus*, ranging from Anatolia,
449 Transcaucasia (Armenia, Georgia and Azerbaijan) and southeast Dagestan to
450 northwest Iran (Qazvin in the east, Lorestan in the south; Lay, 1967). This
451 species is found at altitudes from sea level up to 2,600 m. However, the primary
452 range is from 1,000-2,200 m. *Mesocricetus brandti* is found in arid and semi-
453 arid steppe habitats in lowlands and in mountainous areas (Kryštufek et al.,
454 2015; Kryštufek and Vohralík, 2009; Neumann et al., 2017).

455

456

Family Muridae Illiger, 1811

457

Subfamily Gerbillinae Gray, 1825

458

Genus *Meriones*, Illiger 1811

459

***Meriones cf. persicus* Blanford, 1875**

460

461

462

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464

465

Material: 157 isolated teeth. **Layer 1-3:** three isolated teeth; two left upper
M1 and one right lower m1. **Layer 4:** 65 isolated teeth; 21 m2; four m3; 17 left
lower m1; eight right upper M1, five left upper M1; 10 right lower m1. **Layer 5:**
88 isolated teeth; eight m3; 21 m2; 18 left lower m1, 10 left upper M1, 16 right
upper M1 and 15 right lower m1.

466

467

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472

Description and discussion: the genus *Meriones* is one of the most diverse
among the tribe Gerbillini in the Palaearctic region, particularly in arid regions of
Asia (Darvish et al., 2011; Denys, 2017). The *Meriones* species reported in Iran
are: *Meriones crassus*, *Meriones hurrianae*, *Meriones lybicus*, *Meriones*
meridianus, *Meriones persicus*, *Meriones tristrami*, *Meriones vinogradovi* and
Meriones zarudnyi (Darvish, 2011; Dianat et al., 2017; Kryštufek and Vohralík,
2009; Souttou and Denys, 2012).

473

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481

The material from Kaldar Cave attributed to the genus *Meriones* displays the
typical morphology of this group, including semi-hypsodont molars with
prismatic enamel triangles linked by a longitudinal crest and with no trace of
cusps. In our sample, we identify first upper molars (M1) with three roots, which
is characteristic of *Meriones persicus* and *Meriones tristrami*. Unfortunately, the
dental morphology of *Meriones persicus* and *Meriones tristrami* is very similar;
there are three roots in m1, the second molars have two transverse plates and
two roots, whereas the third molars are simple and rounded with a single root
(Coşkun, 2016; Kryštufek and Vohralík, 2009).

482

483

484

485

Given its current distribution and the morphological traits observed in the
reference collection from Iran, Azerbaijan and Pakistan housed in the Natural
History Museum of London, we provisionally attribute our specimens to
Meriones cf. persicus, especially in the light of the number of roots and the

486 morphology of M1 and m1, pending a revision of the Middle Eastern species of
487 the genus.

488 **Habitat and distribution:** the genus *Meriones* is distributed across North
489 Africa, Central Asia, Transcaucasia, Turkey and Pakistan (Darvish et al., 2014;
490 Stoetzel et al., 2017). It lives mostly in dry steppes of short or tall grass, on
491 open hillside, among rocky outcrops in desolate steppes, or in open dry
492 meadows. The distribution of *Meriones persicus* ranges from the Caucasus
493 (including the southeastern foothills of the Lesser Caucasus and the Talysh
494 Plateau in Azerbaijan) in the west, through northeastern Iraq and Iran to
495 Turkmenistan, Afghanistan (Habibi, 2004) and Pakistan, where it is widely
496 distributed. It generally occurs in arid, rocky or mountainous regions (Kryštufek
497 and Vohralík, 2009; Molur & Sozen, 2016).

498

499

Family Dipodidae Fischer, 1817

500

Genus *Allactaga* Cuvier, 1837

501

***Allactaga* sp.**

502

503 **Material:** two isolated teeth. **Layer 4:** one indet. **Layer 5:** one right lower m3.

504 **Description and discussion:** this rodent group is poorly known in the
505 Middle East (Shenbrot, 2009) and sometimes there is a size overlap between
506 the species. In our sample, we only found two items attributed to *Allactaga* sp.
507 on the basis of the complete lower m3, which presents a morphology with two
508 inner folds and one outer fold; the other tooth is broken, which prevents any
509 precise identification.

510 **Habitat and distribution:** in Iran four species are currently present:
511 *Allactaga elater*, *Allactaga euphratica*, *Allactaga firouzi* and *Allactaga hotsoni*
512 (Karami et al., 2008). The different species are morphologically very close and
513 remain poorly studied. They are mainly found in steppe vegetation and semi-
514 desert areas (Shenbrot, 2009).

515

516

Family Gliridae Thomas, 1897

517

Genus *Myomimus* Ognev, 1924

518

***Myomimus* sp.**

519

520 **Material:** five isolated teeth, **Layer 5:** five isolated teeth, one right lower m1,
521 three right lower m2 and one left lower m2.

522 **Description and discussion:** the genus *Myomimus* is present in Iran with
523 two species, *Myomimus personatus* and *Myomimus setzeri* (Firouz, 2005;
524 Gerrie & Kennerley, 2017; Karami et al., 2008; Kennerley & Kryštufek, 2019).
525 Regarding the remains found at Kaldar, the m1 is of a trapezium-like shape,
526 and its anterior part tends to be narrower than the posterior part. The m1 has
527 three roots, two in the anterior part and one in the posterior part. The m2 is
528 subrectangular, and its occlusal pattern is simpler than in the m1. There are
529 three roots in total, two in the anterior part and one in the posterior part (Kaya

530 and Kaymakçı, 2018; Kryštufek and Vohralík, 2009). The two species are
531 similar to one another and poorly studied. Consequently, we were unable to
532 identify the Kaldar material precisely. Moreover, the reference collection of the
533 Natural History Museum of London only houses *Myomimus personatus*
534 specimens, which could therefore not be compared with *Myomimus setzeri*.

535 **Habitat and distribution:** these species are not well known as regards their
536 distribution. They are mainly found in desert areas (Gerrie & Kennerley, 2017;
537 Kennerley & Kryštufek, 2019).

538

539

Family Muridae Illiger , 1811
Genus Apodemus Kaup, 1829
Apodemus sp.

541

542

543 **Material:** 13 isolated teeth. **Layer 1-3:** two isolated teeth; one left lower m1
544 and one left lower m2; **Layer 4:** six isolated teeth; three left lower m1, two right
545 lower m1 and one left upper M1. **Layer 5:** five isolated teeth; two left lower m1,
546 one right lower m1, one right upper M1 and one m2.

547 **Description and discussion:** the first lower molar (m1) can be seen to
548 present a low occlusal surface with six main cusps. The anterolabial and
549 posterolabial cusps of m1 converge in an X-shape. The posterior cusp of m1 is
550 low, rounded and well developed, with two or three secondary cusps in the
551 labial part, and a mesial tubercle. We attribute the remains found in Kaldar
552 Cave to *Apodemus* sp. because they present the traits characteristic of the
553 genus *Apodemus* (Amori et al., 2016; Bogicevic et al., 2011; Knitlová and
554 Horáček, 2017; Kryštufek and Vohralík, 2009; López-García, 2008).

555 **Habitat and distribution:** five *Apodemus* species are currently recognized
556 in Iran: *A. hyrcanicus*, *A. flavicollis*, *A. witherbyi*, *A. avicennicus* and *A.*
557 *uralensis*, all belonging to the *Sylvaemus* sub-genus (Jangjoo et al., 2011).
558 *Apodemus* has a large distribution range extending from Great Britain across
559 much of continental Europe to the Urals. It also extends east through Turkey to
560 western Armenia, the Zagros Mountains of Iran and south to Syria, Lebanon
561 and Israel. It inhabits a variety of woodland habitats (Amori et al., 2016).

562

563

Genus Mus Linnaeus, 1758
Mus cf. musculus Linnaeus, 1758

564

565

566 **Material:** three isolated teeth. **Layer 4:** one isolated tooth; one left upper M1.
567 **Layer 5:** two isolated teeth; one indeterminate and one left lower m1.

568 **Description and discussion:** as in other murines, the first upper molar (M1)
569 has three rows of tubercles: the first (t1, t2, t3) and second (t4, t5 and t6) groups
570 situated in the anterior part have three tubercles, and the third group (t7 and t9)
571 has two tubercles (Darviche et al., 2006). In Iran (Kryštufek and Vohralík, 2009)
572 both *Mus musculus domesticus* and *Mus macedonicus* may be found.

573 The specimens from Kaldar Cave fit well with *M. musculus* as regards the upper
574 M1 morphology: the lingual row of cusps (t1 and t4) is shifted posteriorly; cusp
575 t7 is reduced to an enamel ridge; distal cusps t8 and t9 leave no space for a
576 posterior cingulum or posterolabial cusp t12 (Siahsarvie and Darvish, 2008).
577 The dental ends of the mesial and central cusps on m1 fuse early; the
578 mesiolabial cusp is small. Upper molars normally have three roots each, one
579 lingual and two labial, whereas lower molars are two-rooted (one anterior and
580 one posterior) (Kryštufek and Vohralík, 2009). Despite these observations,
581 bearing in mind the high intra-specific morphological variability, the low quantity
582 of material and the bad state of preservation of some teeth (Fig. 2.13), we only
583 attribute the Kaldar material to *M. cf. musculus*.

584 **Habitat and distribution:** *Mus musculus* is a commensal species, well
585 distributed throughout the world: it is present over all the continents except
586 Antarctica. It is found in a wide range of habitats but tends not to be found in
587 forest and deserts. *Mus musculus* is ecologically highly opportunistic but a weak
588 competitor; it can cope with aridity and can also expand into the desert
589 (Kryštufek and Vohralík, 2009). It is also found in arid habitats along the border
590 with Syria and Iraq, in desert landscapes and near the Euphrates River
591 (Kryštufek & Vohralík, 2009; Denys, 2017).

592

593 **4.2. Past landscape and climate at Kaldar Cave**

594

595 The small-mammal assemblages from Layers 4 and 5 of Kaldar Cave are
596 dominated by the genus *Microtus* (60 individuals in Layer 4 and 79 in Layer 5),
597 followed by *Ellobius* in Layer 4 (17 individuals) and *Meriones cf. persicus* (17
598 individuals in Layer 4 and 18 in Layer 5). These species indicate that the
599 environment in the area was mainly composed of open dry and steppe areas,
600 although we also found *Apodemus* sp. and *Mus cf. musculus*, which are related
601 rather to a dense vegetation cover (including trees/bush). All the species
602 identified at Kaldar Cave still occur in the area today.

603 Layers 1-3 do not yield enough material to draw palaeoclimatic inferences
604 (MNI < 30). For Layers 4 and 5, the *bioclimatic model* shows similar results
605 (Table 6). It should be pointed out that some species are not included in the *BM*
606 data matrix, such as *Myomimus* (present in Layer 4) and *Microtus guentheri*
607 (Layer 5), because their values did not appear in the *BM* and could not be used
608 in the analysis. The *BM* based on the small mammals from Kaldar Cave
609 suggests lower temperatures and lower precipitation than at present in both
610 Layers 4 and 5 (Table 6). The MAT is around 6°C lower, and there is a higher
611 temperature amplitude between maximum and minimum mean temperatures.
612 This indicates that Layers 4 and 5 of Kaldar Cave were deposited during a
613 colder period, which is not in agreement with the preliminary interpretations of
614 Bazgir et al. (2017) suggesting a temperate “interstadial”.

615 The climate in Khorramabad nowadays is warm an temperate. The average
616 mean annual temperature is 16.90°C, the maximum mean temperature occurs

617 in July with 29.60°C and the minimum mean temperature is in January with 5°C
618 (<https://en.climate-data.org/asia/iran/lorestan/khorramabad-764550/>). This
619 contrast with the climatic conditions inferred from the *BM* on Kaldar Cave with
620 lower temperatures and drier conditions.

621 Applying the *habitat weighting method*, our data show a palaeoenvironment
622 mainly composed of steppes in both levels. In Layer 4, grasslands are also well
623 represented, notably through the presence of *Microtus guentheri*. In Layer 5,
624 deserts are the second most represented habitat, thanks to the considerable
625 presence of *Myomimus* sp. The proportion of rocky areas is also significant,
626 indicated by the presence of *Chionomys nivalis* and *Meriones* cf. *persicus*
627 (Figure 3).

628 There thus seems to be no major palaeoenvironmental or palaeoclimatic
629 change that can explain the cultural shift between Layer 5 (Middle Palaeolithic)
630 and 4 (Upper Palaeolithic). However, Layer 5 appears slightly colder and drier
631 than Layer 4, with a higher proportion of desert habitats.

632 We can compare these results with previous studies carried out in Kaldar
633 Cave using other palaeoenvironmental proxies. Charcoal analyses (Allué et al.,
634 2018; Bazgir et al., 2017) indicate that there were active water sources or flows,
635 with specific plant communities characteristic of open forest growing in cool and
636 dry conditions (Allué et al., 2018). The presence of forested areas is also
637 supported by the large mammals, with the presence of *Sus scrofa*, *Capreolus*
638 sp. and *Cervus elaphus* (Bazgir et al., 2017). Several amphibian and squamate
639 species have also been found (Bazgir et al., 2017): a toad (*Bufo* sp.), an agamid
640 lizard (Agamidae indet.), a gecko (Gekkonidae indet.), a skink (Scincidae
641 indet.), a lacertid (Lacertidae indet.), a glass lizard (*Pseudopus* sp.), a sand boa
642 (*Eryx* sp.), possibly six types of colubrine snakes (Colubrinae indet.), a cobra
643 (Elapidae indet.), and a viper (Viperidae indet.). Most of these taxa (Agamidae,
644 *Eryx* and Elapidae) live in savannahs, steppes and deserts, with a way of life
645 always linked with warm arid areas in rocky or sandy environments. *Pseudopus*
646 lives in dry and bushy environments, sometimes in open woodlands, but avoids
647 dense forest areas (Bazgir et al., 2017).

648 Our results based on small mammals, combined with previous studies of
649 other proxies, thus suggest a mosaic landscape alternating between dry-steppe
650 areas and wooded patches. Nowadays, the vegetation in the Zagros is a
651 montane grassland-woodland characterised by steppe of grassland and herbs
652 with occasional to fairly common trees. The principal local trees are deciduous
653 oaks and junipers, with maples, walnut, almond and ash at middle elevations,
654 and *Pistacia* and *Olea* in drier areas (Fiacconi and Hunt, 2015). Thus, the
655 landscape during the Middle and Upper Pleistocene at Kaldar Cave was similar
656 to that today, despite a colder climate.

657

658 **4.3. Kaldar Cave in the Middle Eastern context**

659

660 Kaldar Cave is situated in the Khorramabad Valley, which played a
661 significant role in human adaptation and dispersal during the Quaternary. Some
662 other caves close to Kaldar, such as Gilvaran, Ghamari and Gar Arjene rock
663 shelter, have yielded Mousterian and Aurignacian occupations (Bazgir et al.,
664 2014). Moreover, surveys in Kermanshah have also documented Middle and
665 Upper Palaeolithic sites (Heydari-Guran and Ghasidian, 2020). None of them
666 has given rise to small-mammal studies. However, Gilvaran Cave has been
667 studied from a palaeoenvironmental point of view through charcoal analyses
668 (Allué et al., 2018), showing a similar pattern to Kaldar, where *Prunus* is also
669 present and indicates the presence of open forest areas. Similarly, other proxies
670 such as pollens and charcoals have been analysed at Shanidar (Campana and
671 Crabtree, 2019; Fiacconi and Hunt, 2015) and Gilvaran (Allué et al., 2018),
672 indicating similar environmental conditions to Kaldar.

673 Other studies based on small mammals from the Middle East have been
674 performed in Qesem Cave (Maul et al., 2015a; Smith et al., 2015), Hummal
675 (Maul et al., 2015b), Azokh Cave (Fernández-Jalvo, 2016), Aghitu-3 Cave
676 (Frahm, 2019; Kandel et al., 2017; Nishiaki and Akazawa, 2018), Neshar Ramla
677 (Weissbrod and Zaidner, 2014), Amud Cave (Belmaker and Hovers, 2011),
678 Dzudzuana Cave (Belmaker et al., 2016) and Karain Cave (Demirel et al.,
679 2011). These studies did not use *HW* or the *BM* for their palaeoclimatic and
680 palaeoenvironmental reconstructions, and the sites are not always
681 contemporary with Kaldar, except Amud Cave (Belmaker and Hovers, 2011),
682 Aghitu-3 (Djamali et al., 2008; Kandel et al., 2017) and Dzudzuana Cave
683 (Belmaker et al., 2016) (Table 7).

684 Most of these studies highlight problems in identifying Middle Eastern rodent
685 species, as faced in the present work. There are some studies of present-day
686 taxonomy and systematics in Iran, Turkey, Israel, Jordan, Lebanon and Syria
687 (Abi-said et al., 2014; Darvish et al., 2000; Haddadian Shad et al., 2014; Kopij
688 and Liven-schulman, 2013; Obuch and Khaleghizadeh, 2012; Shehab et al.,
689 2013), but these are mostly based on skull morphology and thus not applicable
690 in archaeological or palaeontological contexts where the remains are broken.
691 Very few studies provide descriptions of molars with comparative elements,
692 allowing for the correct identification of fossil specimens. In this context,
693 comparison with modern specimens from museum collections of genetically
694 typed specimens is crucial to establish a correct taxonomic reference.

695 Palaeoenvironmental inferences have been drawn on the basis of small-
696 mammal studies, as well as palynological and anthracological analyses. During
697 the Upper Pleistocene, small-mammal compositions differ from one site to
698 another (Belmaker et al., 2016; Kandel et al., 2017) (Table 8), probably because
699 the sites are not exactly contemporaneous and are likely to belong to different
700 eco-regions. It is noteworthy that the genera *Microtus*, *Chionomys*, *Cricetulus*,
701 *Mesocricetus*, *Ellobius* and *Allactaga* are represented in all the sites, allowing
702 us to reconstruct the species communities of this region. Kaldar is the most
703 diverse site in terms of small-mammal species.

704 We applied the *habitat weighting method* at other Middle Eastern sites where
705 small-mammal studies have been performed, namely Aghitu-3 and Dzudzuana
706 Cave, but these are located in other eco-regions (Figure 1a). Aghitu-3 is located
707 in Armenia, at an elevation of 1601 m a.s.l. and the current climate is
708 continental with considerable seasonality in temperature. Dzudzuana Cave is
709 located in Georgia, at an elevation of 560 m a.s.l., and the current climate is
710 warm and temperate. The estimations obtained with the *habitat weighting*
711 *method* (Figure 4) show similar environmental conditions between Kaldar Cave
712 and Aghitu-3, where the landscape is dominated by steppe (indicated by the
713 presence of *Ellobius lutescens*, *Mesocricetus brandti*, *Cricetulus migratorius*
714 and *Allactaga*), with a relatively high percentage of grassland and forests.

715 To ascertain the palaeoclimatic conditions, we calculated and directly
716 compared our results with Aghitu-3 and Dzudzuana Cave using the *bioclimatic*
717 *method* (Table 9). The results obtained for Aghitu-3 show higher temperatures
718 and precipitation than at present, whereas Dzudzuana Cave shows the same
719 pattern as Kaldar Cave, with drier conditions and lower temperatures than
720 today. For Amud Cave, it was not possible to calculate *HW* and *BM*, but data
721 from the literature (Belmaker and Hovers, 2011) indicate a grassland
722 environment similar to the one that we reconstructed at Dzudzuana Cave.

723

724 **5. Conclusions**

725

726 This work represents the first study of a Late Pleistocene rodent assemblage
727 from the Middle East with palaeoenvironmental and palaeoclimatic
728 reconstructions, using and adapting the *habitat weighting method* and the
729 *bioclimatic model* to this area. We identified 1112 rodent remains,
730 corresponding to a minimum number of 264 individuals. The rodent assemblage
731 is composed of 13 taxa: six arvicoline (*Microtus socialis*, *Microtus irani*, *Microtus*
732 *guentheri*, *Chionomys nivalis*, *Ellobius fuscocapillus* and *Ellobius lutescens*),
733 two cricetine (*Cricetulus migratorius* and *Mesocricetus brandti*), one glirid
734 (*Myomimus* sp.), one gerbilline (*Meriones* cf. *persicus*), one dipodid (*Allactaga*
735 sp.) and two murine species (*Apodemus* sp. and *Mus* cf. *musculus*).
736 Augmenting the preliminary analysis of the material (Bazgir et al., 2017), new
737 species were identified, such as *Microtus socialis*, *Microtus irani*, *Microtus*
738 *guentheri*, *Ellobius fuscocapillus* and *Meriones* cf. *persicus*. We also
739 reconsidered the identification of *Ellobius talpinus*, *Calomyscus* sp. and
740 *Dryomys* cf. *nitedula*, based on modern specimens from museum collections
741 and measurements; this is why they do not appear in the new faunal list of
742 Kaldar Cave.

743 Given the scarcity of studies in this biogeographical region, we encountered
744 some difficulties in the identification of species, which could slightly affect the
745 palaeoenvironmental and palaeoclimatic interpretations. In order to counter
746 these potential errors, further studies of small mammals in this region are

747 necessary, as well as research on discriminant characters in molars, using
748 reference collections including genetically typed specimens.

749 The palaeoecological analysis of the rodents from Kaldar Cave revealed
750 lower temperatures and lower precipitation than present-day conditions, and an
751 environment mainly composed of dry steppes with patches of forested areas.
752 The results obtained are supported by palynological, anthracological and large-
753 mammal studies. At a broader geographical scale, colder conditions were also
754 inferred at Dzudzuana Cave. The genera *Microtus*, *Chionomys*, *Cricetulus*,
755 *Mesocricetus*, *Ellobius* and *Allactaga* are present at all the Middle East sites
756 (Aghitu-3, Dzudzuana and Amud) during the Upper Pleistocene, that have
757 yielded small mammals, allowing us to reconstruct the rodent communities of
758 the area.

759 Considering all the results from Kaldar Cave and other contemporaneous
760 sites, we can conclude that both Neanderthals and AMH lived in dry steppes
761 with patches of forested areas, without major environmental changes occurring
762 between the Middle and the Late Palaeolithic. Climatic shifts during the MIS 4-3
763 transition were of a magnitude that did not have a major impact on small
764 mammals in the region, suggesting that climate change may not have had the
765 hypothesized effect on the Neanderthal extinction in the Levant.

766

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792

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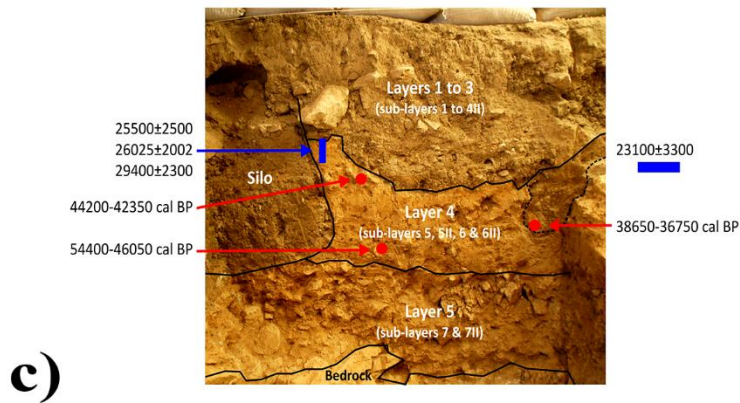
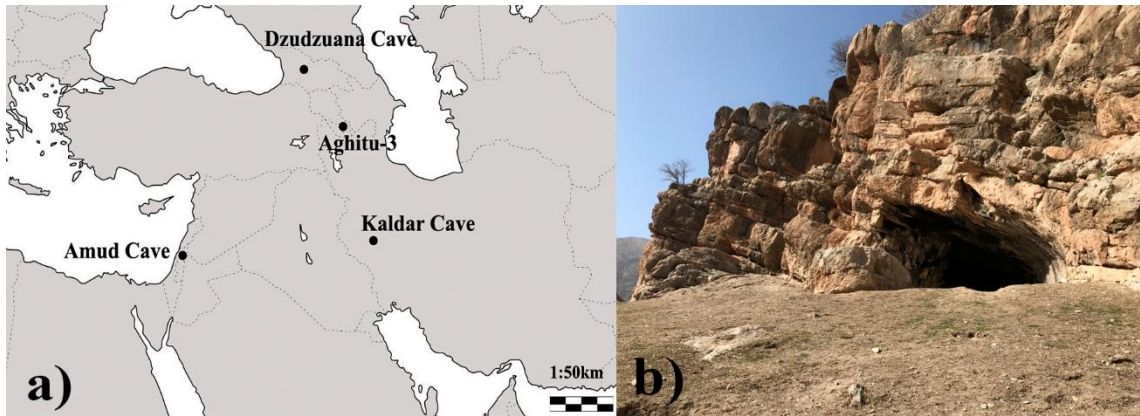


Figure 1: a) Locations of the Late Pleistocene sites with rodent studies in the Middle East, including Kaldar Cave. b) General view of the entrance to Kaldar Cave. c) Stratigraphy of the eastern section of Kaldar Cave, including the location and results of the dated samples, from A. Ollé and B. Bazgir (Bazgir et al., 2017).

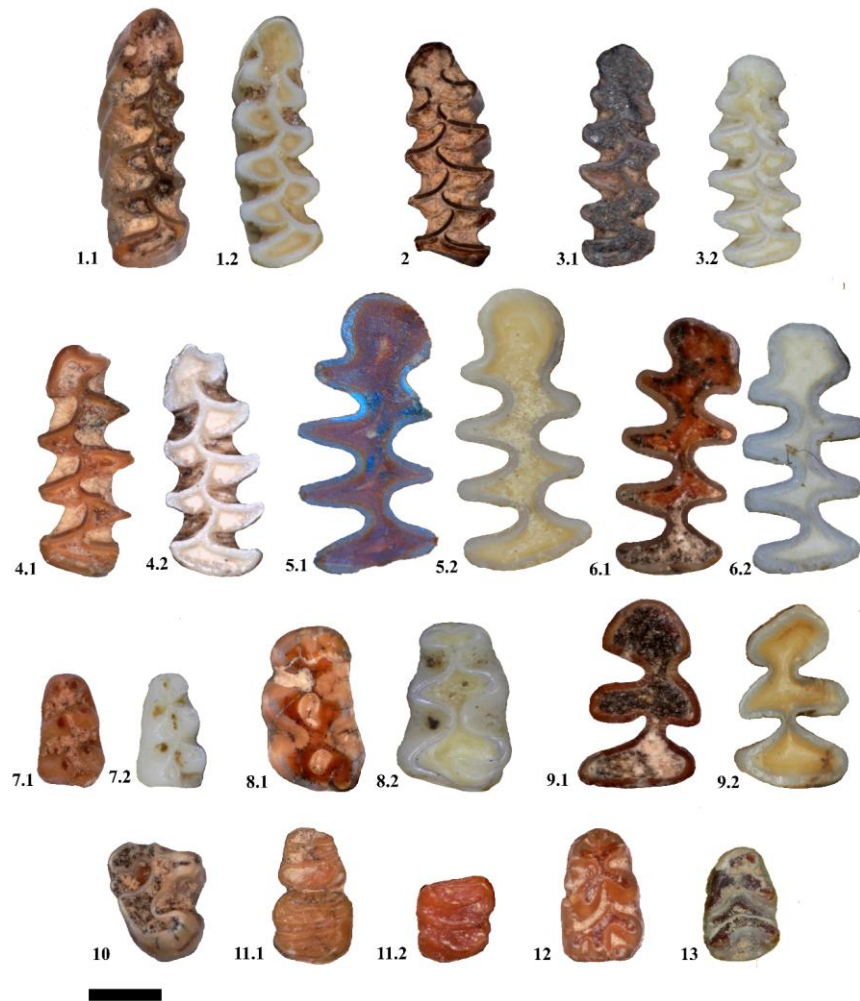


Figure 2: Some rodent species identified at Kaldar Cave in comparison with equivalent (analogue) modern specimens from the NHM of London. **1) *Microtus irani***: 1.1-Kaldar Cave, 2014, Layer 5 (sub-layer 7II), E7, 150-156, right lower m1, number 447. 1.2-modern, NHM205207, Iran (Shiraz), right lower m1; **2) *Microtus guentheri***: 2.1-Kaldar Cave, 2014, Layers 1-3 (sub-layer 4II), F6, 97-107, left lower m1, number 17; **3) *Microtus socialis***: 3.1-Kaldar Cave, 2014, Layer 4 (sub-layer 5II), F7, 115-118, right lower m1, number 106. 3.2-modern, NHM631799, Turkey (Amasya); **4) *Chionomys nivalis***: 4.1-Kaldar Cave, 2014, Layer 4 (sub-layer 5), E6, 94-104, left lower m1, number 542. 4.2-modern, NHM71820, Syria, left lower m1; **5) *Ellobius fuscocapillus***: 5.1-Kaldar Cave, 2014, Layer 4 (sub-layer 5II), E6, 125-130, right lower m1, number 157. 5.2-modern, NHM86101513, Afghanistan, right lower m1; **6) *Ellobius lutescens***: 6.1-Kaldar Cave, 2014, Layer 5 (sub-layer 7II), F6, 130-140, right lower m1, number 319. 6.2-NMH916416, Turkey, right lower m1; **7) *Cricetulus migratorius***: 7.1-Kaldar Cave, 2014, Layer 4 (sub-layer 5II), E6, 135-140, left lower m1, number 259. 7.2-modern, NHM773029, Iran, right lower m1; **8) *Mesocricetus brandti***: 8.1-Kaldar Cave, 2014, Layer 5 (sub-layer 7II), F6, 135-145, left upper M1, number 549. 8.2- modern, NHM193461226, Caucasus, left upper M1; **9) *Meriones cf. persicus***: 9.1-Kaldar Cave, 2014, Layer 5 (sub-layer 7II), F6, 156-166, left lower m1, number 551. 9.2-modern, NHM510434, Iran, left lower m1; **10) *Allactaga* sp.**: 10.1-Kaldar Cave, 2014, Layer 5 (sub-layer 7II), E7, 141-147, right lower m3, number 203; **11) *Myomimus* sp.**: 11.1- Kaldar Cave, 2014, Layer 5 (sub-layer 7II), E7, 141-147, left lower m1 and m2. 11.2-modern, *Myomimus personatus*, NHM67623, Turkey, left lower mandible; **12) *Apodemus* sp.**: 12.1-Kaldar Cave, 2014, Layer 4 (sub-layer 5), E6, 94-104, right m1 and m2, number 547; **13) *Mus cf. musculus***: 13.1-Kaldar Cave, 2014, Layer 5 (sub-layer 7II), 166-174, left lower m1, number 495. Scale 1 mm.

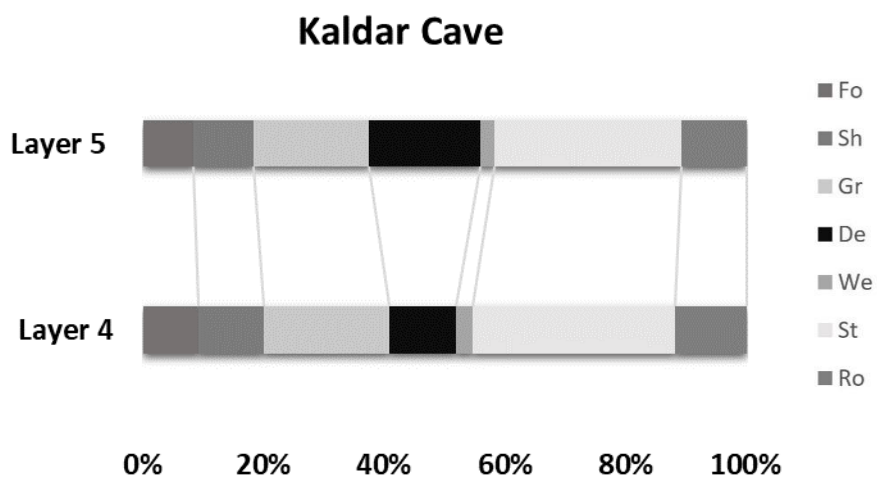


Figure 3: Results of the *habitat weighting method* for Kaldar Cave (Layer 4 and Layer 5). Forest (Fo), Shrubland (Sh), Grassland (Gr), Desert (De), Wetland (We), Steppe (St) and Rocky (Ro).

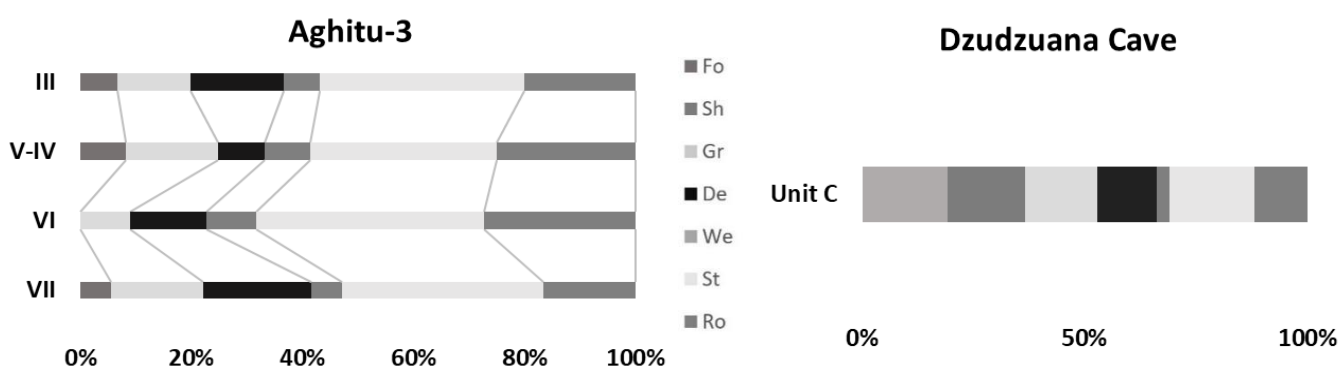


Figure 4: Results of the *habitat weighting method* for Aghitu-3 and Dzudzuana Cave. Forest (Fo), Shrubland (Sh), Grassland (Gr), Desert (De), Wetland (We), Steppe (St) and Rocky (Ro).

Species	Fo	Sh	Gr	De	We	St	Ro
<i>Ellobius lutescens</i>			0.33	0.33		0.33	
<i>Ellobius fuscocapillus</i>						1	
<i>Microtus irani</i>			1				
<i>Microtus guentheri</i>			1				
<i>Microtus socialis</i>		0.5				0.5	
<i>Chionomys nivalis</i>							1
<i>Cricetulus migratorius</i>			0.33	0.33		0.33	
<i>Mesocricetus brandti</i>						1	
<i>Meriones persicus</i>		0.33	0.33				0.33
<i>Allactaga sp.</i>				0.5		0.5	
<i>Apodemus sp.</i>	1						
<i>Mus musculus</i>		0.33	0.33		0.33		
<i>Myomimus sp.</i>				1			

Table 1: scores attributed to each rodent species found at Kaldar Cave according to its ecological requirements, used for the *habitat weighting method*: Forest (Fo), Shrubland (Sh), Grassland (Gr), Desert (De), Wetland (We), Steppe (St) and Rocky (Ro).

Species	I	II	II/III	III	IV	V	VI	VII	VIII	IX
<i>Ellobius lutescens</i>								1		
<i>Ellobius fuscocapillus</i>				0.33	0.33			0.33		
<i>Microtus irani</i>					1					
<i>Microtus socialis</i>					0.5			0.5		
<i>Chionomys nivalis</i>					0.25		0.25		0.25	0.25
<i>Cricetulus migratorius</i>					0.33		0.33	0.33		
<i>Mesocricetus brandti</i>					1					
<i>Meriones persicus</i>				0.5	0.5					
<i>Allactaga sp.</i>				0.5				0.5		
<i>Apodemus sp.</i>							1			
<i>Mus musculus</i>	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	

Table 2: scores attributed to each rodent species found at Kaldar Cave for the bioclimatic model (in accordance with Hernández-Fernández, 2001; Hernández-Fernández et al., 2007). See text for the significance of the Roman numerals corresponding to the climatic groups.

Taxon	Layer 5			Layer 4			Layers 1-3		
	NISP	MNI	%	NISP	MNI	%	NISP	MNI	%
Indet.	3	-	-	11	-	-	-	-	-
<i>Microtus</i> spp.	292	51	52.33	258	31	48.31	4	3	20
<i>Microtus irani</i>	14	9	2.51	0	0	0.00	1	1	5
<i>Microtus guentheri</i>	0	0	0.00	16	9	3.00	1	1	5
<i>Microtus socialis</i>	35	20	6.27	36	20	6.74	3	3	15
<i>Chionomys nivalis</i>	6	3	1.08	17	12	3.18	2	1	10
<i>Ellobius</i> spp.	80	7	14.34	91	8	17.04	2	2	10
<i>Ellobius fuscocapillus</i>	5	4	0.90	5	3	0.94	1	1	5
<i>Ellobius lutescens</i>	10	6	1.79	10	7	1.87	-	-	-
<i>Cricetulus migratorius</i>	5	3	0.90	14	3	2.62	1	1	5
<i>Mesocricetus brandti</i>	7	4	1.25	3	1	0.56	0	0	0
<i>Meriones</i> cf. <i>persicus</i>	88	18	15.77	65	17	12.17	3	2	15
<i>Allactaga</i> sp.	1	1	0.18	1	1	0.19	0	0	0
<i>Myomimus</i> sp.	5	3	0.90	0	0	0.00	0	0	0
<i>Apodemus</i> sp.	5	2	0.90	6	3	1.12	2	1	10
<i>Mus</i> cf. <i>musculus</i>	2	1	0.36	1	1	0.19	0	0	0
Total	558	132	100.00	534	116	100.00	20	16	100.00

Table 3: Representation of the Kaldar Cave rodent species in terms of number of identified specimens (NISP), minimum number of individuals (MNI) and percentage of the NISP (%).

Species	NS	L (Length)		La (Width T4)		Li (Width T5)		Total Width	
		Mean	Min-Max	Mean	Min-Max	Mean	Min-max	Mean	Max-Min
Reference collection									
<i>Microtus irani</i>	4	3.06	2.98-3.23	0.42	0.40-0.44	0.64	0.62-0.67	1.06	1.03-1.08
<i>Microtus socialis</i>	69	2.78	2.29-3.34	0.42	0.32-0.51	0.6	0.44-0.73	1.02	0.78-1.19
<i>Microtus arvalis</i>	25	2.72	2.45-2.96	0.39	0.32-0.46	0.6	0.50-0.70	1	0.83-1.13
<i>Microtus guentheri</i>	70	2.58	2.2-3						
Kaldar Cave									
<i>Microtus guentheri</i>	17	2.52	2.18-3.01	0.35	0.27-0.43	0.54	0.40-0.68	0.90	0.70-1.10
<i>Microtus irani</i>	15	2.89	2.52-3.39	0.41	0.37-0.50	0.62	0.54-0.70	1.05	0.92-1.18
<i>Microtus socialis</i>	74	2.54	2.06-3.01	0.37	0.28-0.48	0.55	0.40-0.70	0.92	0.70-1.16

Table 4: Measurements of *Microtus* specimens (in mm): NS, number of specimens; L, length; La, T4 width; Li, T5 width.

		<i>Ellobius fuscocapillus</i>				<i>Ellobius lutescens</i>		<i>Ellobius talpinus</i>	
		Layer 5 NISP=5	Layer 4 NISP=5	Layer 1-3 NISP=1	NHM NISP=12	Layer 5 NISP=9	Layer 4 NISP=10	NHM NISP=14	NHM NISP=14
L	Min-Max	3.29-3.84	3.73-3.74	-	3.06-4.05	3.08-3.32	3.05-3.4	3.07-3.3	2.86-3.35
	Mean	3.45	3.74	-	3.53	3.28	3.29	3.21	3.12
W	Min-Max	1.32-1.51	1.40-1.54	-	1.3-1.59	1.20-1.45	1.13-1.48	1.11-1.52	1.09-1.72
	Mean	1.45	1.48	1.5	1.41	1.34	1.32	1.34	1.24

Table 5: Measurements of *Ellobius* specimens (in mm): L, total length; W, width. NHM: Natural History Museum of London. NISP: number of identified specimens.

	Layer 5	SD	Layer 4	SD	Current values
Mean annual temperature	10.90 °C	3.39	11.73°C	3.39	16.90 °C
Maximum mean temperature	23.45 °C	4.77	23.10°C	4.77	29.60 °C
Minimum mean temperature	-1.69 °C	4.66	0.25°C	4.66	5°C
Mean annual precipitation	258.68mm	533.24mm	104.08mm	533.24mm	488mm

Table 6: Bioclimatic model estimates for Kaldar Cave. SD, standard deviation. Current values obtained from: <https://en.climate-data.org/asia/iran/lorestan/khorramabad-764550/>.

Site/Author	Layer	Human culture	Chronology	Environmental conditions	Rodent
Amud Cave (Belmaker and Hovers, 2011)	B4	Neanderthals	68.5 ± 3.4ka	Grassland vegetation	<i>Microtus guentheri</i>
	B2-B1	Neanderthals	56.5 ± 3.5, 57.6 ± 3.7, respectively	Woodland	<i>Apodemus cf. mystacinus</i> and <i>Mus macedonicus</i>
Dzudzuana Cave (Belmaker et al., 2016)	Unit C	Modern human	27-24ka cal BP	Mild and humid	<i>Microtus</i> , <i>Ellobius</i> , <i>Arvicola</i> , <i>Apodemus</i> and <i>Allactaga</i> .
Aghitu-3 (Djamali et al., 2008; Kandel et al., 2017)	Level VII-III	Modern human	The oldest layer is VII with a chronology between 39-36,000 cal BP and the most recent is layer III, between 29-24,000 cal BP	This sequence documents that the climate becomes colder	<i>Microtus</i> spp., <i>Chionomys</i> sp., <i>Arvicola amphibius</i> and <i>Ellobius lutescens</i>

Table 7: Comparison between Middle Eastern sites with small-mammal studies

Taxon	Kaldar Cave			Aghitu-3			Dzudzuana	
	Layers 1-3	Layer 4	Layer 5	VII	VI	V-IV	III	Unit C
<i>Microtus</i> spp.	X	X	X	X	X	X	X	
<i>Microtus</i> cf. <i>arvalis</i>								X
<i>Microtus irani</i>	X		X					
<i>Microtus guentheri</i>	X	X						
<i>Microtus socialis</i>	X	X	X					
<i>Chionomys nivalis</i>	-	X	X	X	X	X	X	X
<i>Clethrionomys glareolus</i>								X
<i>Ellobius</i> spp.	X	X	X					
<i>Ellobius fuscocapillus</i>	X	X	X					
<i>Ellobius lutescens</i>	-	X	X	X				X
<i>Cricetus cricetus</i>								X
<i>Cricetulus migratorius</i>	X	X	X	X		X	X	X
<i>Mesocricetus brandti</i>		X	X	X	X	X	X	X
<i>Meriones</i> cf. <i>persicus</i>	X	X	X					
<i>Allactaga</i> sp.		X	X	X	X		X	X
<i>Myomimus</i> sp.			X					
<i>Apodemus</i> sp.	X	X	X					X
<i>Mus musculus</i>		X	X					X
<i>Arvicola amphibius</i>				X	X	X	X	X

Table 8: comparison of the small-mammal lists from several Upper Palaeolithic sites in the Middle East.

	Aghitu-3						Dzudzuana Cave		
	VII	VI	V-IV	III	SD	Current Values	Unit C	SD	Current Values
Mean annual Temperature	15.46 °C	19.44 °C	19.21 °C	17.87 °C	3.386	8.5 °C	5.09 °C	3.39	9.7 °C
Maximum mean temperature	23.59 °C	24.44 °C	24.09 °C	24 °C	4.772	20.2 °C	18.55 °C	4.77	20.3 °C
Minimum mean temperature	7.31 °C	14.67 °C	14.72 °C	11.96 °C	4.656	-3.8 °C	-8.26 °C	4.66	-1.6 °C
Mean annual precipitation	1169.04 mm	1729.48 mm	1825.99 mm	1484.60 mm	533.236	532 °C	194.98 mm	533.24	868 mm

Table 9: Estimates using the *bioclimatic method* for Aghitu-3 and Dzudzuana Cave. SD, standard deviation. Current values obtained from Kandel et al. (2017) for Aghitu-3 and <https://es.climate-data.org/asia/georgia/imereti/jria-414325/?amp=true> for Dzudzuana Cave.

