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

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ABSTRACT

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

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

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

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

The results obtained with the rodent assemblages show that there is no major palaeoenvironmental or palaeoclimatic change that would explain the cultural shift between Layer 5 (Middle Palaeolithic) and Layer 4 (Upper Palaeolithic).

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1. Introduction

Small vertebrates are recognized to be good palaeoecological indicators due to their rapid evolution, the limited geographic range of a species and unique niche requirements, as well as their frequent preservation in archaeological and palaeontological sites.

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They might be excellent indicators of palaeovegetation type and provide a high-resolution proxy for palaeoenvironmental changes (e.g. Belmaker and Hovers, 2011). Studies of small vertebrates from archaeological sites in the Middle East are still scarce (Belmaker and Hovers, 2011; Belmaker et al., 2016; Demirel et al., 2011; Fernández-Jalvo, 2016a; Kandel et al., 2017; Maul et al., 2015a, 2015b; Smith et al., 2016; Weissbrod and Zaidner, 2014), and they mainly propose preliminary lists of taxa. On the other hand, some studies of extant owl pellet assemblages have been performed in the Middle East (Abi-said et al., 2014; Darvish et al., 2000; Haddadian Shad et al., 2014; Kopij and Liven-schulman, 2013; Obuch and Khaleghizadeh, 2012; Rey-Rodríguez et al., 2019; Shehab et al., 2013), providing taxonomic and some taphonomic reference data in Iran, Lebanon, Israel, Turkey and Syria.

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

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

2. Kaldar Cave

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

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

Layer 4 (including sub-layers 5, 5II, 6 and 6II) consists of a silty but compact dark-brown sediment with cultural remains attributed to the Upper and early Upper Palaeolithic. In the uppermost parts of this layer, two fireplaces made of clay were recovered and dated through thermoluminescence, yielding ages that ranged from 23,100 ± 3300 to 29,400 ± 2300 BP (Bazgir et al., 2017). The dates obtained show that these fireplaces were made or re-used from existing older sediment from the upper part of this layer in the later stages of the Upper Palaeolithic. AMS radiocarbon dates of 38,650–36,750 cal BP, 44,200–42,350 cal BP, and 54,400–46,050 cal BP have been obtained from charcoal material located below this layer (Bazgir et al., 2017; Becerra-Valdivia et al., 2017).

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

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

3. Material and methods

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

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

3.1. Taxonomy

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

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

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

3.2. Taphonomy

A preliminary study was performed on the Kaldar Cave

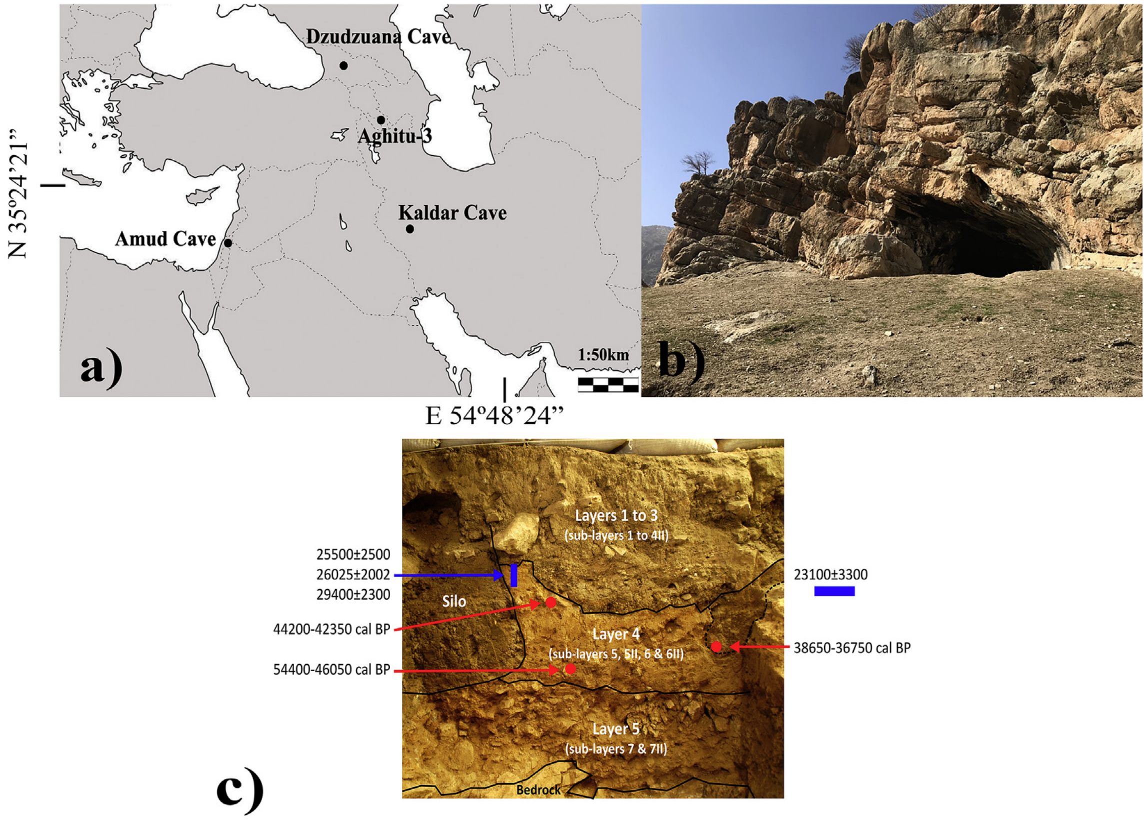

Fig. 1. a) Locations of the Late Pleistocene sites with rodent studies in the Middle East, including Kaldar Cave. b) General view of the entrance to Kaldar Cave. c) Stratigraphy of the eastern section of Kaldar Cave, including the location and results of the dated samples, from A. Ollé and B. Bazgir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

micromammal remains. This was based on the systematic descriptive method that examines the modifications of prey bones induced by predation, focusing on the degree of digestion observed in teeth during the identification (Andrews, 1990; Fernández-Jalvo et al., 2016a,b). This study showed a significant number of digested teeth (Bazgir et al., 2017), indicating that predation activity was the origin of at least part of the accumulation.

3.3. Palaeoenvironmental and palaeoclimatic reconstructions

3.3.1. Habitat weighting method

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

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

3.3.2. Bioclimatic model

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

The different climatic groups defined by Hernández Fernández (2001) and Hernández Fernández et al. (2007) are: I *equatorial*; II *tropical with summer rains*; II/III *transition tropical semiarid*; III *subtropical arid*; IV, *subtropical* with winter rains and summer droughts; V, *warm temperate* with not very severe winters but high humidity; VI, *typical temperate* with winters that are cold but not very long, but summers that are cool; VII, *arid-temperate* with large temperature contrasts between winter and summer; VIII, *cold-temperate* with cool summers and long cold winters (boreal) and IX, *artic* (Table 2).

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

4. Results and discussion

4.1. Taxonomic identifications

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

Order Rodentia Bowdich, 1821

Rodentia indet.

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

Family Cricetidae Fisher, 1817

Subfamily Arvicolinae Gray, 1821

Genus *Microtus* Schrank, 1798

***Microtus* spp.**

Material: 554 isolated teeth**. Layer 1–3:** four isolated teeth; three left lower m1 and one right lower m1. **Layer 4:** 258 isolated teeth; 81 m^2; 101 m^3, 13 right upper M1, 31 right lower m1; four left upper M1 and 28 left lower m1. **Layer 5:** 292 isolated teeth; 119 m^2; 53 m^3; nine left upper M1, 51 left lower m1; 10 right upper M1; 50 right lower m1.

***Microtus socialis* Pallas, 1773**

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

***Microtus irani* Thomas, 1921**

Material: 15 isolated teeth. **Layer 1–3:** one isolated tooth, one right lower m1. **Layer 5:** 14 isolated teeth; nine right lower m1 and five left lower m1.

***Microtus guentheri* Danford and Alston, 1880**

Material: 17 isolated teeth. **Layer 1–3:** one isolated tooth, one left lower m1. **Layer 4:** 16 isolated teeth; nine right lower m1 and seven left lower m1.

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; Firouz, 2005; Golenishchev et al., 2002, 2019).

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).

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

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).

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

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

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.

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

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 (%).

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

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).

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

Genus *Chionomys* Miller, 1908

***Chionomys nivalis* Martins, 1842**

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

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

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

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

Genus *Ellobius* Fischer, 1814

***Ellobius* spp.**

Material: 173 isolated teeth. **Layer 1–3:** two isolated teeth; two left lower m1. **Layer 4:** 91 isolated teeth; seven indet.; eight right lower m1; five left lower m1; 11 upper M1; 43 m^2; 17 m^3. **Layer 5:** 80 isolated teeth; seven left lower m1; three upper M1; 45 m^2; 25 m^3.

***Ellobius fuscocapillus* Blyth, 1843**

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

***Ellobius lutescens* Thomas, 1897**

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

Description and discussion: 204 isolated teeth show the typical traits of the genus *Ellobius* (Miller, 1896; Hinton, 1926; Kretzoi, 1969; Coşkun, 2016; Kryštufek and Shenbrot, 2016; Kryštufek and Vohralík, 2009; Rusin, 2017; Shenbrot et al., 2016; Tesakov, 2016). *Ellobius* molars are notably characterized by the presence of roots that are well visible in adults and old individuals, but not always apparent in young specimens (Coşkun, 2016). Moreover, *Ellobius* molars lack cement in the re-entrant angles. The *Ellobius* m1 is composed of the anterior cap (AC), five triangles (T) with three buccal and four lingual salient angles, and one posterior lobe (PL). Both M3 and m3 are reduced and smaller than the other molars, with three triangles on the labial side and two triangles on the lingual side. M1 has three inner and outer folds, and M2 and M3 have two inner and two outer re-entrant folds. The first and second upper molars have three triangles on the lingual and labial sides. However, the re-entrant angle between the first and the second triangles on the lingual side is more superficial (Gharkheloo and Kıvanç, 2003).

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

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

In our sample we identify as *Ellobius* spp. those m1s that are too broken or digested to distinguish, as well as all the m2, m3, M1, M2 and M3 because of the lack of discriminant characters. The identification of *Ellobius lutescens* and *Ellobius fuscocapillus* in the Kaldar

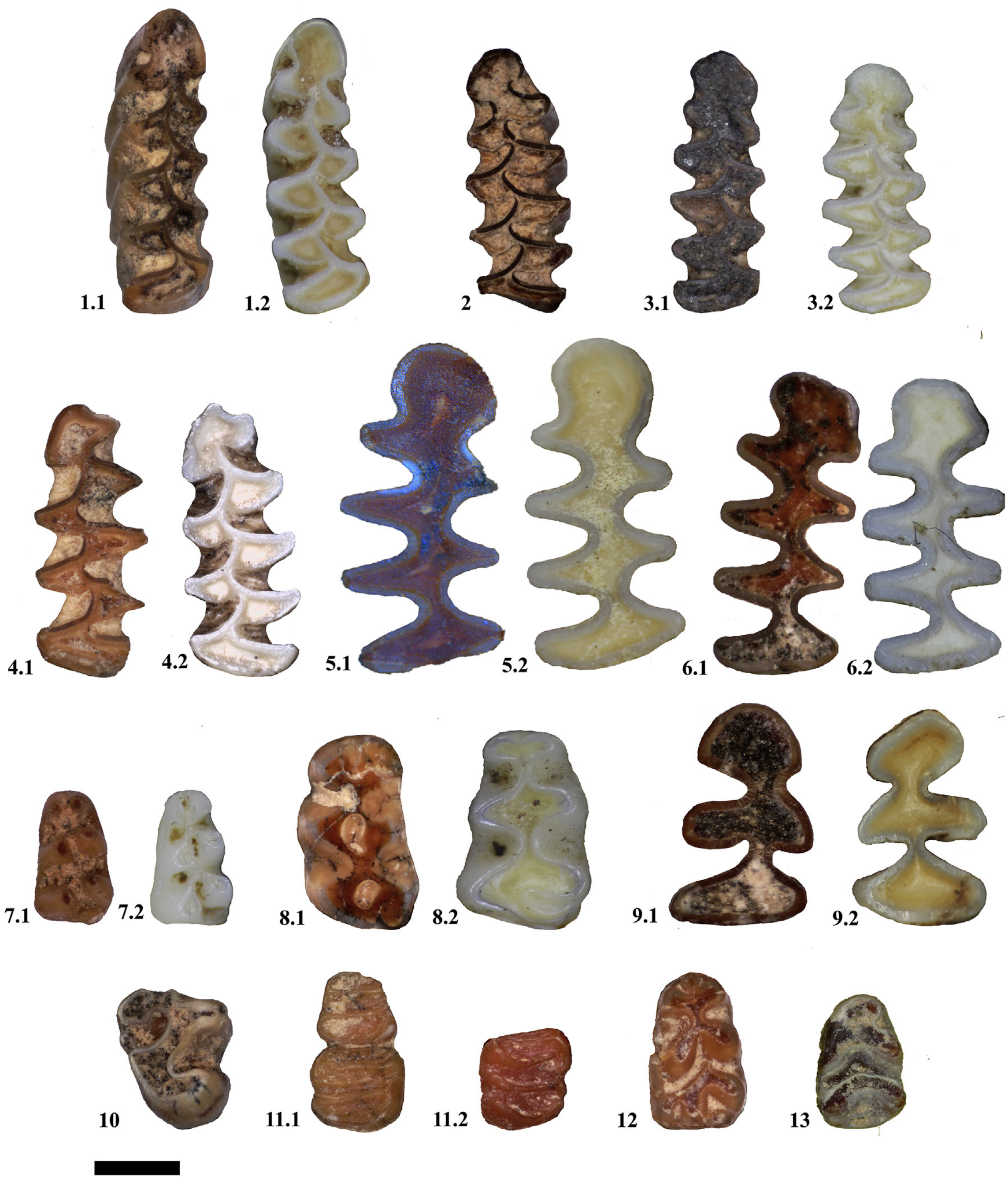

Fig. 2. Some rodent species identified at Kaldar Cave in comparison with equivalent (analogue) modern specimens from the NHM of London. **1)** ***Microtus irani***: 1.1-Kaldar Cave, 2014, Layer 5 (sub-layer 7II), E7, 150–156, right lower m1, number 447.1.2-modern, NHM205207, Iran (Shiraz), right lower 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.

material is based on the morphology of the AC and the measurements (L and W). We do not identify *Ellobius talpinus* in our sample, as no specimen displays morphological features characteristic of this species, such as the narrow AC, and because the measured specimens are larger than *E. talpinus*.

Habitat and distribution: *Ellobius* species frequent steppes, grasslands and semi-deserts in eastern Europe and central Asia; these fossorial species are specialised in subterranean life (Coşkun,

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

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									
Microtus irani	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
Microtus socialis	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
Microtus arvalis	25	2.72	2.45–2.96	0.39	0.32–0.46	0.6	0.50–0.70	1	0.83–1.13
Microtus guentheri	70	2.58	2.2–3						
Kaldar Cave									
Microtus guentheri	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
Microtus irani	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
Microtus socialis	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 5
Measurements of *Ellobius* specimens (in mm): L, total length; W, width. NHM: Natural History Museum of London. NISP: number of identified specimens.

		Ellobius fuscocapillus				*Ellobius lutescens*		*Ellobius talpinus*	
		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

2016; Kryštufek and Vohralík, 2009). *Ellobius lutescens* is a Palaearctic species distributed across Iran, Iraq, Azerbaijan, Armenia, Transcaucasia and East Anatolia (Thomas, 1905; Ellerman and Morrison-Scott, 1951; Darlington, 1957; Osborn, 1962; Walker, 1964; Lay, 1967; Hassinger, 1973; Roberts, 1977; Corbet, 1978; Corbet and Hill, 1991; Wilson and Reeder, 2005; Coşkun, 1997, 2016; Nowak, 1999; Kryštufek and Shenbrot, 2016). In Iran, this species is found in mountain grasslands, sandy semi-deserts and steppe areas (Kryštufek and Shenbrot, 2016; Tesakov, 2016). *Ellobius fuscocapillus* shows a wide range across eastern Iran, Turkmenistan, Afghanistan and Pakistan. In Iran it is found in open steppes with loose soil (Shenbrot et al., 2016).

Subfamily Cricetinae Fischer, 1817

Genus *Cricetulus* Milne-Edwards, 1867

***Cricetulus migratorius* Pallas, 1773**

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

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

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

Genus *Mesocricetus* Nehring, 1898

***Mesocricetus brandti* Nehring, 1898**

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

Description and discussion: the specimens from Kaldar Cave are attributed to *Mesocricetus brandti* on the basis of the size and morphology of the teeth. The molars present a similar morphological pattern to *Cricetulus migratorius*, but are significantly larger in size. The first molars have six tubercles, the second and third molars only four. The largest molars are m1 and M1, whereas m2/M2 and m3/M3 are reduced (Kryštufek and Vohralík, 2009). In Iran we also find *Mesocricetus raddei*, which presents a similar morphology of the teeth to *Mesocricetus brandti*, but compared with the NHM reference collection of the latter, *Mesocricetus raddei* is bigger.

Habitat and distribution: *Mesocricetus brandti* has the largest distributional area of the species belonging to the genus *Mesocricetus*, ranging from Anatolia, Transcaucasia (Armenia, Georgia and Azerbaijan) and southeast Dagestan to northwest Iran (Qazvin in the east, Lorestan in the south; Lay, 1967). This species is found at altitudes from sea level up to 2600 m. However, the primary range is from 1000–2200 m. *Mesocricetus brandti* is found in arid and semi-arid steppe habitats in lowlands and in mountainous areas (Kryštufek et al., 2015; Kryštufek and Vohralík, 2009; Neumann et al., 2017).

Family Muridae Illiger, 1811

Subfamily Gerbillinae Gray, 1825

Genus *Meriones*, Illiger 1811

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

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 m^2; 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 m^2; 18 left lower m1, 10 left upper M1, 16 right upper M1 and 15 right lower m1.

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).

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).

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

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

Family Dipodidae Fischer, 1817

Genus *Allactaga* Cuvier, 1837

***Allactaga* sp.**

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

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

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

Family Gliridae Thomas, 1897

Genus *Myomimus* Ognev, 1924

***Myomimus* sp.**

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

Description and discussion: the genus *Myomimus* is present in Iran with two species, *Myomimus personatus* and *Myomimus setzeri* (Firouz, 2005; Gerrie and Kennerley, 2017; Karami et al., 2008; Kennerley and Kryštufek, 2019). Regarding the remains found at Kaldar, the m1 is of a trapezium-like shape, and its anterior part tends to be narrower than the posterior part. The m1 has three roots, two in the anterior part and one in the posterior part. The m2 is subrectangular, and its occlusal pattern is simpler than in the m1. There are three roots in total, two in the anterior part and one in the posterior part (Kaya and Kaymakçı, 2018; Kryštufek and Vohralík, 2009). The two species are similar to one another and poorly studied. Consequently, we were unable to identify the Kaldar material precisely. Moreover, the reference collection of the Natural History Museum of London only houses *Myomimus personatus* specimens, which could therefore not be compared with *Myomimus setzeri.*

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

Family Muridae Illiger, 1811

Genus *Apodemus* Kaup, 1829

***Apodemus* sp.**

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

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

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

Genus *Mus* Linnaeus, 1758

***Mus* cf. *musculus* Linnaeus, 1758**

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

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

The specimens from Kaldar Cave fit well with *M. musculus* as regards the upper M1 morphology: the lingual row of cusps (t1 and t4) is shifted posteriorly; cusp t7 is reduced to an enamel ridge; distal cusps t8 and t9 leave no space for a posterior cingulum or posterolabial cusp t12 (Siahsarvie and Darvish, 2008). The dental ends of the mesial and central cusps on m1 fuse early; the mesiolabial cusp is small. Upper molars normally have three roots each, one lingual and two labial, whereas lower molars are two-rooted (one anterior and one posterior) (Kryštufek and Vohralík, 2009).

Despite these observations, bearing in mind the high intra-specific morphological variability, the low quantity of material and the bad state of preservation of some teeth (Fig. 2.13), we only attribute the Kaldar material to *M.* cf. *musculus*.

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

4.2. Taphonomic remarks

According to the different degrees of digestion (mostly light, moderate and, heavy in a few cases) observed in the molars previously studied by one of the authors (M. F.-G) and published in Bazgir et al. (2017), the predator responsible for this accumulation could be a category 3 predator such as the tawny owl (*Strix aluco*) or the Eurasian eagle owl (*Bubo bubo*). Both species are currently present in the area, have opportunistic hunting habits, and are sedentary, so their prey spectrum is assumed to be a good representation of the ecosystem in which they live.

4.3. Past landscape and climate at Kaldar Cave

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

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

The climate in Khorramabad nowadays is warm and temperate. The mean annual temperature is 16.9 °C, the maximum mean temperature occurs in July with 29.6 °C and the minimum mean temperature is in January with 5 °C (https://en.climate-data.org/asia/iran/lorestan/khorramabad-764550/). This contrast with the climactic conditions inferred form the *BM* on Kaldar Cave with lower temperatures and drier conditions. For layer 5, mean annual temperature is 6 °C lower than nowadays, the maximum mean temperature 6.15 °C lower than the current values and the minimum mean temperature is 6.69 °C lower than the extant temperatures; the mean annual precipitation is 229.32 mm lower than at present. This tendency is also observable on the Layer 4 mean annual temperature is 5.17 °C lower than at present, the maximum mean temperature 6.5 °C lower than nowadays and the minimum mean temperature is 4.75 °C lower than the extant temperatures; the mean annual precipitation is 383.92 mm lower than at present. (Table 6). Comparing both levels Layer 5 is slightly colder than Layer 4, and Layer 4 is drier than Layer 5.

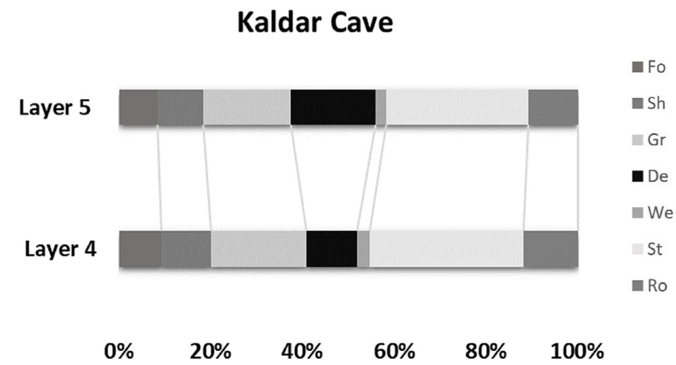

Fig. 3. Results of the *habitat weighting method* for Kaldar Cave (Layer 4 and Layer 5). Forest (Fo), Shrubland (Sh), Grassland (Gr), Desert (De), Wetland (We), Steppe (St) and Rocky (Ro).

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

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

We can compare these results with previous studies carried out in Kaldar Cave using other palaeoenvironmental proxies. Charcoal analyses (Allué et al., 2018; Bazgir et al., 2017) indicate that there were active water sources or flows, with specific plant communities characteristic of open forest growing in cool and dry conditions (Allué et al., 2018). The presence of forested areas is also supported by the large mammals, with the presence of *Sus scrofa*, *Capreolus* sp. and *Cervus elaphus* (Bazgir et al., 2017). Several amphibian and squamate species have also been found (Bazgir et al., 2017): a toad

Table 6
Bioclimatic model estimates for Kaldar Cave. SD, standard deviation. Δ (difference between the values obtained by analysing the rodents from Kaldar Cave and current values).Current values obtained from: https://en.climate-data.org/asia/iran/lorestan/khorramabad-764550/.

	Layer 5	SD	Δ	Layer 4	SD	Δ	Current values
Mean annual temperature	10.90 °C	3.39	−6 °C	11.73 °C	3.39	−5.17 °C	16.90 °C
Maximum mean temperature	23.45 °C	4.77	−6.15 °C	23.10 °C	4.77	−6.5 °C	29.60 °C
Minimum mean temperature	−1.69 °C	4.66	−6.69 °C	0.25 °C	4.66	−4.75 °C	5 °C
Mean annual precipitation	258.68 mm	533.24 mm	−229.32 mm	104.08 mm	533.24 mm	−383.92 mm	488 mm

(*Bufo* sp.), an agamid lizard (Agamidae indet.), a gecko (Gekkonidae indet.), a skink (Scincidae indet.), a lacertid (Lacertidae indet.), a glass lizard (*Pseudopus* sp.), a sand boa (*Eryx* sp.), possibly six types of colubrine snakes (Colubrinae indet.), a cobra (Elapidae indet.), and a viper (Viperidae indet.). Most of these taxa (Agamidae, *Eryx* and Elapidae) live in savannahs, steppes and deserts, with a way of life always linked with warm arid areas in rocky or sandy environments. *Pseudopus* lives in dry and bushy environments, sometimes in open woodlands, but avoids dense forest areas (Bazgir et al., 2017).

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

4.4. Kaldar Cave in the Middle Eastern context

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

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

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

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

We applied the *habitat weighting method* at other Middle Eastern sites where small-mammal studies have been performed, namely Aghitu-3 and Dzudzuana Cave, but these are located in other eco-regions (Fig. 1a). Aghitu-3 is located in Armenian Highlands (46°08′22″ E, 39°51′38″ N), at an elevation of 1601 m a.s.l. and the current climate is continental with considerable seasonality in temperature. Dzudzuana Cave is located in Georgian Caucasus foothills (43°06′11″ E, 42°13′27″ N), at an elevation of 560 m a.s.l., and the current climate is warm and temperate. The estimations obtained with the *habitat weighting method* (Fig. 4) show similar environmental conditions between Kaldar Cave and Aghitu-3, where the landscape is dominated by steppe (indicated by the presence of *Ellobius lutescens*, *Mesocricetus brandti*, *Cricetulus migratorius* and *Allactaga*), with a relatively high percentage of grassland and forests.

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

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

Site/Author	Layer	Human culture	Chronology	Environmental conditions	Rodent
Amud Cave (Belmaker and Hovers, 2011)	B4	Neanderthals	68.5 ± 3.4ka	Grassland vegetation	*Microtus guentheri*
	B2−B1	Neanderthals	56.5 ± 3.5, 57.6 ± 3.7,respectively	Woodland	*Apodemus* cf. *mystacinus* and *Mus macedonicus*
Dzudzuana Cave (Belmaker et al., 2016)	Unit C	Modern human	27-24ka cal BP	Mild and humid	*Microtus*, *Ellobius*, *Arvicola*, *Apodemus* and *Allactaga*.
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	*Microtus* spp., *Chionomys* sp., *Arvicola amphibius* and *Ellobius lutescens*

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

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

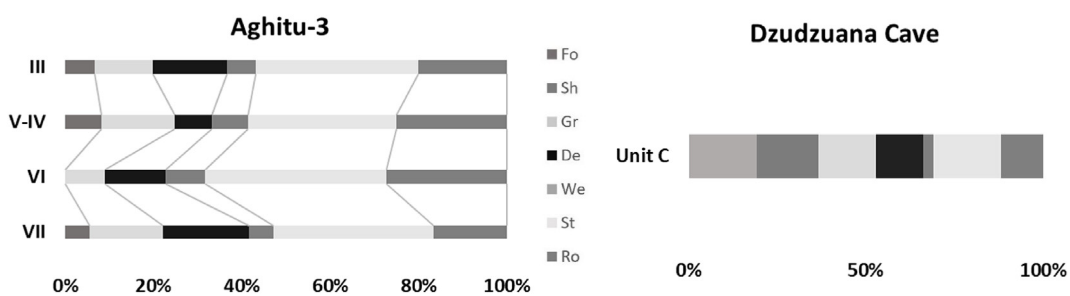

Fig. 4. Results of the *habitat weighting method* for Aghitu-3 and Dzudzuana Cave. Forest (Fo), Shrubland (Sh), Grassland (Gr), Desert (De), Wetland (We), Steppe (St) and Rocky (Ro).

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.

	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

5. Conclusions

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

Given the scarcity of studies in this biogeographical region, we encountered some difficulties in the identification of species, which could slightly affect the palaeoenvironmental and palaeoclimatic interpretations. In order to counter these potential errors, further studies of small mammals in this region are necessary, as well as research on discriminant characters in molars, using reference collections including genetically typed specimens.

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

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

Author statement

Regarding the contributions of the authors I.R.R. and J.M.L-G. analysed the rodent assemblage and wrote the article; H.B. analysed amphibian and squamate species, M.F.G performed taphonomic studies; C.D., E.S., L.T, A.O. and B.B. designed the research.

Declaration of competing interest

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

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Appendix 1

Climatic Parameters	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX	SE
Mean annual temperature in °C (MAT)	26.686	0.024	−0.029	−0.024	−0.074	−0.12	−0.135	−0.217	−0.404	−0.386	3.637
Mean temperature of the warmest month in °C (MTW)	26.219	0.07	0.021	0.02	0.031	−0.212	−0.113	−0.037	−0.121	−0.287	4.754
Mean temperature of the coldest month in °C (MTC)	27.538	−0.033	−0.096	−0.08	−0.175	−0.032	−0.141	−0.418	−0.71	−0.465	5.081
Mean annual precipitation in mm (MAP)	2978.195	−21.237	−27.563	−33.05	−32.648	−6.678	−5.076	−28.4	−33.109	−25.98	470.615

b: intercept.
aIV-aIX: slopes of the different bioclimatic components.
SE: standard error of estimate.
Modified from Hernández Fernández (2001) and Hernández Fernández and Peláez-Campomanes (2003).

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