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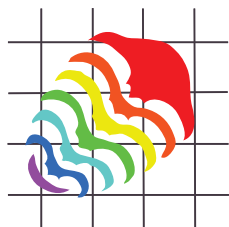
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Distinguishing between three modern *Ellobius* species (Rodentia, Mammalia) and identification of fossil *Ellobius* from Kaldar Cave (Iran) using geometric morphometric analyses of the first lower molar

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Emmanuelle Stoetzel, Christiane Denys, Raphaël Cornette, and Behrouz Bazgir

ABSTRACT

Ellobius remains are common and often abundant in southeastern Europe, western and central Asia archaeological sites. A correct identification of species is crucial for our understanding of the evolution of species and communities through time, including biostratigraphic sequences to be established.

This study applies geometric morphometric methods (GMM) to *Ellobius* first lower molars, with the objectives: 1) to discriminate modern species and explore morphological and size differences in reference samples; and 2) to identify fossil specimens recovered in archaeological sites, based on the aforementioned analysis. The reference dataset used in this paper includes specimens belonging to the three species that today occur in the southeastern Europe, western and central Asia: *Ellobius fuscocapillus*, *E. lutescens* and *E. talpinus*. The archaeological material comes from Late Pleistocene Iranian site of Kaldar Cave (Khorramabad valley, Lorestan Province, western Iran).

Our study shows that the shape of the anterior cap and the arrangement of the following triangles allow discriminating the three studied extant *Ellobius* species. The shapes of *E. fuscocapillus* and *E. lutescens* m1 appear rather similar, whereas *Ellobius talpinus* is well separated from these two species. The total length and the anterior cap of m1 in *E. fuscocapillus* is greater than in *Ellobius lutescens*.

The GMM analyses performed on the modern reference dataset allowed us to identify fossil specimens from Kaldar Cave as *Ellobius lutescens* and some as *E. fuscocapillus*, and excluding *E. talpinus*.

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INTRODUCTION

This study focuses on three species of the vole genus *Ellobius* (Rodentia, Cricetidae, Arvicolinae) nowadays occurring in Iran, and on fossil material from Late Pleistocene Kaldar Cave site in the Zagros mountains. This region is a key area for human evolution and lies at the conjunction of potential migration routes between Africa, Europe and eastern Asia. A well-based characterization of the palaeoenvironmental context is crucial for a good understanding of human occupations (subsistence, cultural adaptations, site occupations, territory, and resource management, dispersal events, etc.). Small mammals may serve as good palaeoenvironmental and palaeoclimatic indicators of the surroundings of an archaeological site. Moreover, voles (arvicolines) in particular are commonly used in Quaternary biostratigraphy because of their rapid evolution and their abundance in the fossil record.

Ellobius is an interesting vole genus since its Pleistocene distribution reached North Africa (Stoetzel, 2013) and the southern Levant (Weissbrod and Weinstein-Evron, 2020), where it is absent now. Nowadays it occurs in southeastern Europe, western and central Asia (e.g., Rey-Rodríguez et al., 2020). It is often abundant in Middle Eastern archaeological sites, and has biostratigraphic potential for this region.

However, the identification of fossil *Ellobius* material is not yet elaborated satisfactory. The identification of most *Ellobius* specimens in museums collections is based on criteria which is usually not applicable to fragmented fossil material. Previous studies on *Ellobius* have mainly focused on chromosomes (Romanenko et al., 2007, 2018, 2020; Coşkun, 2016) and species discrimination based on external characters, not applicable to fossils (Gharkheloo, 2003; Kryštufek and Vohralík, 2009; Tesakov, 2016). In the archaeological literature, taxonomic attributions are often restricted to *Ellobius* sp. (e.g., Maul et al., 2015; Weissbrod and Weinstein-Evron, 2020).

The most common and diagnostic element in fossil vole samples are the teeth, in particular the first lower molars (m1). However, in *Ellobius* m1s morphological differences are hard to find, and there are apparently broad overlaps between the species (Maul et al., 2015; Kandel et al., 2017; Weissbrod et al., 2017).

With the geometric morphometric methods (GMM), fine morphological differences can be detected and variations in shape and size can be quantified, which would have been undetectable by conventional approaches, such as linear measurements or morphotype scores (Adams et al., 2009; Kaya et al., 2018). Previous GMM analyses of various fossil rodent groups (e.g., *Microtus* spp. Cucchi et al., 2014; Luzi et al., 2019; *Meriones* spp.

Stoetzel et al., 2017; and *Rattus* spp. Hulme-Beaman et al., 2018) provided more comprehensive identifications compared to conventional investigations.

The purpose of this study is to investigate morphological and size differences between three species of the genus *Ellobius* from Iran and to apply the results to specimens of the archaeological site of Kaldar Cave. With this article we hope to demonstrate the potential of the GMM approach to the *Ellobius* genus and discuss its use in combination with other morphological criteria.

THE GENUS *ELLOBIUS* FISCHER, 1814

Distribution and Ecological Remarks of the Extant *Ellobius* Species

Nowadays, the genus *Ellobius* Fischer, 1814, occurs in southeast Europe, western and central Asia with five species (Coşkun, 2001, 2016; Wilson et al., 2017, Kaya et al., 2018): *E. talpinus* (Pallas, 1770), *E. tancrei* Blasius, 1884, *E. alaicus* Vorontsov et al., 1969, *E. fuscocapillus* (Blyth, 1843) and *E. lutescens* Thomas, 1897. These fossorial species inhabit steppes, grasslands and semi-deserts, and are highly adapted to subterranean life (Kryštufek and Vohralík, 2009; Coşkun, 2016).

In Iran, where the Kaldar Cave is located and the fossil material under study come from, *Ellobius* is currently represented by *E. lutescens*, *E. fuscocapillus* and *E. talpinus* (Gharkheloo, 2003; Firouz, 2005; Kryštufek and Vohralík, 2009; Kryštufek and Shenbrot, 2016; Rusin, 2017).

Ellobius lutescens (western mole vole) is distributed in northwestern Iran, Iraq, Azerbaijan, Armenia and eastern 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; Coşkun, 1997; Nowak, 1999; Wilson and Reeder, 2005; Kryštufek and Shenbrot, 2016; Wilson et al., 2017). In Iran, this species is found in mountain grasslands, sandy semi-deserts and steppe areas (Kryštufek and Shenbrot, 2016; Tesakov, 2016).

Ellobius fuscocapillus (southern mole vole) shows a range across northeastern Iran, Turkmenistan, Afghanistan and Pakistan. In Iran it is found in open steppes with loose soil (Gharkheloo, 2003; Shenbrot et al., 2016).

Ellobius talpinus (northern mole vole) is distributed in southeastern Ukraine and Russia, Kazakhstan, Uzbekistan, Turkmenistan and in the

small part of northern Iran. Its habitat requirements are similar to that of *Ellobius lutescens* (Rusin, 2017).

The geographical areas occupied by the three species show differences in mean annual temperatures and precipitations (Table 1). *Ellobius talpinus* is found in regions with drier conditions and lower maximum annual temperature than that of the other two species. The geographic ranges of *E. fuscocapillus* and *E. lutescens* display similar temperatures, but *E. fuscocapillus* occurs in wetter environments. All the temperatures and precipitation levels are estimations, consistent with the above-described type of habitat. However, since their subterranean life makes them relatively insensitive to high variations in surface temperatures and precipitations, we can consider that all three species have essentially the same habitat requirements. What can make differences is the resulting vegetation cover, which is of course important for the survival of the animals. But all what we can assume in the current state of knowledge is that the *Ellobius* species provide significant information as indicators for steppe environments. Further studies are needed to evaluate more precisely the potential of the different *Ellobius* species as palaeoenvironmental and palaeoclimatic indicators.

Fossil Record of *Ellobius*

Arvicolines are commonly used in Quaternary

TABLE 1. Ranges of month precipitations and mean annual temperatures within the geographic distribution area of various *Ellobius* species (<https://eol.org/>).

	Temperature (Max/Min)	Precipitation (mm per month)
<i>E. fuscocapillus</i>	11.62/ 0.1°C	36.01
<i>E. lutescens</i>	10.79/ 0.1°C	28.17
<i>E. talpinus</i>	4.75 /0.1°C	24.94

biostratigraphy because of their rapid evolution and their abundance in the fossil record. The genus *Ellobius* may represent a crucial biostratigraphic yardstick in the Zagros mountain range, which marks the western limits of its extant distribution range in the western Asia (Weissbrod and Weinstein-Evron, 2020). However, the palaeobiogeographic and stratigraphic range of the genus in this region is still debated.

Remains of cf. *Ellobius* have been reported in early Pliocene (Ruscinian) sites in Kotovka, Odessa in the Ukraine (Nesin and Nadachowski,

2001), and in two late Pliocene (Late Villanyian) sites, in the west of Ukraine and in Rivoli Veronese, northeastern Italy (Sala et al., 1994). However, Tesakov (1998) believes that the *Ellobius* record from Italy belongs to *Ungaromys dehmi*.

According to several authors (compiled in Topachevsky and Rekovets, 1982; Maul and Markova, 2007; Tesakov, 2016), there was a succession of several *Ellobius* species during the early Pleistocene in Eastern Europe: *E. paleotalpinus*, *E. melitopoliensis*, *E. primigenis*, *E. lakhutensis*, *E. tauricus*, *E. kujalnikensis* and *E. tarchancutensis*. The morphology of *E. tarchancutensis* suggests that it could be the ancestor of *E. lutescens* (Topachevsky and Rekovets, 1982; Tesakov, 2016).

In western Asia, *Ellobius* has been recognized in several Middle Pleistocene archaeological sites in Sel'-Ungur in Kyrgyzstan (*Ellobius* ex gr. *tancrei*; Markova, 1992), in Hummal layer G in Syria (*Ellobius* sp.; Maul et al., 2015), Azokh-1 units Vm, Vu, III, II/III, II (*Ellobius* sp.; Fernández-Jalvo, 2016) in Nagorno Karabakh and Krasarin (*Ellobius* (*Bramus*) *pomeli*; Tesakov, 2016).

During the Middle Pleistocene, *Ellobius* extended its range westwards to Israel, Tabun C and D (Bate, 1937; Frumkin and Comay, in press), Misliya Cave (Weissbrod and Weinstein-Evron, 2020) and North Africa as far as to the Moroccan Atlantic coast (Jaeger, 1988; Stoetzel, 2013). It probably arrived there from western Asia via the Libyco-Egyptian route during a cooling and aridification of North Africa favouring the development of steppes at the beginning of the Middle Pleistocene (Stoetzel, 2013). The North African species then evolved independently from the Asian ones, through the succession of *E. africanus*, *E. atlanticus*, *E. barbarus* and *E. zimae* (Jaeger, 1988). In most studies, it is concluded that *Ellobius*, outside its current range, disappeared at the end of the Middle Pleistocene at the latest (Stoetzel, 2013; Maul et al., 2015; Weissbrod and Weinstein-Evron, 2020).

In the Late Pleistocene, *Ellobius tancrei* has been described from the Mousterian site of Ogzy-Kichik, Tadzhikistan (Markova, 1992). The modern species *E. lutescens* was found in Iraq (Bate, 1930) in the layers of Hazar Merd, dated to 25,000 years ago (Coşkun, 2016). Hashemi et al. (2006) noted that remains of *E. lutescens* have been found in several Late Pleistocene and early Holocene sites in western and northwestern Iran: Kani Mikaeil (Kordestan), Qalaloun near Kouhdasht, Yafteh Gar, and Arjeneh near Khoramabad (Lor-

estan). *Ellobius lutescens* has also been documented in Upper Palaeolithic and Neolithic units of Dzudzuana Cave (Georgia, 34.4-6 ka cal BP; Belmaker et al., 2016), and also in Aghitu-3 level VII (Armenia, Upper Palaeolithic, 39-36 ka cal BP; Kandel et al., 2017). *Ellobius* sp. has been described in Azokh-1 unit I (157 ± 26 ka BP) and in the Holocene site Azokh-5 (Nagorno Karabakh, Parfitt, 2016).

Description of Tooth Morphology

We restricted our analysis to the first lower molar, the most diagnostic tooth in arvicoline. The *Ellobius* lower m1 is composed of the anterior cap (AC), five triangles (T) with three buccal (BRA) and four lingual (LRA) re-entrant angles, and one posterior lobe (PL) (Figure 1A). *Ellobius* molars are notably characterized by broadly confluent triangles, and the presence of roots that are visible in adult and old individuals (Figure 1B). Moreover, *Ellobius* molars lack cement in the re-entrant angles (Coşkun, 2016).

For modern representatives, the skull morphology (Kaya et al., 2018) and external characters (Kryštufek and Vohralík, 2009) contain the main diagnostic features, whereas fossil samples mostly consist of isolated molars or broken jaws. The occlusal morphology of the lower m1 is rather similar in the various *Ellobius* species (especially the three Iranian species *E. fuscocapillus*, *E. lutescens* and *E. talpinus*). However, some specific morphological characters have been pointed out in previous studies: the AC is broad in *Ellobius lutescens*, narrow in *Ellobius talpinus* and elongated in *Ellobius fuscocapillus* (Maul et al., 2015); the distance between T4 and T5 (W) and the total length (L) differ between the species, *Ellobius fuscocapillus* showing the largest teeth and *Ellobius talpinus* the smallest (Rey-Rodríguez et al., 2020). However, these varying morphological and biometric characters are not always clear nor reliable distinction is possible.

MATERIAL AND METHODS

Modern and Fossil Material Studied

For this study we compared modern reference collections and fossil material of *Ellobius* using dental morphometric markers, because teeth represent the most abundant and diagnostic elements in fossil assemblages (Stoetzel et al., 2017). A total of 111 first lower molars (m1s) were measured. In our analysis, we took into account the individual age of the specimens using the classification of

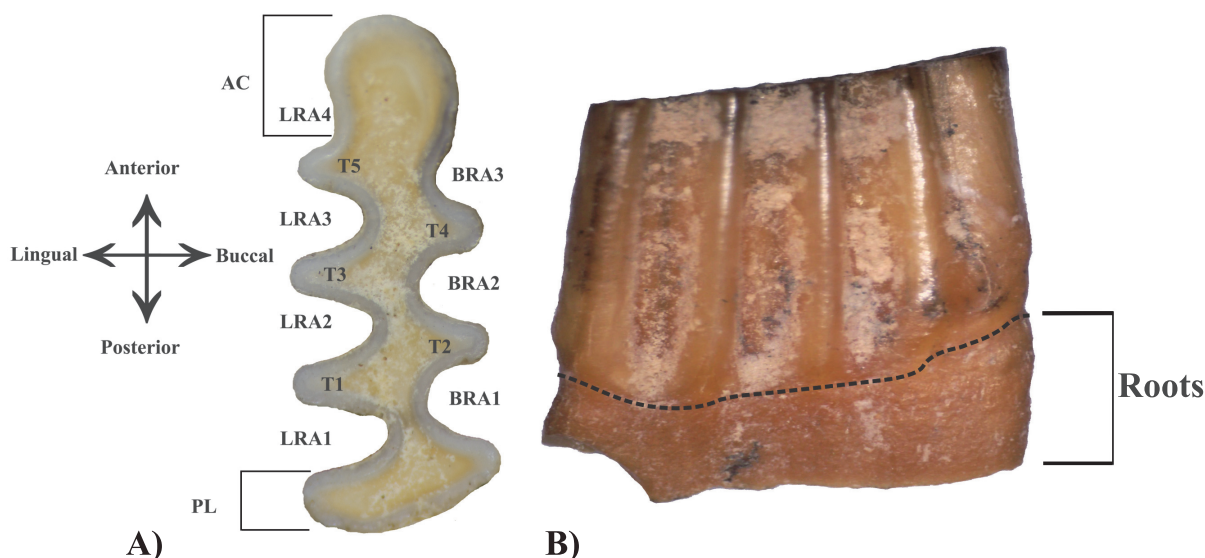


FIGURE 1. A) Occlusal surface of *Ellobius* right lower m1: triangle (T); buccal re-entrant angle (BRA); lingual re-entrant angle (LRA); anterior cap (AC); posterior lobe (PL); **B)** Lingual view of left lower m1.

Coşkun (2016). We observed a striking difference in the occlusal pattern between young and old individuals, so we only used adult individuals, in order to avoid any bias (Stoetzel et al., 2017). Damaged and/or digested molars were not considered. In the reference collections, both males and females were used because no significant sexual dimorphism is known for *Ellobius* (Gharkheloo, 2003). Figure 2 shows the most frequent morphotypes of the three extant and fossil analysed species.

We used specimens from the modern reference collections of the Natural History Museum of London (NHM), the Field Museum of Chicago (FM) and the American Museum of Natural History of New York (AMNH) (Table 2); all the specimens were captured in the field, not bred in captivity.

The archaeological samples come from the Iranian site of Kaldar Cave (Table 2), located in the Zagros Mountains, in the northern part of Khorramabad Valley, Lorestan Province, western Iran (Becerra-Valdivia et al., 2017) (Figure 3). The material is hosted at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES, Tarragona, Spain). More information on the archaeological context and the discoveries from this site can be found in Bazgir et al (2014, 2017) and Rey-Rodríguez et al. (2020).

The study material comes from Layer 5 (attributed to the Middle Palaeolithic) and Layer 4 (attributed to the Upper Palaeolithic) (Bazgir et al., 2014, 2017; Rey-Rodríguez et al., 2020). A total of 264 minimum number of individuals were identified

from the small-mammal assemblages of Kaldar Cave. Layers 4 and 5 are dominated by *Microtus* spp. (60 individuals in Layer 4 and 79 in Layer 5), followed by *Ellobius* spp. (18 individuals in Layer 4 and 17 in Layer 5) and *Meriones* cf. *persicus* (17 individuals in Layer 4 and 18 in Layer 5). Other species were found in lesser proportions: *Chionomys nivalis*, *Cricetulus migratorius*, *Mesocricetus brandti*, *Allactaga* sp., *Myomimus* sp. These species indicate that the environment in the area was mainly composed of open dry and steppe areas. However, we also found *Apodemus* sp. which are related rather to a dense vegetation cover (including trees/bush), as well as few remains of *Mus* cf. *musculus* in both Layers 4 and 5. In this cave, there are also other levels, as Layers 1-3, that did not yield enough material to draw palaeoclimatic inferences (MNI < 30). All the species identified at Kaldar Cave still occur in the area today (Rey-Rodríguez et al., 2020).

Small-mammal remains were collected in the field by water screening, using superimposed 5 and 0.5-mm mesh screens. In subsequent years (2018, 2019), the sediment was sorted by hand and under microscope in order to identify and count the small-mammal elements and extract *Ellobius* remains for the present study.

Data Acquisition

The *Ellobius* lower molars were all photographed under constant conditions with a digital camera (Canon EOS 700D) coupled with a binocu-

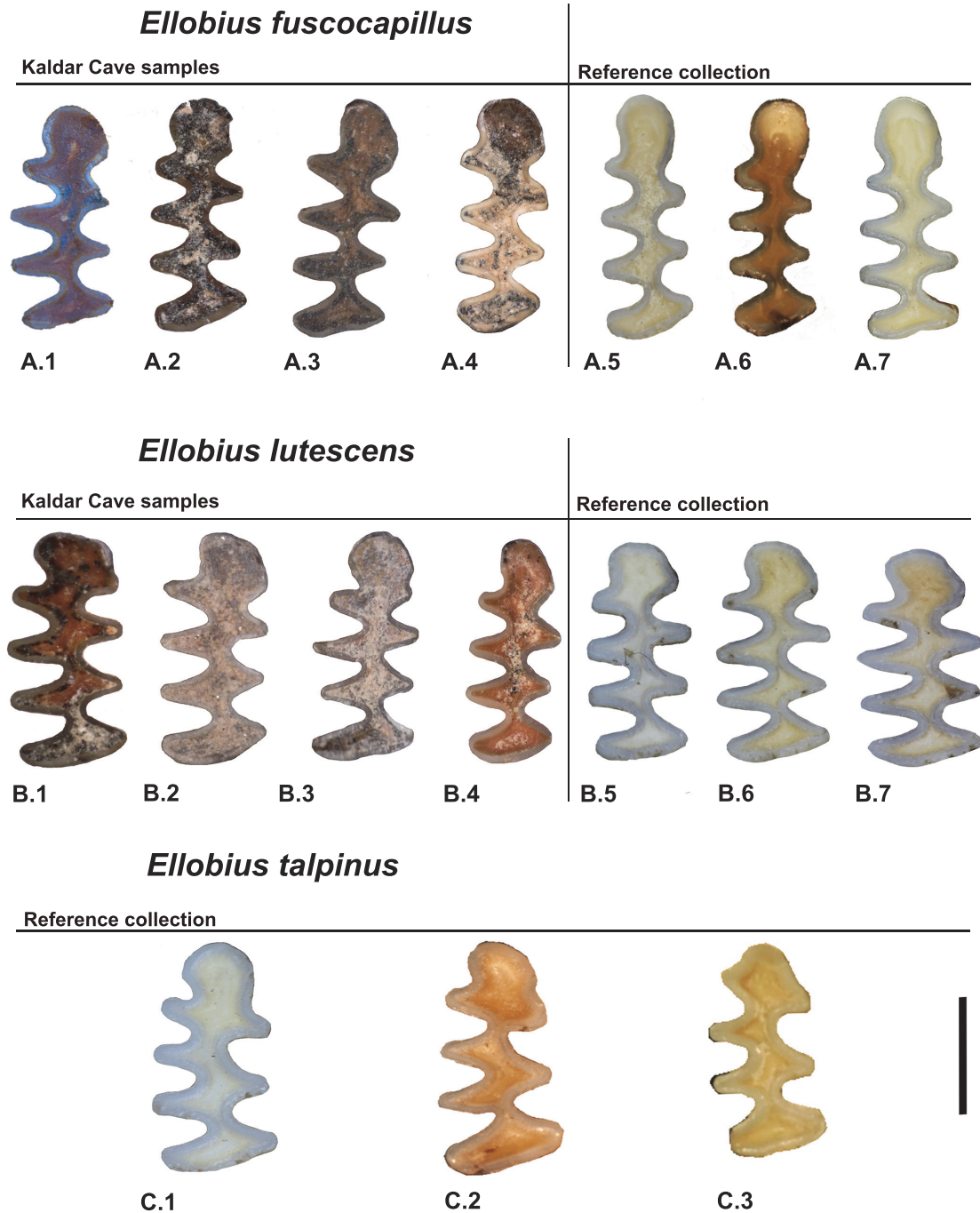


FIGURE 2. *Ellobius* lower m1s (all figured as right ones) from the extant reference collections and Kaldar Cave. **A)** *Ellobius fuscocapillus*: A.1-Kaldar Cave, 2014/4/SL5II/E6/125-130, right lower m1, number 157. A.2-Kaldar Cave, 2014/4/SL5/E5/109-111, right lower m1, number 520. A.3-Kaldar Cave, 2014/5/SL7II/E7/170-180, right lower m1, number 104. A.4- Kaldar Cave, 2014/5/SL7II/F6/135-145, right lower m1, number 547. A.5-modern, NHM86101513, Afghanistan, right lower m1. A.6-modern, FM111846, Iran, right lower m1. A.7-modern, NHM86101512, Afghanistan, right lower m1; **B)** *Ellobius lutescens*: B.1-Kaldar Cave, 2014/5/SL7II/F6/130-140, right lower m1, number 319. B.2-Kaldar Cave, 2014/4/SL5II/F7/115-118, right lower m1, number 90. B.3- Kaldar Cave, 2014/4/SL5II/F7/115-118, right lower m1, number 91. B.4- Kaldar Cave, 2014/5/SL7II/E7/145-150, right lower m1, number 436. B.5-modern, NMH916416, Turkey, right lower m1. B.6-modern, NMH916414, Turkey, right lower m1. B.7-modern, NMH916412, Turkey, right lower m1; **C)** *Ellobius talpinus*: C.1-modern, NHM3421126, Russia, right lower m1. C.2-modern, FM103163, Afghanistan, right lower m1. C.3-modern, AMNH59797, Mongolia, right lower m1. Scale 1 mm.

TABLE 2. Modern reference collection for each museum specimen. Natural History Museum of London (NHM), Field Museum of Chicago (FM) and American Museum of Natural History of New York (AMNH). Archaeological specimens from Kaldar Cave, MP = Middle Palaeolithic, UP = Upper Palaeolithic.

Right lower m1	Reference collection			Total
	NHM	AMNH	FM	
<i>Ellobius fuscocapillus</i>	6	-	34	40
<i>Ellobius lutescens</i>	6	-	-	6
<i>Ellobius talpinus</i>	7	11	20	38
Total	19	11	54	84

Kaldar Cave			
Right lower m1	Level 5(MP)	Level 4(UP)	Total
<i>Ellobius fuscocapillus</i>	1	1	2
<i>Ellobius lutescens</i>	6	2	8
Total	7	3	10

Left lower m1	Level 5(MP)	Level 4(UP)	Total
<i>Ellobius fuscocapillus</i>	4	2	6
<i>Ellobius lutescens</i>	4	7	11

lar microscope (Leica M125). All the pictures of the first lower molars were taken in occlusal view, and right molars were used; when they were not available (only in the fossil material), the left lower molars were used and successively mirrored before the positioning of the landmarks and semi-landmarks. A scale bar was included in all the photographs in order to facilitate the extraction of a scaling factor, which can be used to estimate the centroid size (Tabatabaei Yazdi and Alhajeri, 2018). We took into account the lateral side for the age classification.

To investigate the first lower molar size and shape we combined two-dimensional (2D) landmarks (LM) and semi-landmarks (SLM) on the pho-

tographs using TPSdig2 v.2.32 software package (Rohlf, 2016) for 2D geometric morphometric analyses (we include our data on a TPS file, Appendix 1). The methodology was adapted from the previous studies of Klenovšek and Kryštufek (2013), Cucchi et al. (2014, 2017), Cornette et al. (2015), Maul et al. (2015), Kryštufek et al. (2016), Stoetzel et al. (2017) and Dianat et al. (2017, 2020).

Fourteen landmarks were placed at the maximum curvature on the salient and re-entrant lingual and buccal angles, on the posterior lobe and the anterior cap, where the landmarks were positioned on the outline (Figure 4A).

In order to characterize the size and shape of the anterior cap, 60 equidistant semi-landmarks



FIGURE 3. A) Kaldar Cave location. **B)** Entrance from the south of Kaldar Cave.

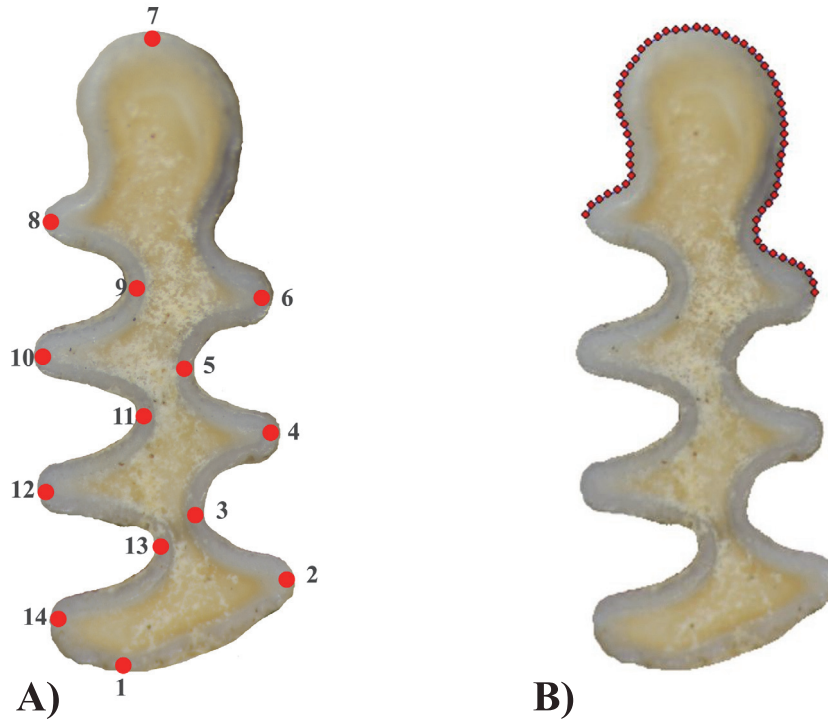


FIGURE 4. *Ellobius* right lower m1. **A)** 14 landmarks: Landmarks on the outermost turning point of buccal (2, 4, 6) and lingual (8, 10, 12, 14) salient angles, and on the innermost turning point of buccal (3, 5) and lingual (9, 11, 13) re-entrant angle. **B)** 60 semi-landmarks on the anterior cap.

were automatically positioned along the curve corresponding to the external outline of the tooth enamel from buccal salient angle 3 to lingual salient angle 4 (Figure 4B).

To test the repeatability of the procedure, we re-digitized the set of landmarks and semi-landmarks 10 times on three randomly selected teeth. We estimate the measurement error on this new set of variables from the Procrustes ANOVA mean squares following the method proposed by Fruciano (2016). The procedure has been retained highly repeatable ($R=0.97$).

Shape Analyses

All the following analyses were performed with R (R Core Team, 2020) using the Geomorph (Adams et al., 2020) and Morpho (Schlager, 2017) packages.

Before undertaking the statistical analysis, the 2D landmark and semi-landmark coordinates were scaled through a general Procrustes analysis (GPA), allowing the semi-landmarks to slide along the outline (Gunz and Mitteroecker, 2013). A principal component analysis (PCA) was then performed on the new normalized landmark and semi-landmark coordinates of the reference collection.

Archaeological specimens were added *a posteriori* as supplementary individuals in the PCA shape space. A canonical variate analysis (CVA) was then performed on the PC scores, keeping 90 % of the overall shape variation (Baylac and Frieß, 2006). To assess the classification accuracy, a cross-validation test was performed on the CVA scores. Finally, the allometric effect was investigated through univariate and multivariate linear regression of the PC scores on the log of the centroid size.

RESULTS

The PCA (Table 3) performed on the normalized landmarks and sliding semi-landmarks of the first lower molar reveals significant differences between the analysed species, the first two principal components (PCs) account for 52.7% of the total variance (Figure 5). Component 3 was also analysed but the variance was too low, and there was no differentiation between the species. We included the complete table with all statistical data in Appendix 2.

The main variation along the PC1 (38.2%) regards the morphology of the Anterior Cap, which is more flattened for the positive values and more

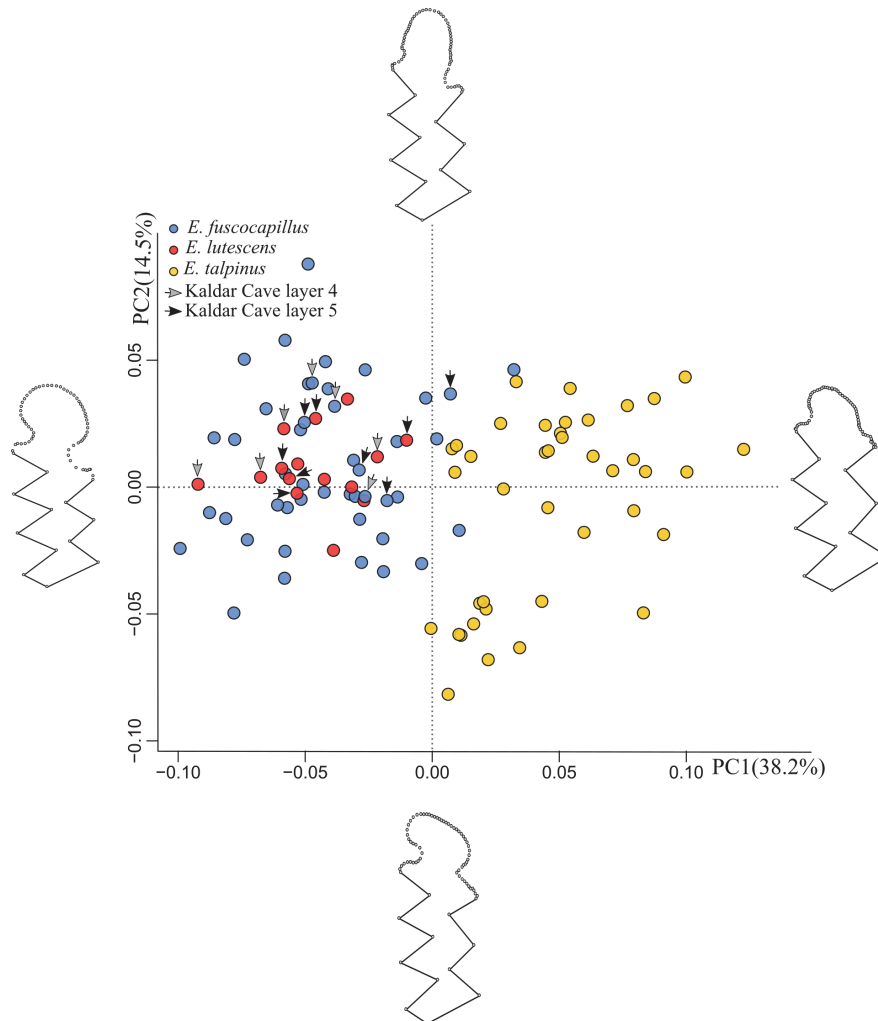
TABLE 3. Contribution of the first 10th PCs to the total variance (%). PCA: principal component analysis.

PC	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
%	38.2	14.5	8.1	6.9	4.2	2.8	2.6	2.2	1.6	1.5

rounded for the negatives ones. *Ellobius talpinus* occur on the positive part of the PC1 axis while *E. fuscocapillus* and *E. lutescens* are located on the negatives ones reflecting a broader and more rounded AC. Along the PC2 (14.5%) scores, the positive values show an AC elongated and pronounced on the buccal side, negative values display a more rounded AC with a clear constriction between BRA3 and LRA4. On PC2 there is not a clear differentiation between the three species. However, *E. lutescens* specimens are located principally in the upper half of the *E. fuscocapillus* and *lutescens* cloud, with positive PC2 values.

The shape of *Ellobius talpinus* with narrower AC (Figure 5) is significantly different from that of *E. fuscocapillus* and *lutescens*, which appear morphologically very close one to another. The Kaldar Cave specimens are well distributed in the cloud of *E. lutescens* and *E. fuscocapillus*, with all of them having negative PC1 values. We can conclude that *Ellobius talpinus* is not present in the archaeological sample.

In order to estimate possible allometric effects on the samples, we performed a linear regression of the PCs onto the log of the centroid size (following the approach of Mitteroecker et al., 2015). Only PC1 shows a significant correlation with size ($R^2 =$

**FIGURE 5.** Principal component analysis on the normalized landmarks and sliding semilandmarks and shape configuration at the extreme ends of the two first PCs.

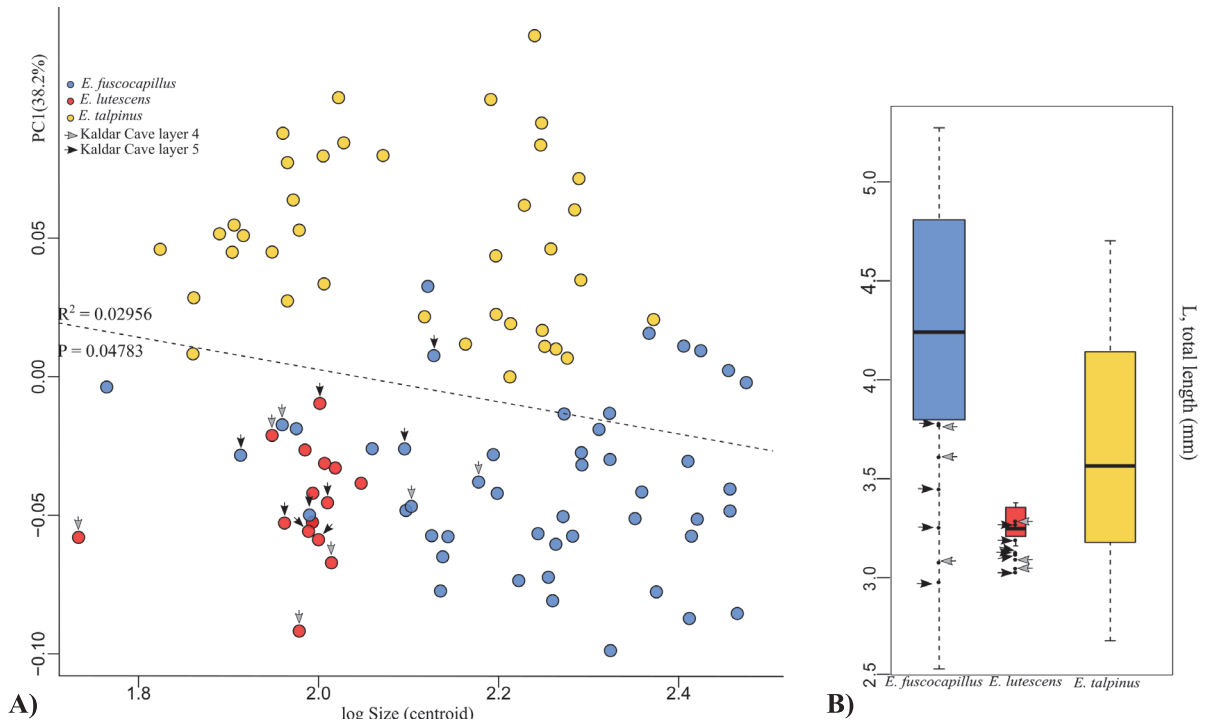


FIGURE 6. A) First two PCs from the Principal component analysis performed on the size and shape including the reference collection and Kaldar Cave material. **B)** Boxplot of the total length of *Ellobius* from the extant reference collections and Kaldar Cave.

0.02956, $p=0.04783$). In this graph (Figure 6A), it is possible to discriminate *Ellobius lutescens* from *E. fuscocapillus*, the latter showing larger dimensions. *E. talpinus* presents a wide size range overlapping the ranges of the two latter (Figure 6). The archaeological remains are placed again in the cloud of *E. lutescens* and *E. fuscocapillus* but with some ambiguous identifications. We have also evidenced this confusion in the reference dataset with three *E. fuscocapillus* individuals from the Field Museum that were replaced among *E. lutescens* in our analysis, indicating a possible misidentification of the museum specimens. On Figure 6B, Kaldar Cave fossil specimens appear in general smaller than the reference specimens, but inside the standard deviation.

The canonical variate analysis of 90% of the total variation (PCs1 to 16) in the sample and the relative cross-validation procedure give an overall

classification accuracy of 86 % (with almost 100% correct classification for *Ellobius talpinus*) (Table 4).

DISCUSSION

Our results indicate that it is possible to accurately identify *Ellobius* species by applying GMM to m1 shape and size. The main differences between species concern the AC shape, the size and the general disposition of the triangles.

One result of the performed GMM is that the shape of *Ellobius fuscocapillus* and *E. lutescens* clusters in one cloud, and *E. talpinus* in another. This is in agreement with the distinction of two clades among the genus *Ellobius*: the subgenus *Bramus* Pomel, 1892 (with *E. fuscocapillus* Blyth, 1843, and *E. lutescens* Thomas, 1897) and the subgenus *Ellobius* Fischer, 1814 (with *E. talpinus*

TABLE 4. Cross-validated classification results in frequencies and %.

Taxon	<i>E. fuscocapillus</i>		<i>E. lutescens</i>		<i>E. talpinus</i>		None	
	N	%	N	%	N	%	N	%
<i>E. fuscocapillus</i>	37	78.72	10	21.27	0	-	0	-
<i>E. lutescens</i>	2	13.33	13	86.66	0	-	0	-
<i>E. talpinus</i>	0	-	0	-	36	94.73	2	5.26

Pallas, 1770; *E. tancrei* Blasius, 1884; and *E. alaiicus* Vorontsov et al. 1969) (Carleton and Musser, 2005).

The shape differences between *Ellobius fuscocapillus* and *E. lutescens* is grossly in agreement with some earlier considerations based on conventional methods. Previously, Maul et al. (2015) considered the AC shape as a discriminant criteria, being broad in *Ellobius lutescens*, narrow in *Ellobius talpinus* and elongated in *Ellobius fuscocapillus*. Tesakov (2016) found that the size of *E. lutescens* is slightly smaller than *E. fuscocapillus*. Rey-Rodríguez et al. (2020) reported that the confluence between T4 and T5 differs among the species, with T1-T2 and T3-T4 being slightly less pairwise opposed in *E. lutescens*.

Our GMM analyses allowed these previously examined criteria to be assessed all together, in taking into account the size, the morphology of the AC and the general disposition of the triangles. In our fossil samples many teeth are fragmented, and could not have been included in our GMM. However, it could be possible to consider fragments of *Ellobius* m1s in further analyses, for example by focusing only on the shape of the anterior cap.

Sliding Semi-Landmarks and Anatomical Landmarks Compared with Previous Systematic Methods of *Ellobius* Identification

Despite classic methods enable to distinguish between many m1s of some of the species, a throughout discrimination remains unclear. According to Maul et al. (2015), morphological features of the AC (without performing GMM analyses) would be enough to permit species identification, and especially to differentiate *Ellobius talpinus* from *Ellobius lutescens* and *fuscocapillus*, because *Ellobius talpinus* has a less developed and narrower AC than in the other two species. But in the present study, we have seen that there is a morphological overlap between *E. lutescens* and *E. fuscocapillus*. So, while “classic” morphological criteria often result in unclear features or overlaps between species, our GMM analysis of *Ellobius* m1 allowed two groups to be accurately differentiated, *Ellobius talpinus* on the one hand and *Ellobius lutescens* and *fuscocapillus* on the other. The distinction between these two latter species is more complex, and indeed no straightforward grouping was observed with the first PCA (Figure 5). However, morphological differences between them could have been detected by comparing the mean shapes of their m1s (Figure 7) and by including the size parameter (Figure 6).

Figure 7 shows the means (dots) and variations (arrows) of the different landmarks and semi-landmarks between *Ellobius fuscocapillus* and *E. lutescens*. Major morphological differences are seen in points 1 (posterior lobe), 3, 4, 5 and 6 (BRAs and BSAs). This means that T1-T2 and T3-T4 are less parallel in *E. lutescens* than in *E. fuscocapillus*, as observed in the buccal part. Rey-Rodríguez et al. (2020) proposed that the width between T4 and T5 (W) and the total length (L) of the two species are different. The configuration of the AC shows that the transition between T4-T5 is narrower in *E. lutescens* than in *E. fuscocapillus*, which generates a smaller and more closed AC in *E. lutescens* than in *E. fuscocapillus*, in accordance with the observations of Maul et al. (2015). Finally, also the previous observation of Tesakov (2016) is confirmed that size is a valid criterion for distinguishing *Ellobius fuscocapillus* (larger) and *Ellobius lutescens* (smaller).

Combining shape and size allowed us identifying the fossil *Ellobius* m1s from Kaldar Cave. The morphology of the AC, the size and the W (width between T4 and T5) are valid criteria in most of the cases, but we have seen that GMM analyses allowed them all to be combined and a number of previous identifications to be re-analysed (Bazgir et al., 2014, 2017; Rey-Rodríguez et al., 2020). The results of the present analysis allowed some *E. lutescens* from the archaeological material to be re-assigned to *E. fuscocapillus* (five *E. fuscocapillus*, three from Layer 4 and two from Layer 5 were re-assigned). These misclassifications were due to the fact that *E. fuscocapillus* and *E. lutescens* are quite similar from a morphological point of view, and because the previous identifications were based on the W, L and the AC, subjected to overlapping problems, which have subsequently been clarified with the GMM.

In this study we have not seen morphological differences between specimens from Layer 4 and 5. As we are working in an archaeological site, the fact that we have two species in the same levels does not mean that they were deposited at the same time. Layer 4 has a chronological range of 54,400–46,050 cal BP at the bottom and 23,100 ± 3,300 to 29,400 ± 2,300 BP at the top, so we have a gap where one species could be replaced by the other one. The same observation can be made for Layer 5, whose chronology is still under review. Moreover, the fact that we have two species in the same levels does not mean that they lived in the exact same place, because the small mammal assemblages from Kaldar Cave were accumulated

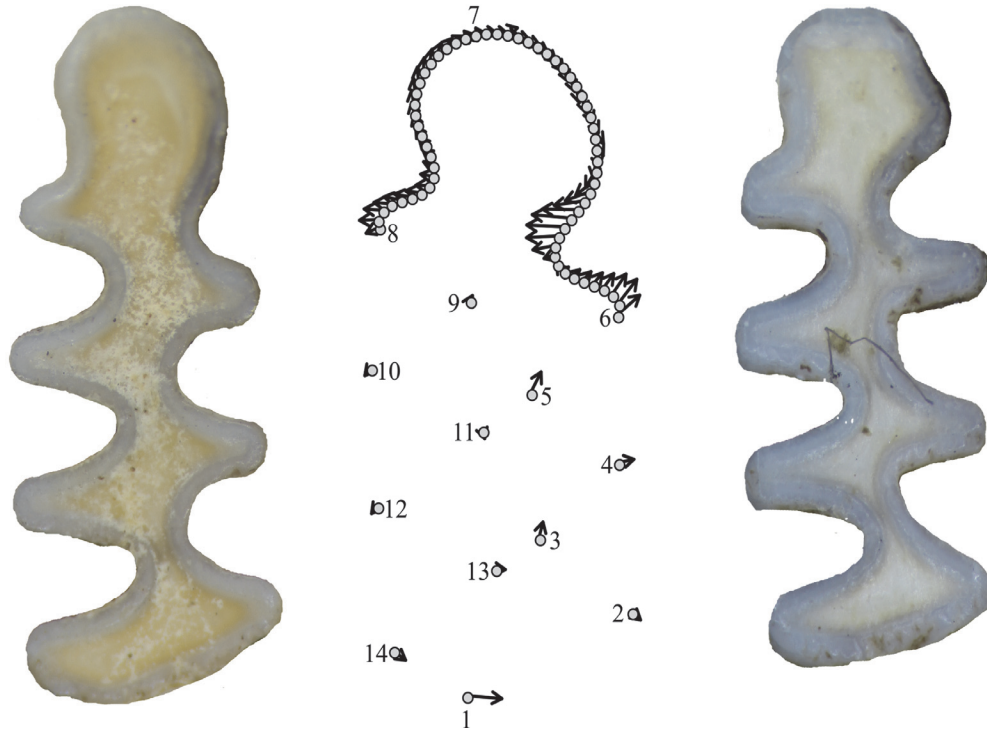


FIGURE 7. Morphological differences between *Ellobius fuscicapillus* (left) and *Ellobius lutescens* (right). Arrows depict the displacements between corresponding landmarks in the reference (dots) and *Ellobius lutescens* as target specimens.

by nocturnal raptors (Rey-Rodríguez et al., 2020), which could hunt in different habitats on a territory of several (tens of) km².

Ellobius fuscicapillus is not present in the area nowadays, but it may have lived there in the past. Indeed, at Kaldar Cave, the palaeoenvironmental data (obtained with the *habitat weighting* method) have shown that the landscape was mainly composed of steppes in both levels, which are favorable habitats for the *Ellobius* species (Rey-Rodríguez et al., 2020). The absence of *E. talpinus* in our archaeological sample could be linked to the climatic requirements of the species, but this hypothesis remains to be deepened.

CONCLUSIONS

In the present study, based on modern and fossil specimens of *Ellobius* species, we found potential size and shape differences within the examined material thanks to GMM analyses. On the basis of the m1 shape alone, we were able to differentiate two groups: *E. talpinus* on the one hand, and *E. fuscicapillus* and *E. lutescens* on the other. Taking size into account, moreover, it was possible to distinguish *E. fuscicapillus* from *E. lutescens*. However, we agree that it would be nec-

essary to increase the reference dataset, particularly for *E. lutescens*, which may help us find further discriminative patterns between these three species in future studies.

GMM enabled us to obtain good results in fossil species attributions. Here, only complete teeth were used, i.e. not the whole fossil *Ellobius* sample from Kaldar Cave. We obtained better results in the classifications in including all the teeth landmarks instead of the AC alone. It would thus be really useful to improve the results in order to be able to identify broken or digested molars, albeit with the caveat that when only the anterior cap of the molar is preserved we cannot discriminate between *E. fuscicapillus* and *E. lutescens*. Accordingly, it would be necessary to combine this method with other techniques and use all the criteria together.

It would be interesting to extend this GMM study to other modern and fossil *Ellobius* species, especially from Middle Pleistocene sites, in order to obtain a more complex overview of their morphological differences and their evolution throughout their current and past geographic range, and to explore the potential and usefulness of this tool in the archaeological sites of southeastern Europe, western and central Asia.

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APPENDICES

APPENDIX 1.

TPS data. The appendix material is available online as a zipped file at <https://palaeo-electronica.org/content/2021/3265-ellobius-and-gmm>.

APPENDIX 2.

Complete statistical data for the PCA. The appendix material is available online as a zipped file at <https://palaeo-electronica.org/content/2021/3265-ellobius-and-gmm>.