



## On the trail of Neolithic mice and men towards Transcaucasia: zooarchaeological clues from Nakhchivan (Azerbaijan)

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Transcaucasia comprises a key region for understanding the history of both the hybrid zone between house mouse lineages and the dispersal of the Neolithic way of life outside its Near Eastern cradle. The opportunity to document the colonization history of both men and mice in Transcaucasia was made possible by the discovery of mouse remains accumulated in pits from a 6000-year-old farming village in the Nakhchivan (Autonomous Republic of Nakhchivan, Azerbaijan). The present study investigated their taxonomy and most likely dispersal path through the identification of the *Mus* lineage to which they might belong using a geometric morphometric approach of dental traits distances between archaeological and modern populations of the different *Mus* lineages of South-West Asia. We demonstrate that the mouse remains trapped in the deep storage pits of the dwelling belong to the *Mus musculus domesticus* from the Near East, with dental shapes similar to current populations in Northern Syria. These results strongly suggest that the *domesticus* lineage was dispersed into Transcaucasia from the upper Euphrates valley by Neolithic migration, some time between the 7th and 5th millennium BC, providing substantial evidence to back up the scenario featuring near-eastern *stimuli* in the emergence of agriculture in the South Caucasus. The *domesticus* mitochondrial DNA signature of the current house mouse in the same location 5000 years later, as well as their turnover towards a subspecies *musculus/castaneus* phenotype, suggests that early *domesticus* colonizers hybridized with a later *musculus* (and maybe *castaneus*) dispersal originating from south of the Caspian Sea and/or Northern Caucasasia. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **108**, 917–928.

**ADDITIONAL KEYWORDS:** colonization history – geometric morphometric – house mouse – hybridization – *Mus musculus*.

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## INTRODUCTION

The ancestors of the house mouse (*Mus musculus* L.) originated in the North of the Indian subcontinent 0.5 Mya. In the course of their adaptive radiation, they diversified approximately 250 000 years ago into three main lineages: *Mus musculus domesticus* (*domesticus* hereafter), *Mus musculus musculus* (*musculus* hereafter) and *Mus musculus castaneus* (*castaneus* hereafter), all three commensal of humans (Bonhomme & Searle, 2012). In the Western Palaeartic, human induced dispersal is at the origin of the occurrence of *musculus* from Central and Northern Europe to Northeast Asia, and *domesticus* throughout Southwest Asia, the Mediterranean, and Western Europe. These two sub-species currently hybridize along a line running from Bulgaria (Orsini *et al.*, 1983) to Norway (Jones *et al.*, 2011), as well as in Transcaucasia (Milishnikov, Lavrenchenko & Lebedev, 2004; Orth *et al.*, 1996). The origin of *domesticus* synanthropization, 11 000 years ago, as a side effect of the near eastern Neolithic niche construction, is now well documented by zooarchaeological data (Cucchi, Auffray & Vigne, 2012). Its dispersal towards Western Europe, along with the Mediterranean maritime traffic, between the third and last millennium BC, is also well documented (Cucchi, Vigne & Auffray, 2005; Cucchi, 2008; Cucchi *et al.*, 2012). On the other hand, the arrival of *musculus* in South Eastern Europe has been demonstrated in a fifth millennium BC village (Cucchi *et al.*, 2011), although its synanthropization centre remains hypothetical (Cucchi *et al.*, 2012).

Documenting the colonization history of the house mouse through their genes and morphology provides relevant proxies for tracking human migration (Searle *et al.*, 2009a; Bonhomme & Searle, 2012) because much of the range of these sub-species has been attained through human transports. The mitochondrial (mt)DNA phylogeography of commensal mice has already proved useful for unravelling obscure voyaging stories of the Vikings (Gündüz *et al.*, 2001; Searle *et al.*, 2009b; Jones *et al.*, 2012), whereas the tooth morphology of a stowaway house mouse found in a Bronze Age shipwreck has provided major clues regarding the vessel's last journey (Cucchi, 2008).

The Transcaucasian isthmus is a crucial area for house mouse evolutionary biologists, as well as archaeologists interested in the role of Near Eastern influence in the emergence of agriculture in this region at the end of the seventh millennium BC (Lombard & Chataigner, 2004). Different hypotheses are considered concerning the hybridization between *musculus*, originating from Northern Caucasus or the southern coast of the Caspian Sea (Bonhomme &

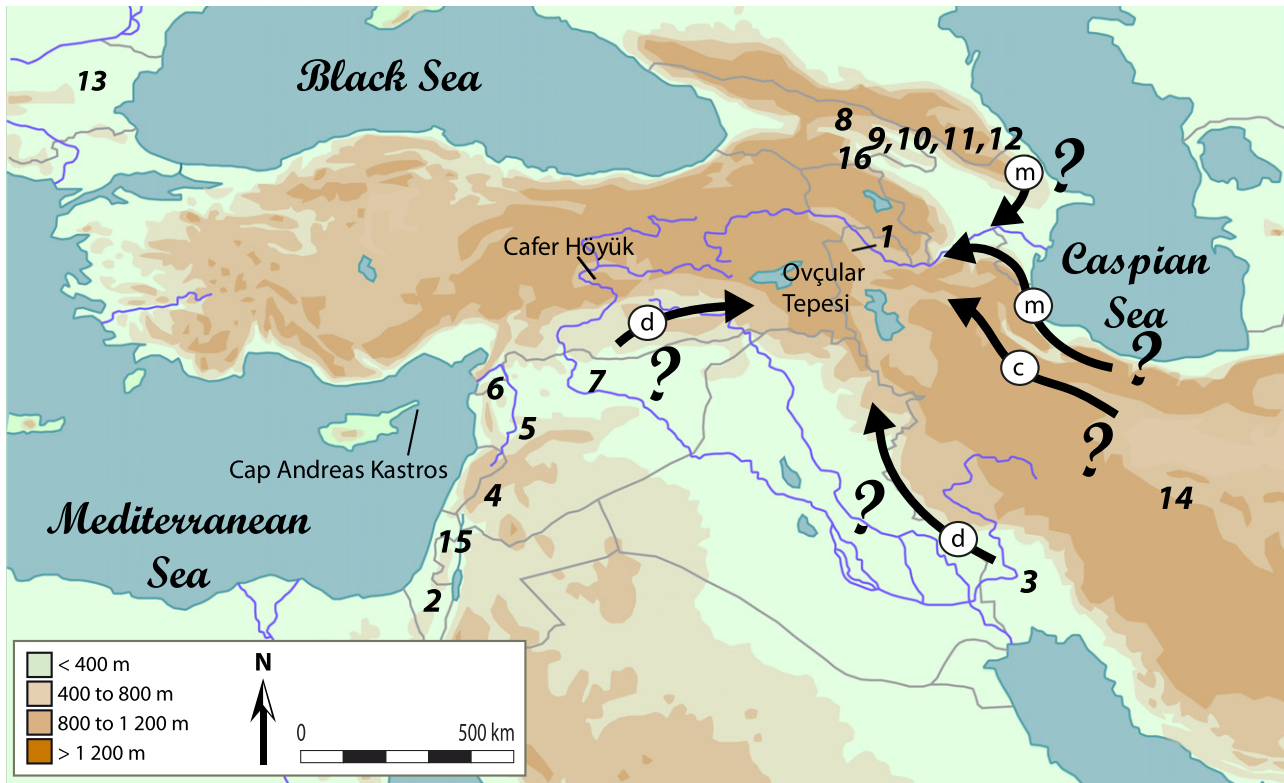
Searle, 2012), and *domesticus* originating from a south-western route (Rajabi-Maham, Orth & Bonhomme, 2008) or from Northwest Iran (Fig. 1). Hybridization may result from a recent post-glacial secondary contact (Orth *et al.*, 1996; Mezhzherin, Kotenkova & Mikhailenko, 1998) or a centre of differentiation for an ancient autochthonous *musculus* gene pool that has incurred successive hybridization events through time (Milishnikov, Lavrenchenko & Lebedev, 2004). For this debate to move away from speculation, zooarchaeological evidence dating the house mouse colonization history in Transcaucasia is required (Milishnikov *et al.*, 2004).

The recent discovery of numerous mice remains collected from a 6000-year-old village (Ovçular Tepesi) in Southwest Transcaucasia (Marro, Bakhshaliyev & Ashurov, 2009, 2011) provides new insights into the dispersal path of both the house mouse and the Neolithic migration in Transcaucasia as a result of the chronological, taxonomical, and biogeographical information encapsulated in the mice remains. The present study aimed to use molar traits, which are heritable and not remodelled through life, to observe the phenotypic relationships of Ovçular Tepesi mice with other ancient and current mouse sub-species and populations from Southwest Asia: (1) to identify the sub-specific status of what is allegedly one of the first commensal house mouse populations in Southwestern Transcaucasia; (2) to assess its most likely geographical origin and dispersal route; and (3) to discuss the house mouse colonization history in Transcaucasia.

## MATERIAL AND METHODS

Ovçular Tepesi is located in the Nakhchivan Autonomous Republic (Azerbaijan) (Fig. 1), at the crossroads of major routes linking the Iranian plateau to Anatolia and the Caucasus to Mesopotamia (Marro *et al.*, 2009, 2011). This location makes this site a focal point for documenting the different dispersal routes of human groups and their commensal animals towards Transcaucasia.

Ovçular Tepesi was occupied from the Late Chalcolithic (LC) to the Early Bronze Age, between the end of the fifth millennium BC and the fourth to third millennium BC. Small mammals have been collected (Kovacs *et al.*, in press) from the filling sediment of three LC pits (locus: 01.171, 02.070, and 08.051) in the vicinity of domestic buildings (Fig. 2). Each of them was approximately 60 cm in diameter and more than 150 cm deep. In total 800 litres of sediments have been collected, floated, and sorted with a 1 mm-mesh (Berthon *et al.*, in press; Kovács *et al.*, in press). The filling of the pits, and indirectly the small



**Figure 1.** Map of South-West Asia and the location of the modern and archaeological samples of *Mus*. Numbers indicate the sample location, as described in Table 1. Arrowed lines give the hypothetical colonization paths towards Transcaucasia that are investigated in the present study. d, *domesticus*; m, *musculus*; c, *castaneus*.

mammals remains, have been radiocarbon dated between 4350 and 3970 calibrated years BC. (Marro *et al.*, 2009).

#### TAPHONOMY OF THE OVÇULAR TEPESI SMALL MAMMALS

The deposit in the pits was assessed together with the small mammal diversity of the collected assemblage, its taphonomic signature (bone fragmentation and bone preservation) (Andrews, 1990), and the age class distribution of the mice.

The identification of the small mammal remains, except for the *Mus* sp., was based on morphoscopic and morphometric criteria (Chaline *et al.*, 1974; Niethammer & Krapp, 1978; Kryštufek & Vohralík, 2001, 2005, 2009).

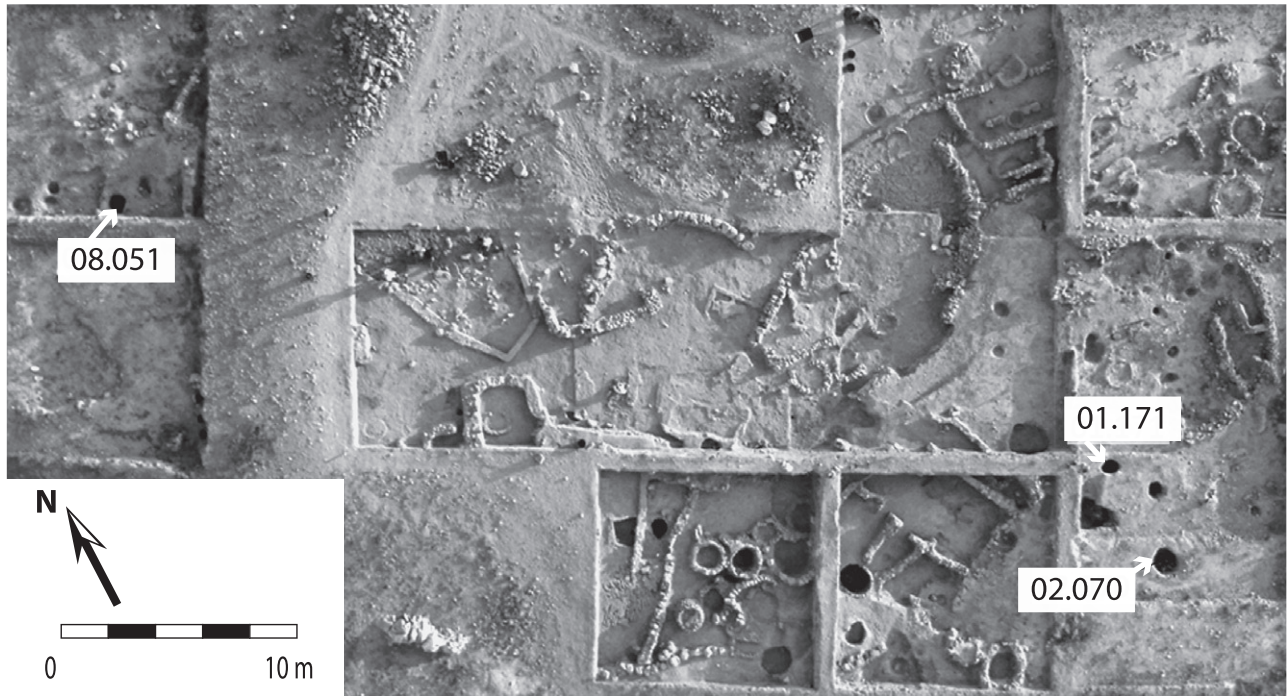
Bone fragmentation was estimated through the relative frequency of different anatomical elements in each taxon using an estimated percentage of representation (Dodson & Wexlar, 1979). The level of preservation (excellent, fair, good, mediocre, and bad) was assessed by the degree of surface porosity and exfoliation and differential surface alteration (root or digestion marks). We observed with a light stereo-

microscope whether bone fragments have a worn appearance (e.g. an indication of strong digestive effects) or retained sharply angular edges indicating either recent fragmentation or short transportation (O'Connor, 1991). Lastly, the age-distribution of the mice was estimated through stage of tooth-wear because the continual attrition of molars during the feeding process is age-related (Morris, 1972). The ageing method of Lidicker (1966), based on the wear pattern of upper molars, was also adapted for the lower molars.

#### TAXONOMY OF THE OVÇULAR TEPESI MOUSE

Among the three pits excavated in Ovçular Tepesi, pit 01.171 has yielded the largest sample of mouse remains, with a total of 31 specimens (pit 02.070: six specimens; pit 08.051: nine specimens). Their taxonomy within the *Mus* complex and their phenotypic relationship with current and past sub-species and populations of Southwest Asia (Table 1) was examined using the first lower molar (m1), in accordance with previous studies (Cucchi *et al.*, 2006, 2011; Cucchi, 2008).

Ancient samples of synanthropic house mice from Early Near Eastern Neolithic contexts have been



**Figure 2.** Aerial view of the Ovçular Tepesi site with the localization of the different pits where small mammal remains were collected (image courtesy of S. Sanz, CNRS).

**Table 1.** Localities, sites, and specimens of *Mus* species used for molar shape analysis

Taxon	Country	Map number	Localities/site	N	HG
<i>Mus</i> sp.	Azerbaijan-Nakhchivan (A)		Ovçular Tepesi	46	
<i>Mus musculus domesticus</i>	Azerbaijan-Nakhchivan (TG)	1	Dize village	6	3.4
	Israel (TG)	2	various	33	1.2.4.11
	Iran (TG)	3	Ahvaz	21	3.7.9
	Syria (TG)	4	Damascus	2	3
		5	Hamah	5	3.6.10
		6	Latakia	5	6.10
	Syria (P)	7	Halula	32	
	Turkey (A)		Cafer Höyük	23	
	Cyprus (A)		Cap Andreas Kastros	3	
<i>Mus musculus musculus</i>	Georgia (TG)	8	Alazani	1	
		9	Lagodekhi	5	
		10	Vachlavan	2	
		11	Tbilissi	4	
		12	Chiracskaya	3	
	Bulgaria (TG)	13	Dobromir	11	
<i>Mus musculus castaneus</i>	Iran (TG)	14	Espahan	36	
<i>Mus macedonicus spretoides</i>	Israel (TG)	15	Various	16	
<i>Mus macedonicus macedonicus</i>	Georgia (TG)	16	various	18	

TG, trapped and genotyped; P, owl pellets (*Tyto alba*); A, ancient; map number, location number of the sample; N, number of m1; HG, haplogroups *sensu* Bonhomme *et al.* (2011).

**Table 2.** Mitochondrial DNA typing and haplogroup assignment of the live-trapped specimens from Nakhchivan (Azerbaijan)

Location	Locality	Specimen	Genbank	Mt haplotype	HG*	HG†
Nakhchivan	Dize	Dize1	JX889722	A	HG4	Orkney
Nakhchivan	Dize	Dize2	JX889723	B	HG4	Orkney
Nakhchivan	Dize	Dize3	JX889724	A	HG4	Orkney
Nakhchivan	Dize	Dize4	JX889725	B	HG4	Orkney
Nakhchivan	Dize	Dize5	JX889726	C	HG3	TMC

\*Bonhomme *et al.* (2011), †Jones *et al.* (2010).

included to document past phenotypes of the commensal house mouse in the Near East. They were collected from two sites: Cafer Höyük (CH) in Turkey (approximately 7500 BC) and Cap Andreas Kastros (CAK) in Cyprus (approximately 7000 BC) and identified as *domesticus* by molar shape analysis (Cucchi, 2005).

The modern referential includes the two subspecies of the eastern Mediterranean short-tailed mouse: *Mus macedonicus macedonicus* and *Mus macedonicus spretooides* (Orth, Auffray & Bonhomme, 2002), as well as several geographical samples of the three different commensal house-mouse lineages associated with three potential dispersal routes towards Transcaucasia: *M. m. musculus* for the Northern route, *M. m. domesticus* from the Levant for the south-western route, and from Iran by a the south-eastern route (Fig. 1).

To enhance the sample size of *domesticus* in Syria, we identified 32 mice from Syrian barn-owl (*Tyto alba*) pellets collected in Halula in Northern Syria (A. Haydar, pers. com.). Their identification was assessed by molar shape analysis with discriminant probabilistic approaches against the two current sympatric species in Syria: *M. m. domesticus* and *M. m. macedonicus*. Twenty-nine *M. m. domesticus* and three *M. m. macedonicus* were identified and included accordingly in the modern referential from Syria.

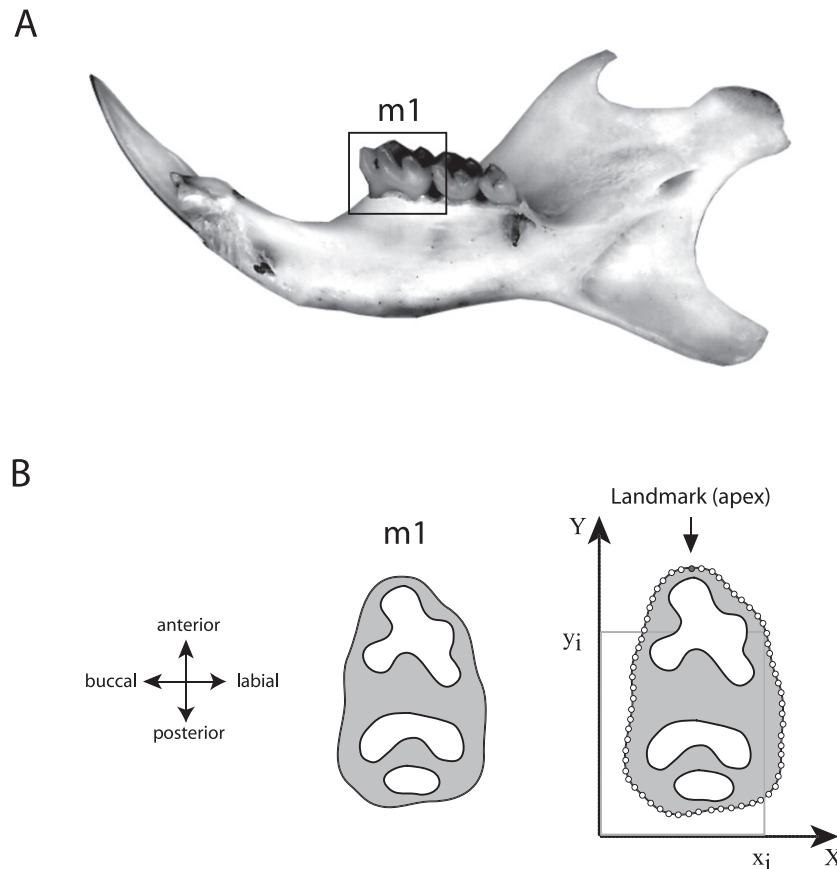
Modern specimens from Azerbaijan have been live-trapped in the immediate vicinity of Ovçular Tepesi site, in the village of Dize (Nakhchivan Autonomous Republic). Their mtDNA (D-Loop) has been identified as *domesticus* using a polymerase chain reaction and sequencing protocol *sensu* Rajabi-Maham *et al.* (2008). Their mtDNA haplotypes have been assessed using a Neighbour-Net unrooted tree (Hudson & Bryant, 2006) implemented in SPLITSTREE, version 4.10, in accordance with the exact same protocol and haplogroup numbering as that reported by Bonhomme *et al.* (2011). Among the five amplifying specimens of Dize (Table 2), four are associated with HG4 and one is associated with HG3. HG4 is an haplo-

group with an extensive distribution not only well represented in North Western Europe, but also found in Cyprus or in Asia Minor. HG3 is also widely dispersed but occurs mainly in Southwest Asia, first at a low frequency in the Northern Levant (Syria, Lebanon) but predominate over Northwest Iran, coastal Black Sea, and Central Anatolia (Bonhomme *et al.*, 2011).

#### GEOMETRIC MORPHOMETRICS

Molar shape analyses use a landmarks and sliding semi-landmarks approach. Two-dimensional images of m1 occlusive views were acquired with a Leica Microscope. The Cartesian co-ordinates were recorded on the images, starting from the furthest point of the anterior lobe (landmark) and along the crown's external outline of the m1 as 63 equally spaced semi-landmarks (Fig. 3) using TPSDIG, version 2.12 (Rohlf, 2010). The position, orientation, and scaling information from the raw coordinates were standardized by a generalized Procrustes analysis (GPA) with TPSRELW, version 1.45 (Rohlf, 2005). The semi-landmarks were constrained to slide along an estimated tangent at each sliding point using the Bending Energy method (Bookstein, 1997). Molar shape variables are the Procrustes co-ordinates obtained after the GPA superimposition on the 64 Cartesian co-ordinates of the m1 configuration.

The numerical taxonomy of *Mus* specimens from Ovçular Tepesi (called OT mice hereafter) was performed using predictive linear discriminant analyses (LDA). Differences between the current taxa of the *Mus* complex were assessed by multivariate analysis of variance. Predictions for the OT mice were performed over discriminant functions computed for a referential of three house mouse taxa (*domesticus*, *musculus*, and *castaneus* from Iran) and two Macedonian mice taxa (*M. macedonicus macedonicus* and *M. macedonicus spretooides*) (Table 1). We estimated the classification accuracy of the referential using



**Figure 3.** A, house mouse mandible (lingual view). B, lower first molar (m1) orientation and location of the semilandmarks (see text).

a leave-one-out cross validation procedure (Ripley, 1996) of a canonical variate analysis. Because LDA are affected by sample size and the number of variables used as group predictors (Mitterocker & Bookstein, 2011), we reduced the dimensionality of the variables *sensu* Baylac & Friess (2005) by defining the number of predictors as the  $N$  first Procrustes coordinates that both maximize the variability between groups without overestimating the cross validation percentage as a result of unbalanced sample sizes with 100 repetitions (Evin *et al.*, 2013). Predictive discriminant analyses provide *a posteriori* probabilities of membership to one of the groups. Specimens classified with posterior probabilities below 0.9 were excluded from the subsequent analyses. Above this threshold, each specimen is assigned to its predicted group in the subsequent analyses.

Phenetic relationships between taxa and populations are assessed by principal component analysis (PCA) on the Procrustes coordinates coupled with an unrooted Neighbour-joining (NJ) tree (Saitou & Nei, 1987) computed on the Procrustes distances between group means (taxa of various geographical origins).

The robustness of key bifurcations in the NJ unrooted tree was assessed using the correct cross-validation percentage (CVP) of a discriminant function computed between the cluster of interest and the external data. To avoid over-estimation of the CVP as a result of unbalanced sample sizes, 100 sub-samples of the external data set were randomly selected to match the number of individuals in the group of interest. The robustness was then expressed as the maximum of the upper limits of the confident intervals of the CVP distribution obtained for balanced samples (2013).

Statistical analyses were carried out with R, version 2.13.0 (R development Core Team), RMORPH library (Baylac, 2012) and ADE4 (Thioulouse *et al.*, 1997) packages. Discriminant functions are available in Evin *et al.* 2013.

## RESULTS

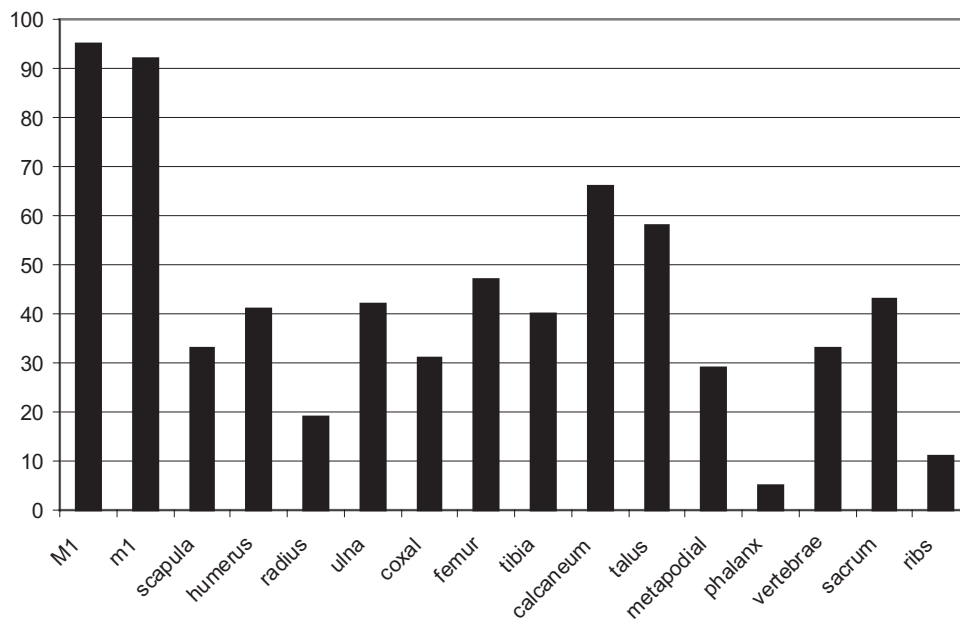
### ORIGIN OF THE OVÇULAR TEPESI SMALL MAMMALS

Among the 2127 identified bone fragments of small mammals, only four taxa of rodents and two taxa of

**Table 3.** Small mammal spectra pooled from the three pits of Ovuçular Tepesi

Family	Species	Vernacular names	Pit 02.070		Pit 01.171		Pit 08.051	
			NISP	MNI	NISP	MNI	NISP	MNI
Muridae	<i>Mus</i> sp.	House mouse	77	6	245	38	171	14
	<i>Meriones</i> sp.	Jird indet.			2	1	38	3
Cricetidae	<i>Cricetulus migratorius</i>	Grey hamster			8	1	1	1
	Arvicolinae indet.	Vole indet.					1	1
Soricidae	<i>Suncus etruscus</i>	Pygmy white-toothed shrew			5	2		
	<i>Crocidura</i> sp.	White-toothed shrew			9	2		
	Soricidae indet.	Shrew, genus indet.					1	
Total identified			<b>77</b>	<b>6</b>	<b>169</b>	<b>44</b>	<b>212</b>	<b>19</b>
Total unidentified rodent remains	Rodentia indet.	Hamster-size rodents	17		3		88	
		Mouse-size rodents	7		264		1190	
			<b>24</b>		<b>267</b>		<b>1278</b>	

NISP, number of identifiable fragments of each taxon; MNI, minimum number of individuals. Total number of identified bones and unidentified rodents are displayed in bold.

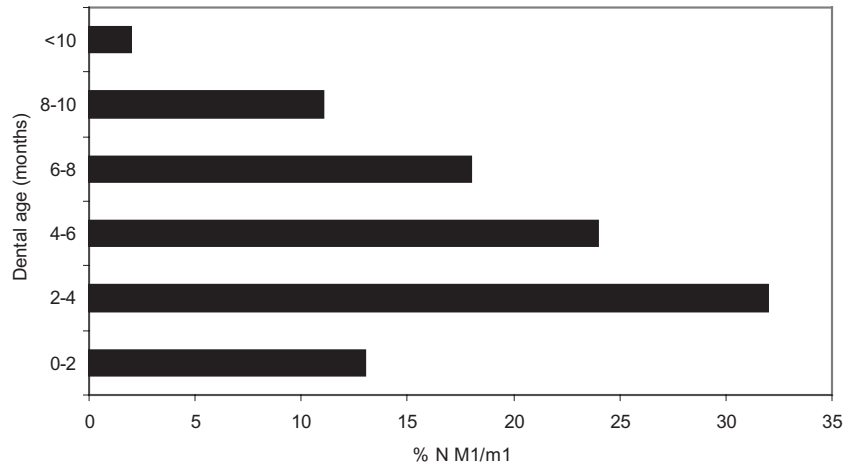


**Figure 4.** Diagram of the percentage of representation (%PR) of the main anatomical elements of mouse-size rodents considering the minimum number of individuals (lateralization only in the cases: long bone – presence of proximal part; talus and calcaneum – intact bone; coxal and scapula – presence of intact articular part).

insectivores could be recognized, indicating a very low diversity (Table 3). Mouse-like rodents (*Mus* sp.) are predominant with 84% of the minimum number of identified individuals, followed by rare occurrences of jird (*Meriones* sp.) and grey hamster (*Cricetulus migratorius*). Only one fragment of a vole molar (Arvicolinae indet.) was found, without possible specific identification. Insectivores are represented by two

taxa of white-toothed shrew (*Crocidura* sp. and *Suncus etruscus*).

Despite the poor level of preservation (95% in the three pits) and rather high fragmentation (75%), most of the post-cranial elements of individual skeleton are preserved (Fig. 4), demonstrating that complete individuals were trapped in the pits. Root and abrasion or digestion marks are low (15% and 4%, respectively),



**Figure 5.** Distribution of different age-classes of mice in Ovçular Tepesi pits (number of m1 = 9; number of M1 = 105).

whereas 6% of the bone assemblage displays charred marks (mainly calcination) indicating prolonged contact with high temperatures, probably a hearth. The intrusive character of certain specimens in the archaeological assemblage (e.g. burrowing rodents such as *Meriones* and *Cricetulus*) can be ruled out because these taxa show evidence of carbonization/calcination.

The age distribution of the mice accumulated in the three pits (Fig. 5) is represented by all the age categories of a population, with a majority of adults (age group 2–6 months), juveniles < 2 months, and older specimens > 10 months old.

#### NUMERICAL TAXONOMY OF THE OT MICE

Probabilistic predictions of the Ovçular Tepesi mice were computed on the discriminant functions for the modern samples of house mouse lineages showing highly significant molar-shape differences (Pillai = 1.5335,  $F = 5.8347$ ,  $P < 0.001$ ) with correct cross-validated classification of 85% on a reduced set of shape variables (41 PCs). Thirty-six specimens out of the 46 OT mice were classified with posterior probabilities above the 0.9 threshold: 31 specimens (86%) to *M. m. domesticus*, three to *M. m. macedonicus*, and two to *musculus*. The occurrence of the two latter taxa must be considered with caution because there are chances of misclassification. Therefore, we decided that only the 31 OT specimens identified as *M. m. domesticus* would be used in the phenotypic relationships study.

The phenetic relationship between ancient and present *Mus* sub-species and populations across Southwest Asia (Fig. 6) demonstrate a central morphogroup including the Iranian lineages (*castaneus*, *domesticus*), the *musculus* lineage (Georgia), the *domesticus* from Nakhchivan, and the Early Neolithic

*domesticus* from Turkey. From this central morphogroup, the *M. macedonicus* phylogroup (Syria, Georgia and Israel) diverge on one side and the Near Eastern modern (Syria, Israel) and ancient (Cyprus, Azerbaijan) *domesticus* diverge on the other. This trend is visible on both the PCA (Fig. 6A) and the NJ unrooted tree (Fig. 6B). These main divergences are supported by the highly significant morphological difference computed by the discriminant analyses (Fig. 6A). Both PCA and NJ demonstrate the OT house mice phenetic relationships with the Near eastern *domesticus* morphogroup and, more precisely, with the Syrian population, whereas the CAK *domesticus* from Cyprus are related to Israel. Both links are supported by a highly significant morphological difference of these two branches (Fig. 6A), suggesting a different dispersal origin for the Neolithic colonization of Cyprus and Southern Caucasia.

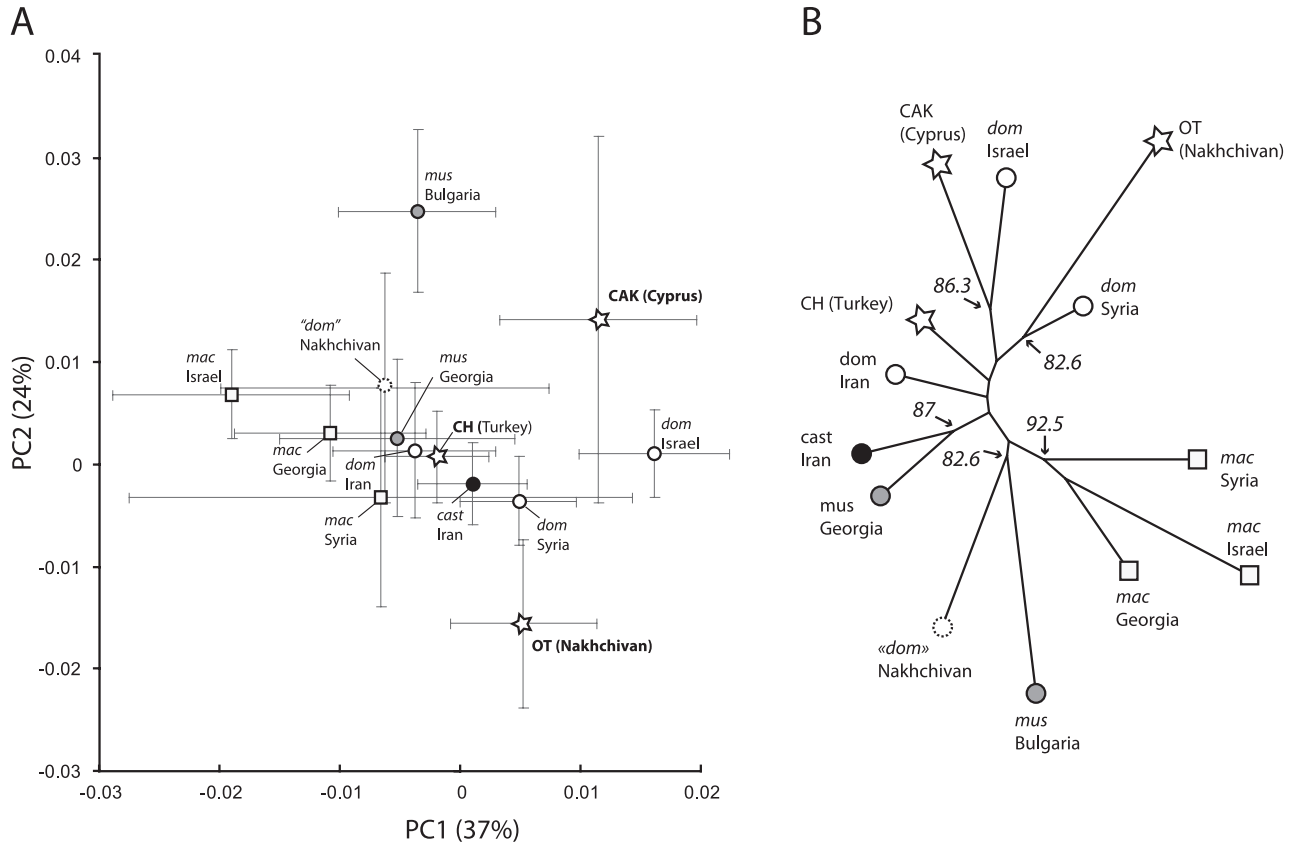
The phenetic relationships also demonstrate the drastic phenotypic shift of the house mouse population in Nakhchivan between the Late Chalcolithic and the present time. Indeed, the present-day specimens from Nakhchivan, despite a *domesticus* mtDNA, display phenetic relationships with the central morphogroup close to the *musculus* lineages in both the PCA and the NJ unrooted tree.

## DISCUSSION

### SYNANTHROPIC SMALL MAMMALS IN LATE CHALCOLITHIC AZERBAIJAN

The deep pits of Ovçular Tepesi have acted as open traps into which rodents and insectivores fell and died, sampling a small mammal community of low diversity (six identified taxa) compared to approximately 40 small mammal species identified in the natural habitat of Azerbaijan (Kryštufek & Vohralík,





**Figure 6.** A, scatter plot of the two first principal components (PCs) performed on the molar shape variables (Procrustes coordinates). Each symbol corresponds to the mean value of a modern or ancient group, bracketed by the 95% confidence interval. B, Neighbour-joining unrooted tree inferred from Procrustes distances between molar mean-shape of modern populations and archaeological samples of *domesticus*. Each bifurcation in the unrooted tree shows the maximum of the upper limits of the confident intervals for the percentage of correct cross validation distribution of the discriminant analyses (for more details, see Material and methods). CH, Cafer Höyük; CAK, Cap Andreas Kastros; OT, Ovçular Tepesi; *mac*, *Mus macedonicus*; *dom*, *Mus musculus domesticus*; *mus*, *Mus musculus musculus*; *cast*, *Mus musculus castaneus*; stars, archaeological samples of *domesticus*.

2005, 2009). According to recent ecological studies, few small mammals are pre-adapted to close interactions with humans and all the taxa from the OT pits, except for the jirds, are currently recognized as synanthropic species (Evstafiev, 2006). Among these species, the house mouse is the main commensal rodent, constantly living in man-made habitats, whereas the others occur only seasonally or occasionally. In the case of the pygmy white-toothed shrew, its presence in human settlements has only been rarely documented (Molur *et al.*, 2005). The same community of synanthropic species has been identified in a Chalcolithic village from Southern Romania (Cucchi *et al.*, 2011), providing evidence that the synanthropization process affected identical taxa in Chalcolithic Transcaucasia and Romania.

The proportion of house mice in the Late Chalcolithic settlement of Ovçular Tepesi is similar to that

found in areas dedicated to dwelling or food storage in the anthropogenic habitat of Ukraine (Evstafiev, 2006), providing indirect clues with respect to the function of the pits, at some point during the occupation of the settlement, as food storage or silos for grain storage.

#### THE ORIGIN OF THE OVÇULAR TEPESI HOUSE MOUSE AND THE NEOLITHIZATION OF TRANSCAUCASIA

The molar shape of the Ovçular Tepesi house mouse diverges from the ancestral morphotype of central lineages of *musculus* (Georgia), *castaneus* of Central Iran or even the *domesticus* from Southwest Iran (Siahsarvie *et al.*, 2012) but relates to the Near Eastern *domesticus* lineage and especially to the current *domesticus* morphotype of the Northern Levant (Syria). On the other hand, the Neolithic

*domesticus* of Cyprus are related to the Southern Levant (Israel), suggesting a different dispersal origin for the founding population of Cyprus more likely situated in Southern Levant, a route supported by the mitochondrial make-up of the current *domesticus* populations in Cyprus (Bonhomme *et al.*, 2011).

These phenotypic relationships exclude *de facto* dispersal routes from the Northern Caucasus or Northwest Iran during the initial phase of the invasive process of Southern Caucasia 6000 years ago. The Northern Near Eastern footprint encapsulated in the molar shape variation of the Ovuçular Tepesi *domesticus* rather suggests a dispersal origin that coincides with the upper Tigris/Euphrates basin, where mtDNA markers pinpoint the cradle of modern day commensal *domesticus* (Rajabi-Maham *et al.*, 2008). It is also the region where wild populations of *domesticus*, probably already present in the natural habitat ever since their natural dispersal about 200 000 years ago (Duvaux *et al.*, 2011), evolved towards full commensal behaviour (Cucchi *et al.*, 2012), at a time when Neolithic niche construction emerged with the first villages of farmers (Willcox, Fornite & Herveux, 2008; Willcox, Buxo & Herveux, 2009). The *domesticus* dispersal towards Nakhchivan from this Near Eastern commensal epicentre could result from the transfer of domestic animals and plants that indirectly testify to the existence of a human migration. This new insight into the early biogeographical history of the house mouse in Nakhchivan thus brings substantial evidence to support a scenario that features decisive near-eastern *stimuli* in the emergence of Neolithic cultures in Transcaucasia, at least in the Araxes basin. At Kültepe I, for example, the presence of rectangular mud-brick architecture, *terracotta* spindle-whorls, and chaff-tempered pottery has been interpreted as evidence of interactions between South Caucasian and Near-Eastern communities that may have triggered a process of Neolithization in Transcaucasia from the beginning of the sixth millennium BC onwards (Lombard & Chataigner, 2004: 76). The finding of a Near Eastern morphotype of *domesticus* in the Late Chalcolithic pits of Ovuçular Tepesi could be an indication that human migrations from the Near-East, and not just knowledge diffusion, are at the root of these Neolithization processes.

#### HOUSE MOUSE COLONIZATION AND HYBRIDIZATION HISTORY IN NAKHCHIVAN

Six thousand years later, the commensal house mouse population from the same locality in Nakhchivan displays a molar phenotype that is related to the sub-species *musculus*, whereas its *domesticus* mitochondrial signature is associated with haplogroup present in the Near East and the Black Sea coasts,

suggesting that the commensal house mouse of Nakhchivan is now predominantly a *musculus* population with *domesticus* mtDNA. This hypothesis would be in agreement with the nuclear signature of mice caught further north in Azerbaijan (Milishnikov *et al.*, 2004) and Eastern Georgia (Orth *et al.*, 1996) showing predominantly *musculus* populations forming a large intergradation zone between the two subspecies. A similar molar phenotype shift has been detected in Northwest Iran, this time from *castaneus* to *domesticus*, occurring sometime during the mid Holocene (Shabani *et al.*, 2010). These shifts suggests that, in the Middle East, sometime during the Middle/late Holocene, an important phase of expansion and secondary contact between house mouse lineages occurred, probably as a result of a new regime of human movements that contributed to facilitating the house mouse dispersal in this area.

Such discordance between mtDNA variation and nuclear markers is well documented for the house mouse populations of Sweden, Denmark, and most of Finland, where all the *musculus* populations have a *domesticus* mtDNA background as a result of founding events from a dispersal process originating from a hybrid zone in the far North of Germany (Gyllensten & Wilson, 1987; Prager *et al.*, 1993). On the other hand, recent studies conducted on nuclear markers and mitochondrial sequences of the house mice in Norway (Jones *et al.*, 2010) show that, beyond the hybrid zone, *musculus* genes are found in the *domesticus* territory, and suggest that this occurred as a consequence of relictual alleles of a first *musculus* colonization followed by passive transport of *domesticus*, probably during the Viking period (Jones *et al.*, 2010). The molar shape shift of the house mouse of Nakhchivan, from a '*domesticus*' to a '*musculus-like*' phenotype, likely results from secondary contact, whereby the original *domesticus* colonizers, probably made of small founding population via a Neolithic migration from the Northern Levant, would have been genetically displaced by an asymmetrical gene flow after hybridization with *musculus* intruders at a later time. The *musculus* dispersal, with a greater migrant flow, would have originated from the Northern Caucasus or South of the Caspian Sea, at the favour of human transport.

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