



Evolution of an invasive rodent on an archipelago as revealed by molar shape analysis: the house mouse in the Canary Islands

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ABSTRACT

Aim The aim of this paper is to identify the patterns in the morphological differentiation in Canary Island mice, based on fossil and modern samples. In order to achieve this, the mouse species present on the archipelago were first compared with a set of continental mice. The differences between the continental and Canary Island samples, and among the Canary Island samples, provide insights into the processes of colonization and the subsequent insular evolution.

Location Canary archipelago.

Methods An outline analysis based on Fourier transformation was used to quantify shape differences between lower molars. Together with the fossil and modern Canary Island samples, a reference set of genotyped continental populations of the commensal *Mus musculus* and the wild *Mus spretus* was used for comparison.

Results The morphometric analysis showed that all the mouse specimens from the Canary Islands and Cape Verde belonged to *Mus musculus domesticus*. Lower molars of extant mice from La Gomera, El Hierro, Gran Canaria, Tenerife, and to a lesser degree from Lanzarote, were similar to those of genotyped *M. m. domesticus* from the continent, while teeth of extant mice from Fuerteventura were more divergent. Fossil mice from Fuerteventura were very similar to the extant representatives on this island, and similar to the fossil mice on the nearby islands of Lobos and La Graciosa.

Main conclusions The mouse present on the Canary archipelago has been identified as the house mouse *M. m. domesticus*. Based on the shape of the lower molar, the Canary Island mice are divergent from the continental ones, but the degree of divergence varies with the geography of the archipelago. Overall, populations from eastern islands are more divergent from the continental mice than populations from western ones. Fossil populations indicate that this situation was established several centuries ago. Two main factors may have contributed to this pattern: the appearance of different types of environment on the islands since the successful settlement of the mouse, and/or the number of subsequent introductions of continental individuals via shipping.

Keywords

Anthropization, colonization, Fourier transform, geometric morphometry, human migration, insular syndrome, island biogeography, Late Holocene, *Mus musculus domesticus*, zooarchaeology.

INTRODUCTION

The expansion of human populations during the last millennia of the Holocene was accompanied by a massive turnover of faunas, resulting both from the active and passive transportation of animals and from the extinction of many species (Blondel & Vigne, 1993; Dobson, 1998; Masseti, 1998, 2002; Vigne, 1999; Gippoliti & Amori, 2006). Humans even reached islands that were at considerable distances from the continents, and here their impact on the biodiversity was particularly strong: multiple examples of extinction of endemic island mammals and birds have been recorded (Quammen, 1996). Among the mammal species introduced into the islands, the synanthropic small mammal species with commensal or anthropophilous behaviours have been the unwelcome accompaniment of human dispersal. The most common of these anthropochorous species are rats and mice, whose current ubiquity results in their strong dependence upon the anthroposphere (human environment). Both of these groups have been ranked by the IUCN as among the world's hundred worst invasive species for both biodiversity and human health (Lowe *et al.*, 2000).

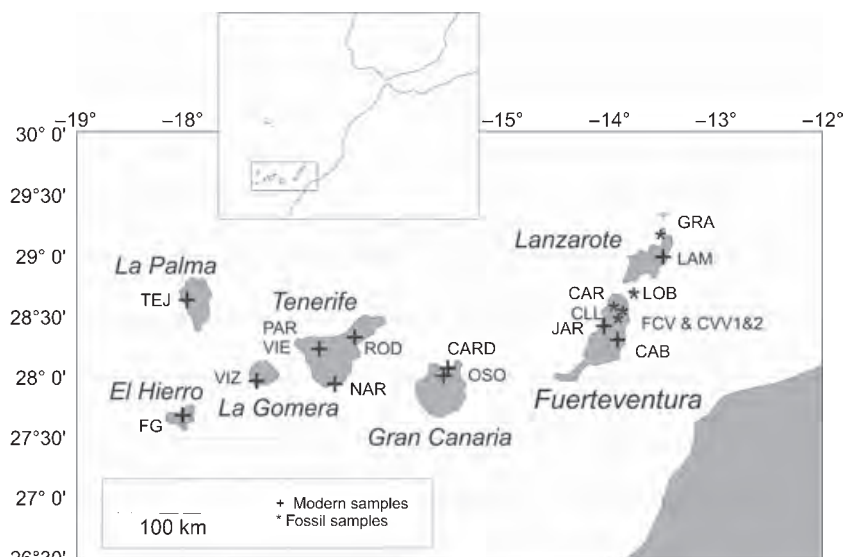
Many of the islands onto which these animals were introduced were characterized by a fauna devoid of, or poor in, mammalian species. Their impact as new competitors thus had dramatic consequences on the local small mammal fauna (Vigne & Valladas, 1996; Dowler *et al.*, 2000). At the same time, human expansion provided unintentional evolutionary experiments, allowing the invasive species to colonize the new environment, or at least a large part of it, as is the case, for example, for the house mouse. Did the new migrant evolve effectively, and what was the ensuing evolutionary pattern? Are we able to demonstrate and quantify its morphological evolution? Such questions can be addressed in the context of the Holocene colonization of islands: an absolute dating of fossil remains is possible, a detailed ecogeographical context is

accessible, and climatic variations are well known. Finally, islands can be expected to provide better laboratory conditions than continental areas in which to trace complex histories associated with human migrations.

The Canary Islands (Fig. 1) provide a suitable case study for addressing such questions since they were only colonized by humans late in the Holocene. This colonization had dramatic consequences on the autochthonous fauna of terrestrial vertebrates, many of which have become extinct during the last three millennia. The giant lizards and the three autochthonous rodents were particularly affected. The rodents were members of the Old World rats and mice subfamily (Murinae). They colonized several islands of the Canary archipelago by natural means, leading to endemic genera and species: *Canariomys bravoii* on Tenerife (Crusafont & Petter, 1964), *Canariomys tamarani* on Gran Canaria (López-Martínez & López-Jurado, 1987), and *Malpaisomys insularis* on the oriental Canary Islands, Fuerteventura and Lanzarote (Hutterer *et al.*, 1988). The youngest fossils of these endemic rodents are frequently found in association either with archaeological remains or with a mouse, considered to be the house mouse, *Mus musculus* Linnaeus, 1758, the only species among the Eurasian *Mus* genus complex that has a commensal interaction with humans (Bonhomme *et al.*, 1984). However, on Fuerteventura, one of the eastern Canary Islands, the mouse found in association with *Malpaisomys insularis* presents some typical characteristics (Carrascosa & López-Martínez, 1988), indicating that the identification requires further clarification.

Two species of the genus *Mus* are potential candidates for the colonization of the Canary Islands as well as of other eastern Atlantic Ocean archipelagos and islands, namely *Mus musculus* and *Mus spretus* Lataste, 1883. Both are present in north-west Africa today (Auffray *et al.*, 1990). The wild species *M. spretus* occupies the western Mediterranean and is considered native to the Maghreb (Dobson, 1998). It is thought to have been present in north-west Africa since the end of the

Figure 1 Canary Islands. Abbreviations: crosses and stars indicate recent and fossil samples, respectively. FG, La Fuga de Gorreta; TEJ, Barranco. Tahona El Jesus; VIZ, La Vizcaina; NAR, Barranco de Narices; ROD, Carretera de Los Rodeos; PAR, Partidos de Franquis; VIE, Montaña del Viento; CARD, Cardones; OSO, Osorio; JAR, Barranco Jarubio; CAB, Barranco de Rio Cabras; CVV, Cueva de Villaverde, upper sample; FCV, Cueva de Villaverde, lower sample; CLL, Cueva del Llano; CAR, Malpais de Arena; LOB, Lobos island; Lam, Malpais de la Corona; GRA, Graciosa (Montaña Amarilla).



Pleistocene (Darviche *et al.*, 2006). If the colonization occurred through natural dispersion, the most probable ancestor for Canary mice is the wild mouse *Mus spretus*. If the colonization occurred through passive transport by humans, the house mouse *Mus musculus* ssp. is the most probable candidate, as suggested by current observations on stowaway transport (Baker, 1994). Its identification as the house mouse would allow both an assessment of insular evolutionary patterns with reference to the mainland ancestor, and conclusions to be drawn about the colonization of the archipelago by man. Indeed, the presence of the house mouse would provide information on past connections between the continent and the islands resulting from human migrations (Cucchi *et al.*, 2002, 2005; Cucchi, 2005).

The time of the aboriginal human settlement on these islands, as well as the nature and importance of the contacts between Guanches and peoples of the nearby continents and Mediterranean area are still under discussion (Mederos Martín & Escribano Cobo, 2002).

The status of the Canary Islands mouse needs to be clarified before it is possible to identify the patterns of space (continent vs. Canary archipelago and eastern vs. western Canary Islands) and time differentiation, and the evolutionary processes involved. Two further topics will be addressed by considering the morphological differentiation of the Canary Islands mouse: human settlement on the Canary Islands; and the degree of isolation of this archipelago before the 15th century.

MATERIALS AND METHODS

Modern and fossil Canary Islands mice are here compared with a genotyped reference set including the house mouse *Mus musculus* and the wild mouse *Mus spretus*. In western Eurasia, the house mouse is represented by two subspecies (sometimes regarded as two species; see, for example, Musser & Carleton, 2005) with parapatric geographical ranges. *Mus musculus musculus* occurs in eastern and central Europe, whereas *M. m. domesticus* occupies western Europe and the Mediterranean basin. Given the location of the Canary Islands, the latter subspecies is the one most likely to have colonized these islands. Hence, *M. m. musculus* is represented in the genotyped reference set by one population from Denmark only. Geometric morphometrics was used, a method that is suitable for interspecific and intraspecific identification of fossil mice remains (Cucchi *et al.*, 2002; Cucchi, 2005).

The study was based on a sample set (Table 1) of 724 first lower molars (m1) of mice (*Mus*). The reference set for known species included 173 house mice, *M. m. domesticus*, from Greece, Israel, France including Corsica, Italy including Sardinia, Algeria and Tunisia. The other subspecies of *Mus musculus*, namely *M. m. musculus*, occupies the Balkans, central and eastern Europe, as far north as Denmark. A sample of 19 animals from Denmark documents this taxon. A sample of 84 animals from France, Spain (including Majorca), and Morocco documents the western Mediterranean wild mouse *Mus spretus*. These samples are part of the ISE collection,

University of Montpellier II. Owl pellets collected on each of the seven islands provide the sample (248 m1) for the study of the modern variation on the Canary archipelago. The sample also includes 171 m1 from the eastern Canary Islands, which were collected in sediments and for that reason are here referred to as fossils (Fig. 1 and Table 1). Finally, a sample of 29 m1 from one island of the Cape Verde archipelago (Santa Luzia Island, site of La Ribeira de Penedo) documents a case of recent colonization of an island previously devoid of rodents. The colonization of this archipelago by humans is known to have occurred around the middle of the 15th century, the islands previously having been uninhabited. This sample was collected at the top of a deposit associated to a still-occupied barn owl nest, the deposit yielding at its base solely bones of autochthonous reptiles, and at its top bones of the house mouse and of the small autochthonous *Tarentola caboverdiana* Schleich, 1984. The environment is very arid, and the island is still uninhabited.

Fossil samples

Seven samples of mice were extracted from sediments deposited in caves or cavities. These sediments also included bones and teeth of the now extinct *Malpaisomys insularis* and of the rare, endemic shrew *Crocidura canariensis* (Hutterer *et al.*, 1987). Either dry or wet sieving was performed, with the smallest mesh usually being 0.7 mm. The localities that provided the samples are as follows:

1. Cueva de Villaverde is an archaeological site. The sediments, which partly filled a collapsed lava tube, are stratified, and *Malpaisomys* is abundant while the mouse is only present in the upper levels (Carrascosa & López-Martínez, 1988; Boye *et al.*, 1992). Three samples come from this site – one (FCV) from outside the entrance of the cave, and two (CVV1 and CVV2, collected in 1988 by R. Hutterer, N. López-Martínez and J. Michaux) from inside the cave.
2. Cueva del Llano, which is not an archaeological site, is a locality within a collapsed lava tube, a few kilometres north of Cueva de Villaverde. The stratigraphy of the filling and taphonomic processes responsible for the accumulation of fossils have already been published (Coello *et al.*, 1999; Castillo-Ruiz *et al.*, 2001). The autochthonous mammals present are abundant, especially *Malpaisomys*, while the mouse is present only in the uppermost level (sample CLL).
3. Malpais de Arena (sample CAR) is a filling of a small lava tube, where *Malpaisomys* and *Mus* were collected together.
4. Lobos (sample LOB) is a small lava mount, where *Malpaisomys* and *Mus* are both present in filled cavities.
5. La Graciosa is in the Montaña Amarilla area. The sample GRA was collected from the sieving of sediments that filled a fissure.

The dating of these mouse samples is critical because the reconstruction of the history of the house mouse and of the colonization of the Canary Islands by humans requires a high power of resolution, at least of the order of a century. Several

Table 1 Samples considered in this study, with abbreviation (Code), large-scale location (Country/island), sample origin (O), taxa analysed (Taxon) and sample size (m1). F, material from sediment filling caves or cavities; P, pellets; T, trapped animals (genotype available). Age of the samples: recent except for F, considered likely to be several centuries old (see text for explanation).

Deposit/trapping locality	Code	Country/island	O	Taxon	m1
Cueva de Villaverde – outside	FCV	Fuerteventura	F	<i>M. sp.</i>	29
Cueva de Villaverde – inside	CVV1	Fuerteventura	F	<i>M. sp.</i>	25
Cueva de Villaverde – inside	CVV2	Fuerteventura	F	<i>M. sp.</i>	28
Cueva del Llano	CLL	Fuerteventura	F	<i>M. sp.</i>	9
Malpais de Arena	CAR	Fuerteventura	F	<i>M. sp.</i>	30
Lobos 4	LOB	Island of Lobos (Fuert.)	F	<i>M. sp.</i>	28
Graciosa (Montaña Amarilla)	GRA	Island of La Graciosa (Lanz.)	F	<i>M. sp.</i>	22
Santa Luzia	SLZ	Cape Verde	F	<i>M. sp.</i>	29
Malpais de la Corona	LAM	Lanzarote	P	<i>M. m. ssp.</i>	25
Barranco Jarubio	JAR	Fuerteventura	P	<i>M. m. ssp.</i>	30
Barranco de Rio Cabras 1	CAB	Fuerteventura	P	<i>M. m. ssp.</i>	20
Cardones	CARD	Gran Canaria	P	<i>M. m. ssp.</i>	6
Osorio	OSO	Gran Canaria	P	<i>M. m. ssp.</i>	12
Barranco de Narices	NAR	Tenerife	P	<i>M. m. ssp.</i>	25
Los Rodeos	ROD	Tenerife	P	<i>M. m. ssp.</i>	22
Montaña del Viento	VIE	Tenerife	P	<i>M. m. ssp.</i>	32
Partidos de Franquis	PAR	Tenerife	P	<i>M. m. ssp.</i>	35
Vizcaina	VIZ	La Gomera	P	<i>M. m. ssp.</i>	13
Fuga de Gorreta	FG	El Hierro	P	<i>M. m. ssp.</i>	22
Barranco Tahona el Jesus	TEJ	La Palma	P	<i>M. m. ssp.</i>	6
Reference samples	MDGRE	Greece	T	<i>M. m. domesticus</i>	22
	MDISRL	Israel	T	<i>M. m. domesticus</i>	23
	MDALG	Algeria	T	<i>M. m. domesticus</i>	14
	Mdpiana	Corsica – Piana islet	T	<i>M. m. domesticus</i>	6
	MDCOR	Corsica	T	<i>M. m. domesticus</i>	31
	MDFR	France	T	<i>M. m. domesticus</i>	20
	MDIT	Italy	T	<i>M. m. domesticus</i>	26
	MDSAR	Sardinia	T	<i>M. m. domesticus</i>	11
	MDTUN	Tunisia	T	<i>M. m. domesticus</i>	20
	MMDEN	Denmark	T	<i>M. m. musculus</i>	19
	MSSP	Spain	T	<i>M. spretus</i>	18
	MSFR	France	T	<i>M. spretus</i>	17
	MSMAJ	Majorca	T	<i>M. spretus</i>	23
	MSMOR	Morocco	T	<i>M. spretus</i>	26

¹⁴C ages of charcoal, bones and shells are already available. The interval time ranges in calibrated calendar ages (95.4% probability; Reimer *et al.*, 2004) are as follows.

Cueva de Villaverde: (1) 861 AD–1042 AD for charcoal from the deposit outside the entrance of the cave (Carrascosa & López-Martínez, 1988); the studied mouse sample FCL was extracted from this deposit; (2) 210 AD–420 AD for charcoal from a level inside the cave (level 3 in Carrascosa & López-Martínez, 1988); (3) 840 BC–484 BC for *Malpaisomys* bones (carbon dating sample GrA-27413: Centre for Isotope Research, University of Groningen, the Netherlands) collected inside the cave together with *Mus* sample CVV1.

Lobos 4: 1296 AD–1409 AD (small mammal bones; carbon dating sample GrA30417);

Graciosa: 123 BC–28 AD (shearwater bones; carbon dating GrA-30215).

Cueva del Llano: 6384 BC–5462 BC and 6266 BC–5309 BC (terrestrial gastropods; calibrated ages based on ages given in Coello *et al.*, 1999 and Castillo-Ruiz *et al.*, 2001) for the level with mouse remains (CLL).

The age of the *Mus* samples collected from these sites is difficult to ascertain because their association with the available radiocarbon ages is not reliable. The main reason for this is the nature of the samples, coming as they do from sediments deposited in caves or lava tubes. In such environments post-depositional disturbance is commonplace. The small vertebrate bones are strongly subject to vertical migration through stratigraphical succession as a result of bioturbation (burrowing, roots, percolation, etc.). These vertical movements can cause contamination of the lower layers by the upper ones. This appears to have happened in the two CVV samples from inside the Villaverde cave, as they contained a small number of *Mus* bones compared with the large numbers of *Malpaisomys* bones. It is possible that the *Mus* remains could belong to mice from upper layers. The same post-depositional disturbances may have affected the charcoal used for radiocarbon dating. The three ¹⁴C ages from Cueva de Villaverde nevertheless agree with the dates for the aboriginal human settlements on the Canary Islands. The Canary Islands have been inhabited for about 2500 years (Mederos Martín &

Escribano Cobo, 2002), and such a time interval is compatible with the occurrence of the house mouse in the north-western Mediterranean area (Cucchi *et al.*, 2005). This is not the case for the two ages provided by Cueva del Llano. If allocated to the mouse, such ages would be several thousands of years older than those stated for the house mouse history in the west of the Old World, a fact already noted by Cucchi *et al.* (2005). The dating of snail shells is generally considered to be unreliable. Like charcoals and small vertebrate bones, the shells can move along the stratigraphic column, and, furthermore, tests of them can incorporate carbonates from older levels and calcareous crusts present in the surrounding area. Therefore, the radio-carbon date of the layer CLL9 where *Mus* appear with *Malpaisomys* should be considered to be unreliable.

The embedding of small mammal bones and teeth in sediments is the result of various processes that follow the primary deposition of owl pellets (Andrews, 1990). As the studied mouse remains are in the process of fossilization, their ages will not be determined until accelerator-based mass-spectrometric (AMS) technique ^{14}C dating can be obtained from mice bones. It can only be suggested that these samples are several hundred years old.

Outline analysis

The morphological variation of murine molars can be efficiently described by the two-dimensional projection of the tooth viewed from its occlusal surface. The outline registers the differences in the relative positions and importance of the main cusps, as well as of any secondary cusps (or conule) if located near the base of the crown. A further advantage is that such an outline does not vary greatly with wear, and thus provides a morphological estimate independent of the age of the animals and of the age structure of the population (Renaud, 2005).

An efficient approach to analysing such outline data is the elliptic Fourier transform (EFT). This method is based on separate Fourier decompositions of the incremental changes along x and y as a function of the cumulative length along the outline (Kuhl & Gardina, 1982; Ferson *et al.*, 1985). Any harmonic corresponds to four coefficients: A_n and B_n for x , and C_n and D_n for y , defining an ellipse in the xy -plane. The coefficients of the first harmonic, describing the best-fitting ellipse to the original outline, are used to standardize the size, orientation, and starting point of the object. These standardizations are a major advantage of the EFT, together with the very accurate reconstructions obtained using the inverse EFT. The possibility of standardizing the orientation of the outline, and especially the location of the starting point, is of great use for the first lower molars of mice. Such teeth do not display an easily recognizable point from which to start the outline, and hence the use of the EFT with the available standardization significantly increases the accuracy of the comparisons between the outlines.

A drawback of the EFT is that the Fourier coefficients of one harmonic cannot be considered as independent because the

variations along x and y are related when considering a closed outline. However, this does not greatly influence the observed patterns of morphological differentiation, which are comparable to results obtained with other methods of outline analysis (Rohlf & Archie, 1984; Renaud & Michaux, 2003).

Seven harmonics were retained because this threshold has been shown to constitute a satisfying compromise between measurement error and information content on mice teeth (Cucchi, 2005). Fourier coefficients from the first harmonic were not retained in the following statistical analyses, because they correspond to residuals after standardization (Crampton, 1995; Renaud *et al.*, 1996). Hence, 24 Fourier coefficients constituted the variables considered in the subsequent analyses.

Statistical analyses

The overall morphology of each tooth is a combination of its size and shape.

The size of the m1 was estimated by a univariate parameter, the area of the ellipse corresponding to the first harmonic. Differences were tested using an analysis of variance (ANOVA). In order to obtain a better picture of the pattern of differentiation between Canary Island and genotyped mice, and among Canary Island mice, pairwise comparisons were also performed. The Tukey correction for multiple comparisons was used, an analogue of the Bonferroni procedure for a large number of pairs of means.

The shape of each outline was described by a set of 24 Fourier coefficients (4 coefficients per 6 harmonics – the coefficients of the first harmonic were not included). This set of coefficients was analysed using multivariate statistics.

A discriminant analysis was performed only on the genotyped specimens of the three modern species considered. Fossil and modern specimens from the Canary Islands and Cape Verde were not taken into account for the calculation of these discriminant axes but were classified into the species they were morphologically closest to.

Differences between localities were further investigated using multivariate analysis of variance (MANOVA; test considered: Wilks' Lambda). In this case, genotyped specimens and fossil or modern teeth from the Canary Islands and the sample from Cape Verde were treated in the same way. Canonical axes were estimated from a MANOVA that displayed the total morphological variation on a few synthetic shape axes. Outlines obtained using an inverse Fourier transform allowed the visualization of the shape differences involved. Outlines have been reconstructed for some group means and for extreme values along the canonical axes. Such reconstructions can be obtained by calculating the multivariate regression parameters of Fourier coefficients (dependent variables) on the relevant canonical axis (independent variable).

A second analysis focused only on mice from the Canary Islands, in order better to assess the pattern of differentiation among the islands, and between modern and fossil samples.

The representations on multivariate axes might be misleading because the information is summarized on the first principal plane(s). The differentiation of a sample on subsequent axes would thus not be visualized. Therefore, the previous analysis was completed by another representation including all the dimensions of differentiation. Euclidean distances were calculated between the means of each modern and fossil group, including the Fourier coefficients from the second to the seventh harmonic. Cluster analyses were applied to this distance matrix and visualized as phenetic trees. Two methods were used: a UPGMA (unweighted pair-group method, arithmetic average), which brings all branches to the same length, and a neighbour-joining method (unweighted), which retains unequal branch lengths.

The statistics were calculated using SYSTAT v.10 and NTSYS-PC.

RESULTS

Classification of the Canary mice in the genotyped reference set

A discriminant analysis with the species and subspecies as grouping variable on the genotyped reference set shows a clear morphological differentiation between the three taxa *M. m. domesticus*, *M. m. musculus* and *M. spretus*, based on the outline of their m1 (Wilks' Lambda test $P < 0.0001$). The classification of the genotyped specimens on the discriminant axes provides satisfying results (Table 2), with some 90% of classifications being correct for the two well-represented taxa *M. spretus* and *M. m. domesticus*. The robustness of the results is confirmed by the high percentage of correct classifications using a jack-knifed test (Table 2). This reference set and the corresponding discriminant axes were used to classify the specimens of unknown genetic origin, i.e. the fossils from the Canary Islands, the sample from the Cape Verde Islands and the modern teeth from owl pellets, documenting the morphological variations on the Canary archipelago.

The results are unambiguous and indicate that all these samples should be considered as *M. m. domesticus* (Table 2). The modern samples from the western Canary Islands, namely FG (El Hierro), VIZ (La Gomera) and CARD (Gran Canaria), are classified at 100% into *M. m. domesticus*. Among the modern samples, most provide classification rates of above 90% into *M. m. domesticus*: JAR (Fuerteventura), OSO (Gran Canaria), and the four samples from Tenerife (NAR, ROD, VIE, PAR).

The fossils provide lower rates of classification as *M. m. domesticus*, most samples coming into the 70–80% category. The two fossil assemblages from Lobos island, close to Fuerteventura, and La Graciosa island, close to Lanzarote have c. 50% of the specimens classified as *M. m. domesticus*, the rest being classified as *M. spretus* or *M. musculus musculus*. One further case of classification as *M. m. musculus* has been found for the Santa Luzia sample, an island of the Cape Verde

Table 2 Classification matrix (cases in row categories classified into columns) based on a discriminant analysis. The analysis is based on three species of mice: *Mus musculus domesticus* Schwartz & Schwartz, 1943, *M. m. musculus* Linnaeus, 1758, and *M. spretus* Lataste, 1883. The outline of the first lower molar was analysed for a set of genotyped specimens in each case. Teeth from the Canary Islands, from fossil deposits and owl pellets, were classified into any of the three mouse species, based on the morphological distance of each tooth from the genotypic groups. In order to assess the robustness of the classification, specimens from the original data set (genotyped mice) were submitted to the classification (% correct), including a jack-knifed test (percentage correct in brackets).

Group	Sample	<i>M.m.d.</i>	<i>M.m.m.</i>	<i>M.s.</i>	% correct
Genotyped					
<i>M.m.d.</i>	Total	2	17	0	89 (84)
<i>M.m.m.</i>	Total	5	1	78	93 (87)
<i>M. spretus</i>	Total	162	0	11	94 (92)
Canary					% <i>M.m.d.</i>
Modern					
East	FU-JAR	28	0	2	93
	FU-CAB	15	0	5	75
West	LA-LAM	22	0	3	88
	GC-CARD	5	0	0	100
	GC-OSO	10	0	1	91
	TE-NAR	24	0	1	96
	TE-ROD	21	0	1	95
	TE-VIE	28	0	1	97
	TE-PAR	32	0	1	97
	LG-VIZ	13	0	0	100
	HIE-FG	22	0	0	100
	LP-TEJ	4	0	2	67
Fossil					
Canary	FCV	21	0	8	72
	CVV1	19	0	6	76
	CVV2	21	0	7	75
	CLL	7	0	2	78
	CAR	24	0	6	80
	LOB	16	0	12	57
	GRA	11	2	9	50
Cape Verde	SLZ	19	1	9	66

archipelago (SLZ). Overall, 66% of the teeth are attributed to *M. m. domesticus*.

Patterns of shape differentiation of the lower molar

The classification of specimens from the Canary Islands and Cape Verde into the genotyped reference set suggests that these mice should be considered as *M. m. domesticus*. However, numerous teeth were also identified as *M. spretus*. To understand better the pattern of morphological differentiation, a canonical analysis was performed on the total data set, the grouping variable being the modern or fossil sample, or the trapping location (see Table 1). A significant morphological differentiation existed among samples (Wilks' Lambda test, $P < 0.0001$). The first two canonical axes corresponded to 27%

and 17% of the among-group variance, respectively (Figs 2a & 3b). On these axes, which represent most of the morphological differentiation, *M. spretus* clearly separates from *M. m. domesticus* by a shift towards both positive CA1 and negative CA2 values. *Mus musculus musculus* is less clearly differentiated, but isolates along CA4 (10% of variance, data not shown), whereas CA3 (11%, not shown) corresponds to a variation within *M. spretus*. Corsica and the nearby island of Piania document insular populations of *M. m. domesticus*. They cluster within the range of variation of the mainland *M. m. domesticus*.

Compared with this genotyped reference set, the modern and fossil teeth from the Canary archipelago tend to shift towards negative CA1 values. Modern samples from the western Canary Islands cluster together close to the *domesticus* pool. The modern and fossil samples from Fuerteventura display a more definite differentiation compared with *domes-*

ticus, shifting further towards negative CA1 and CA2 values. Among these samples, the fossils from Lobos island (LOB), close to Fuerteventura, diverge slightly more. Mice from Lanzarote, despite the eastern location of the island, resemble those from the western Canary Islands. Finally, the sample from the Cape Verde archipelago (SLZ) clearly falls close to the *domesticus* pool.

Variation of the m1 outline within the Canary archipelago samples

An analysis of the m1 outline on the Canary Island samples (Fig. 2b) allows us to focus on the pattern of differentiation in the archipelago (Wilks' Lambda test $P < 0.0001$). A geographical rather than a temporal signal emerges, with modern and fossil samples from Fuerteventura clustered towards negative

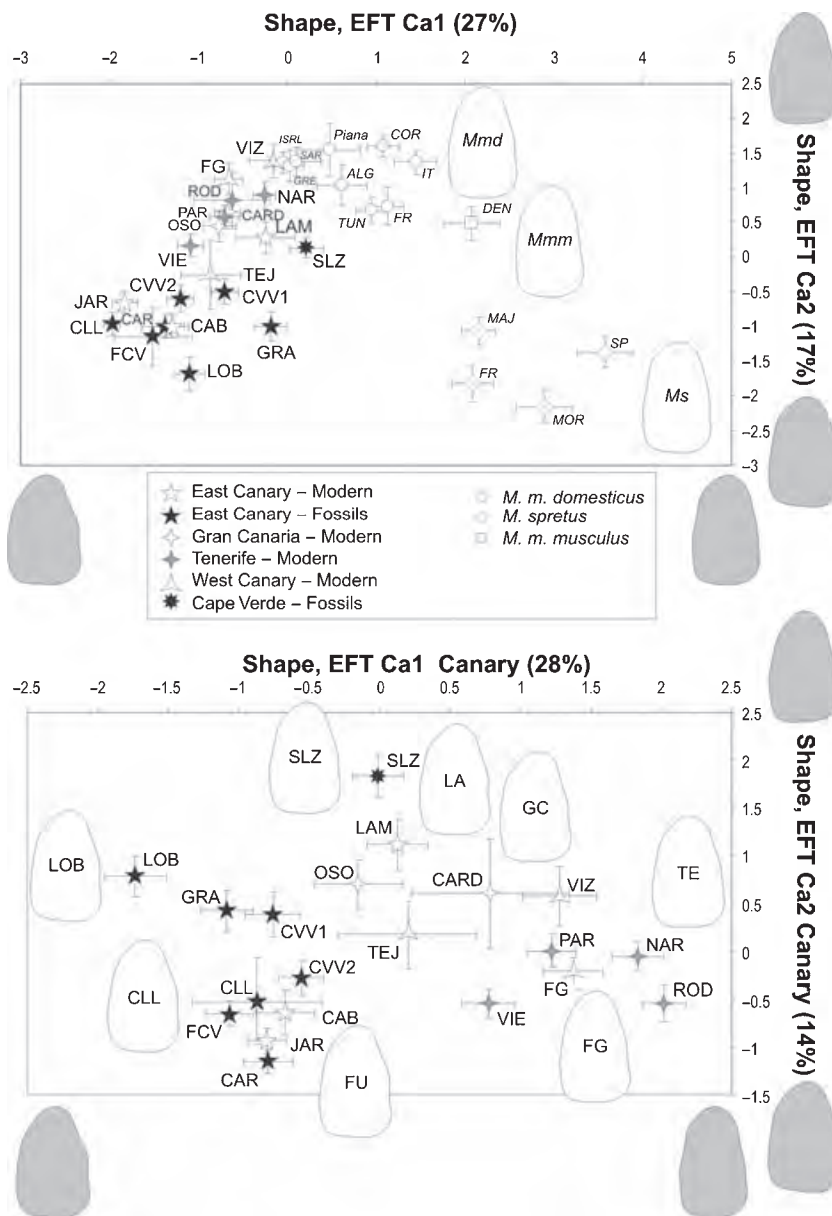


Figure 2 Shape differentiation of the first lower molar on the Canary Islands. (a) Canarian mice compared with the genotyped reference set including samples of *Mus musculus* Linnaeus, 1758 and *Mus spretus* Lataste, 1883. (b) Differentiation within the Canary archipelago. In both parts, the axes correspond to the first and second canonical axes of an analysis performed on the Fourier coefficients (second to seventh harmonics) of an elliptic Fourier transform of the m1 outline. Symbols correspond to the group mean, bracketed by the 95% confidence interval. Reconstructed outlines, obtained by an inverse Fourier transform, visualize the shape changes. Open outlines correspond to some group means; grey outlines, to extreme values along canonical axes (+3/-3).

CA1 (28% of variance) and well differentiated from all the other samples. The samples from Lobos island (near Fuerteventura) and La Graciosa (near Lanzarote) further shift towards negative values along the first canonical axis. Samples from the western Canary Islands including Tenerife, La Gomera and El Hierro constitute the other end-member along the first axis. Samples from Lanzarote, Gran Canaria and La Palma are intermediate in shape.

Phenetic trees calculated on group means complete the representation on the multivariate axes (Fig. 4). Both algorithms (UPGMA and NJ) provide similar patterns, suggesting that the emerging results are robust. The four samples of *M. spretus* are clustered together. These samples and the single

sample documenting *M. m. musculus* constitute the most divergent groups. Most, if not all, genotyped samples of *M. m. domesticus* constitute the other group, among which the Canarian samples are nested. The m1 from Cape Verde (SLZ) fall close to the occidental samples of *M. m. domesticus* (e.g. France, Algeria, Corsica, and Sardinia). The samples from the western Canary Islands (Tenerife, El Hierro and La Gomera) cluster together close to oriental *M. m. domesticus* (Greece and Israel) and the insular house mice from Pianca. The two samples from Gran Canaria cluster together in an intermediate position, close to the western Canary Islands but divergent from the *M. m. domesticus* stock. Finally, the m1 from the eastern Canary Islands constitute a rather isolated group. The fossil and the

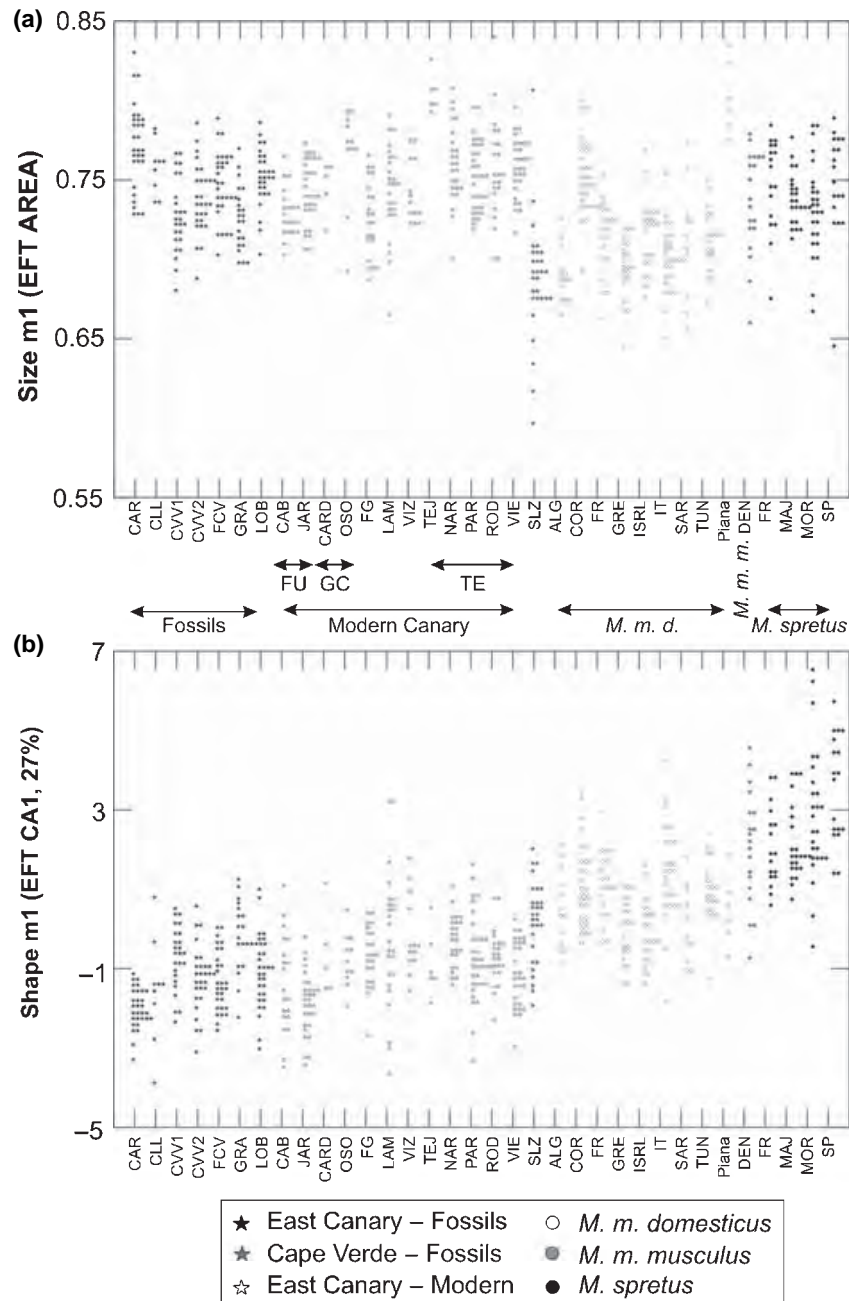


Figure 3 Morphological variation of the first lower molar in fossil and extant samples of mice from the Canary Islands and in samples of genotyped specimens: (a) size of the first lower m1, and (b) shape estimated by scores on the first canonical axis, representing 29% of the among-group variation. For locality and sample abbreviations, see Fig. 1 and Table 1.

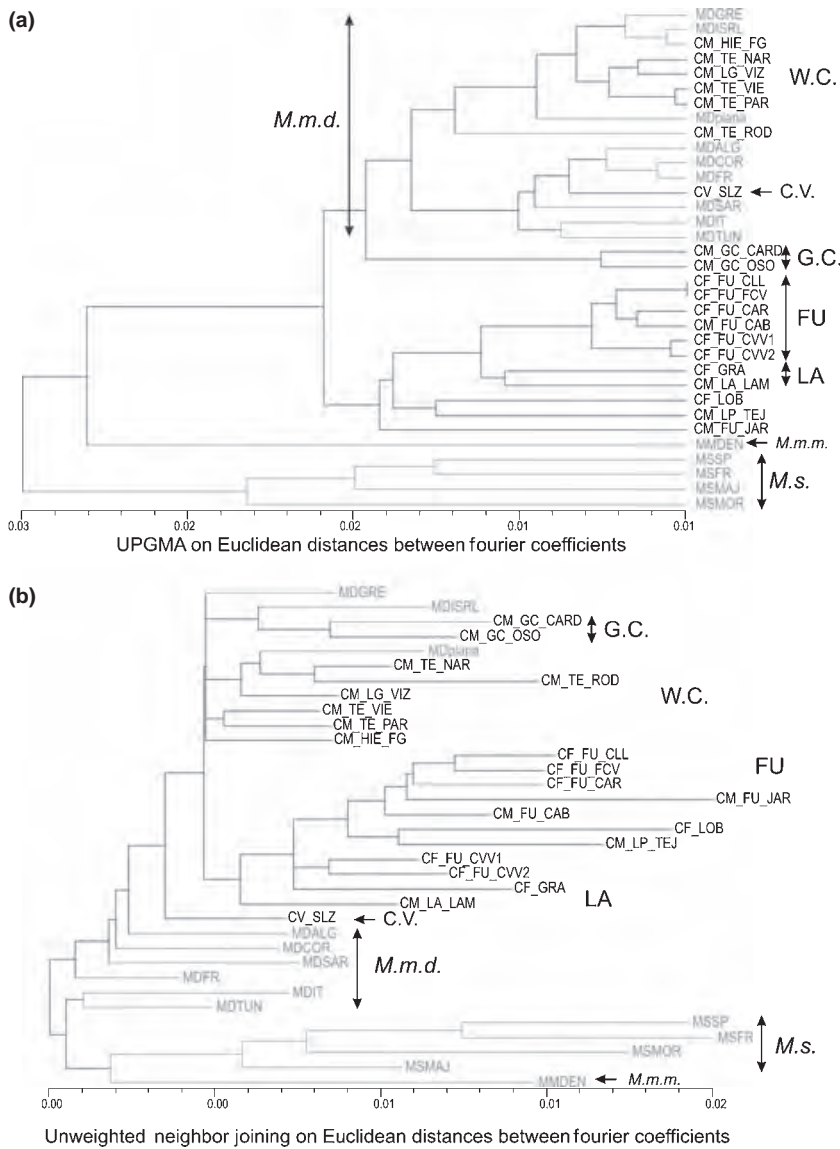


Figure 4 Phenetic trees visualizing the distances among group means. The Euclidean distances between group means were calculated based on the Fourier coefficients of the second to seventh harmonics. A cluster analysis was then applied to this distance matrix and visualized as a phenetic tree. (a) UPGMA. (b) Neighbour-joining algorithm.

modern samples from Fuerteventura cluster together, highlighting the reduced temporal differentiation. Interestingly, whereas on the multivariate axes the sample from Lanzarote was not clearly associated with the m1 of Fuerteventura, both phenetic trees cluster it within the other samples from the eastern Canary Islands, and close to the sample of the nearby island of La Graciosa. The divergence of the sample of Lobos island is confirmed, although it is clearly associated with the eastern Canary Island samples.

Geographical and temporal size differences

The pattern of size variation of the first lower molar completed the shape analysis (Fig. 3a). *Mus musculus domesticus* is smaller than both *M. m. musculus* and *M. spretus*, which share similar size ranges. Mice from Corsica, however, depart from the mainland *domesticus* and exhibit sizes similar to *spretus* and *musculus*. This pattern is confirmed by pairwise comparisons among samples (Table 3). The macrodont trend is even stronger on the islet

Piana, off Corsica, where the molar size exceeds those of *spretus* and *musculus* (Table 3, Fig. 3a). The sample from Cape Verde (SLZ) is characterized by a small size that is comparable to the mainland *domesticus*. In contrast, the fossil and the modern Canary Island mice exhibit large sizes comparable to those of *Mus spretus* and Corsican *Mus musculus domesticus*.

Within the Canary Islands, the size of the m1 is relatively stable from one island to another (Table 4). No size difference separates fossil and modern samples from Fuerteventura, except for the fossil teeth from CAR, which are larger than all other m1 from the Canary Islands.

DISCUSSION

The Canary mouse as a differentiated house mouse

The main result emerging from our study is the identification of all modern and fossil Canary Island mice as *M. m. domesticus*. The mice, however, are differentiated from their mainland

Table 3 Pairwise comparison of m1 sizes (estimated by the area of the ellipse H1) between modern samples of the Canary and genotyped groups of mice. CM: Canary modern, CV: Cape Verde, MM: *Mus musculus musculus* (*M.m.m.*), MS: *Mus spretus* (*M.s.*), MD: *Mus musculus domesticus* (*M.m.d.*). MDeast: eastern samples (GRE and ISRL), MDmag: Maghreb (ALG and TUN), MDwest: western samples (FR, IT, COR, SAR). The probability of Studentized pairwise comparisons is given, corrected for the large number of comparisons (Tukey method). Figures in the grey area give comparisons within the genotyped referenced set. Significant probabilities are in bold.

AreaEFT	Canary					<i>M.m.m.</i>	<i>M.s.</i>	<i>M.m.d.</i>					
	CM_FU	CM_GC	CM_LA	CM_TE	CV_SLZ	MM	MS	MDcorse	MDeast	MDmag	MDpiana	MDsard	MDwest
CM_FU	1.000												
CM_GC	0.156	1.000											
CM_LA	1.000	0.817	1.000										
CM_TE	0.002	1.000	0.648	1.000									
CV_SLZ	0.000	0.000	0.000	0.000	1.000								
MM	1.000	0.314	1.000	0.113	0.000	1.000							
MS	1.000	0.284	1.000	0.003	0.000	1.000	1.000						
MDcorse	0.403	1.000	0.993	1.000	0.000	0.679	0.639	1.000					
MDeast	0.000	0.000	0.000	0.000	0.190	0.002	0.000	0.000	1.000				
MDmag	0.000	0.000	0.000	0.000	0.614	0.001	0.000	0.000	1.000	1.000			
MDpiana	0.000	0.061	0.000	0.004	0.000	0.000	0.000	0.003	0.000	0.000	1.000		
MDsard	0.144	0.000	0.044	0.000	0.393	0.412	0.036	0.001	1.000	1.000	0.000	1.000	
MDwest	0.000	0.000	0.000	0.000	0.154	0.002	0.000	0.000	1.000	1.000	0.000	1.000	1.000

Table 4 Pairwise comparison of m1 sizes (estimated by the area of the ellipse H1) between modern and fossil samples of the Canary Islands. Samples with fewer than 10 specimens were not included. The probability of Studentized pairwise comparisons is given, corrected for the large number of comparisons (Tukey method). Significant probabilities are in bold.

	Fossils					Modern							
	FU_CAR	FU_CVV1	FU_CVV2	FU_FCV	GRA	LOB	FU	GC	HIE_FG	LA_LAM	LG_VIZ	TE	SLZ
FU_CAR	1.000												
FU_CVV1	0.000	1.000											
FU_CVV2	0.000	0.960	1.000										
FU_FCV	0.007	0.166	0.983	1.000									
GRA	0.000	1.000	0.918	0.126	1.000								
LOB	0.109	0.018	0.667	1.000	0.013	1.000							
FU	0.000	0.923	1.000	0.930	0.857	0.392	1.000						
GC	0.954	0.003	0.191	0.911	0.002	0.999	0.078	1.000					
HIE_FG	0.000	1.000	0.915	0.123	1.000	0.013	0.852	0.002	1.000				
LA_LAM	0.002	0.515	1.000	1.000	0.421	0.994	0.999	0.713	0.415	1.000			
LG_VIZ	0.019	0.887	1.000	1.000	0.823	0.996	1.000	0.804	0.819	1.000	1.000		
TE	0.121	0.000	0.027	0.842	0.000	1.000	0.000	1.000	0.000	0.507	0.779	1.000	
SLZ	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000

counterpart to a varied extent. Among the Canary Island mice, those most divergent from their mainland relatives are the extant mice from Fuerteventura, confirming the peculiarity of the mouse on this island, as already noted by Carrascosa & López-Martínez (1988). This differentiation seems to be quite old and to have persisted through time without much change, because all fossil samples from Fuerteventura, and to a lesser extent from the nearby islands of Lobos and La Graciosa, are closely related to the modern mice from Fuerteventura with regard to the shape of their lower molars.

These mice are also differentiated from the continental house mice by the size of the molars. The size of the m1 is

larger for all populations of the Canary Islands compared with the mainland reference. This study also points to shape differences that characterize some island populations, corroborating various observations on teeth (Renaud, 2005) or mandibles (Renaud & Millien, 2001). It is unclear whether these differences are adaptive (Pergams & Ashley, 2001) or random (Renaud & Millien, 2001). All the populations of the various islands diverge in molar shape in a similar morphological direction, although to a different degree (Fig. 3). The divergence concerns the massive first lower molars with a wide back part and a pronounced median cusp on the lingual side (see Fig. 2, right-hand side

on reconstructed outlines). The overall morphology of the m1 of the Canary Islands mice differs from that of the Corsican mice, which shifts in another direction in morphological space (Fig. 3).

Interpretation of the pattern of morphological variation

The distance between islands (except between Fuerteventura, Lanzarote and the islands of Lobos and La Graciosa) and the distance from the continent is of the order of 100 km. A strong and cold north–south sea current strengthens the isolation of the archipelago as well as of the islands. This situation has lasted for at least four millennia, and is connected with the establishment of the Sahara desert (deMenocal *et al.*, 2000). Once settled, the house mouse became adapted to living away from human settlements as in the Mediterranean climate. It now occupies a large part of all of the islands, especially in human environments with dwellings and agricultural fields (Nogales *et al.*, 2006).

The characteristics shared by the various Canary populations may be explained by three different hypotheses. First, the similarity of all Canary Island mice could be the result of a convergent adaptation, after an initial colonization of the individual islands by a heterogeneous stock. Second, the initial colonization of the Canary Islands by a single stock could have been followed by the divergence of the populations, the differential evolution corresponding to differences between the environments of the islands. Third, the initial colonization of the Canary Islands by a single stock could have been followed by an equal degree of divergence of the populations, the divergence being weakened by subsequent contacts between islands or more likely with the continent as a result of increasing maritime exchanges.

The first hypothesis seems more difficult to support than the two others. According to it, a similarity between populations from different islands would be expected owing to similar environmental conditions; this is not the case, for example, with the mice from Lanzarote, which are much less divergent than the mice from Fuerteventura even though the two islands share the same very dry climate. The gradual variation that can be observed from the eastern to the western islands is also not expected from this hypothesis, because the two island groups clearly differ in their environments. A unique colonization event followed by a divergent evolution between islands resulting from environmental conditions is not well supported either. Despite the small-sized sample from La Palma, mice from this island and from Fuerteventura are very similar, although the two islands offer very different climatic conditions. If the eastern Canary Islands are arid and show a uniform landscape, whereas the western islands are characterized by a high relief leading to altitudinal zones of vegetation (Fernández-Palacios, 1999; Juan *et al.*, 2000), it must nevertheless be stressed that all islands offer arid or semiarid vegetation at a low altitude (Juan *et al.*, 2000), a situation that all the mice faced when they settled. This fact would support

an initial equal divergence of the populations. However, the differences between the mice from Gran Canaria, El Hierro, and Tenerife compared with the mice from La Palma contradict such an implication. Compared with the second hypothesis, the third one seems a likely possibility; that is, the introduction of mice via travel by humans between islands and more especially from the nearby continents, as a consequence of an increase in trade. The resulting weakening of the divergence would be proportional to the intensity of contact, for example greater contact in the larger islands (Gran Canaria and Tenerife) than in the others.

The above hypotheses will be difficult to test because they include the intricate effects of numerous factors and may end in quite similar patterns. It would also be interesting to discuss other factors: competition and time. The competition with autochthonous rodents may have occurred only on a few islands (there was one giant rat on Gran Canaria and on Tenerife, and a mouse-sized one on the eastern islands), and this factor probably had little effect as La Palma and Fuerteventura mice are very similar, and no terrestrial mammal has ever been present on La Palma. The date of the settlement of the mouse on the Canary Islands, and the time of colonization, which is likely to differ between islands, raise difficult questions because the available chronological data are still too scarce and unreliable.

Despite the uncertainty regarding the age of the fossil samples, they do not document any temporal variation on Fuerteventura. Such observations support the hypothesis of an early evolution of the invasive species. The lack of data on fossil populations on the other islands does not allow generalizations. The house mouse from Santa Luzia (Cape Verde) could, however, illustrate another example of such an initial early stage of divergence following colonization of a new island: it is chronologically well constrained and shows that in no more than five centuries the mouse population diverged from the continental populations significantly in shape as well as in size (the size decreasing; Fig. 3). The decrease in divergence observed on several islands may be attributed either to more frequent arrivals of house mice from the mainland, leading to the introgression and the weakening of the early morphological divergence, or to a later settlement by the mice.

The mouse as a marker of past human migrations

The first occurrence of the house mouse was reported in the Middle East about 14,000 years ago (Auffray *et al.*, 1988; Auffray & Britton-Davidian, 1992; Cucchi *et al.*, 2005). Because it adapted to the new habitats created by humans, who became sedentary, the mouse followed the human expansion and can be used as a marker of that expansion. The gradual or punctuated rhythm of the house mouse progression to the West has been discussed in the last two decades (Auffray *et al.*, 1988, 1990; Cucchi *et al.*, 2005). The house mouse settlement in western Europe did not take place before the middle of the last millennium BC (Cucchi *et al.*,

2005), and no data for North Africa are available. It nevertheless appears that humans passively transported the house mouse, together with viable domestic stock, shortly after the mouse settled in the Near East, as exemplified by the case of Cyprus (Cucchi *et al.*, 2002). The anthropogenic introduction of commensal species in large Mediterranean islands during the Neolithic period also provides indirect evidence of scheduled maritime exchanges since the beginning of Neolithic (Cherry, 1990; Vigne & Cucchi, 2005).

Even though rodents can cross sea-barriers, as happened with the ancestors of the autochthonous rodents of the Canary Islands or some species of mouse (Cucchi *et al.*, 2006), the zooarchaeological data from Mediterranean islands (Vigne, 1999) have shown that it is likely that human dispersal was responsible for the introduction of commensal species such as mice onto any isolated archipelago. However, which peoples were responsible for the introduction of the house mouse on the Canary Islands? A number of potential migrants or traders could be candidates: from the oldest to the most recent these are the ancestors of the Guanches who introduced domestic animals, Phoenicians, Carthaginians, Romans, European or Arab sailors, European conquerors. Considering the data on the house mouse relative to western Europe, the time of the Phoenician and Carthaginian maritime trade would be favoured, and the discovery in Morocco as well as in Algeria and Tunisia of well-dated fossil mice could be a decisive test for providing further elements in the understanding of the house mouse settlement in the Canary Islands.

CONCLUSION

The morphometric analysis of the first lower molars of modern and fossil mice from the Canary Islands shows that the house mouse *M. m. domesticus* colonized the archipelago. Furthermore, Canary mice all share a morphological trend towards massive m1: this trend is more marked in Fuerteventura populations, whereas mice from the western islands exhibit a dental shape intermediate between the Fuerteventura and the mainland populations. Compared with this spatial structure, the variation registered through time, despite the uncertainty about the documented time interval on Fuerteventura, is of minor importance. The geographical structure observed today among the mice of the Canary Islands may be the result of an early divergence in complete isolation from the mainland stock, followed by an ever-increasing introgression on the largest and most welcoming islands owing to increased human travel. Western islands could have been traditionally more important than eastern islands with regard to commercial exchanges.

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REFERENCES

- Andrews, P. (1990) *Owls, caves and fossils*. Natural History Museum Publications, London.
- Auffray, J.-C. & Britton-Davidian, J. (1992) When did the house mouse colonize Europe? *Biological Journal of the Linnean Society, London*, **45**, 187–190.
- Auffray, J.C., Tchernov, E. & Nevo, E. (1988) Origine du commensalisme de la souris domestique (*Mus musculus domesticus*) vis-à-vis de l'homme. *Comptes Rendus de l'Académie des Sciences, Séries III*, **3**, 517–522.
- Auffray, J.-C., Vanlerberghe, F. & Britton-Davidian, J. (1990) The house mouse progression in Eurasia: a palaeontological and archaeozoological approach. *Biological Journal of the Linnean Society*, **41**, 13–25.
- Baker, A.E.M. (1994) Stowaway transport rates of house mice (*Mus domesticus*) and deermice (*Peromyscus maniculatus*). *Proceedings of the 16th Vertebrate Pest Conference* (ed. by W.S. Halverson and A.C. Crabb), pp. 106–112. University of California, Davis.
- Blondel, J. & Vigne, J.-D. (1993) Space, time and man as determinants of diversity of birds and mammals in the Mediterranean region. *Species diversity in ecological communities. ecological and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 135–146. Chicago University Press, Chicago.
- Bonhomme, F., Catalan, J., Britton-Davidian, J., Chapman, V.M., Moriwaki, K., Nevo, E. & Thaler, L. (1984) Biochemical diversity and evolution in the genus *Mus*. *Biochemical Genetics*, **22**, 275–303.
- Boye, P., Hutterer, R., López-Martínez, N. & Michaux, J. (1992) A reconstruction of the Lava mouse (*Malpaisomys insularis*), an extinct rodent of the Canary Islands. *Zeitschrift für Säugetierkunde*, **57**, 29–38.
- Carrascosa, M.C. & López-Martínez, N. (1988) The house mouse from a prehistoric site in Fuerteventura (Canary Islands). *Bonner Zoologische Beiträge*, **39**, 237–256.
- Castillo-Ruiz, C., Martín-González, E. & Coello, J.J. (2001) Small vertebrate taphonomy of La Cueva del Llano, a volcanic cave on Fuerteventura (Canary Islands, Spain).

- Palaeogeography, Palaeoclimatology, Palaeoecology*, **166**, 277–291.
- Cherry, J.F. (1990) The first colonization of the Mediterranean islands: a review of recent research. *Journal of Mediterranean Archaeology*, **3**, 145–221.
- Coello, J.J., Castillo, C. & Martín González, E. (1999) Stratigraphy, chronology, and paleoenvironmental reconstruction of the Quaternary sedimentary infilling of a volcanic tube in Fuerteventura, Canary islands. *Quaternary Research*, **52**, 360–368.
- Crampton, J.S. (1995) Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia*, **28**, 179–186.
- Crusafont, M. & Petter, F. (1964) Un muridé géant fossile des Iles canaries *Canariomys bravoii* gen. nov., sp. nov. (Rongeurs, Muridés). *Mammalia*, **28**, 608–611.
- Cucchi, T. (2005) Le commensalisme de la souris et les sociétés néolithiques méditerranéennes. PhD thesis, Muséum national d'Histoire naturelle, Paris.
- Cucchi, T., Vigne, J.-D., Auffray, J.-C., Croft, P. & Peltenburg, E. (2002) Introduction involontaire de la souris domestique (*Mus musculus domesticus*) à Chypre dès le Néolithique précéramique ancien (fin IX^e et VIII^e millénaire av. J.-C.). *Comptes Rendus Palevol*, **1**, 235–241 (English abridged version).
- Cucchi, T., Auffray, J.-C. & Vigne, J.-D. (2005) First occurrence of the house mouse (*Mus musculus domesticus* Schwarz & Schwarz, 1943) in the Western Mediterranean: a zooarchaeological revision of subfossil occurrences. *Biological Journal of the Linnean Society*, **84**, 429–445.
- Cucchi, T., Orth, A., Auffray, J.-C., Renaud, S., Fabre, L., Catalan, J., Hadjisterkotis, E., Bonhomme, F. & Vigne, J.D. (2006) A new endemic species of the subgenus *Mus* (Rodentia, Mammalia) on the Island of Cyprus. *Zootaxa*, **1241**, 1–36.
- Darviche, D., Orth, A. & Michaux, J. (2006) *Mus spretus* et *Mus musculus* (Rodentia, Mammalia) en zone méditerranéenne: différenciation biométrique et morphologique et application à des fossiles marocains pléistocènes. *Mammalia*, **70**, 90–97.
- deMenocal, P.B., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L. & Yarusinski, M. (2000) Abrupt onset and termination of the African Humid Period: Rapid climate response to gradual insolation forcing. *Quaternary Science Reviews*, **19**, 347–361.
- Dobson, M. (1998) Mammal distribution in western Mediterranean: the role of human intervention. *Mammal Review*, **28**, 77–88.
- Dowler, R.C., Carroll, D.S. & Edwards, C.W. (2000) Rediscovery of rodents (genus *Nesoryzomys*) considered extinct in the Galapagos. *Oryx*, **34**, 109–117.
- Fernández-Palacios, J.M. (1999) Marco ecológico de las Islas Canarias. *Ecología y cultura en Canarias* (ed. by J.M. Fernández-Palacios, J.J. Bacallado and J.A. Belmonte), pp. 83–105. Organismo Autónomo Complejo Insular de Museos y Centros, Cabildo de Tenerife, Santa Cruz de Tenerife, Spain.
- Ferson, S., Rohlf, F.J. & Koehn, R.K. (1985) Measuring shape variation of two-dimensional outlines. *Systematic Zoology*, **34**, 59–68.
- Gippoliti, S. & Amori, G. (2006) Ancient introductions of mammals in the Mediterranean Basin and their implications for conservation. *Mammal Review*, **36**, 37–48.
- Hutterer, R., Lâpez-Jurado, L.F. & Vogel, P. (1987) The shrews of the eastern Canary Islands: a new species (Mammalia: Soricidae). *Journal of Natural History*, **21**, 1347–1357.
- Hutterer, R., López-Martínez, N. & Michaux, J. (1988) A new rodent from the Quaternary deposits of the Canary Islands and its relationships with Neogene and recent Murids of Europe and Africa. *Palaeovertebrata*, **18**, 241–262.
- Juan, C., Emerson, B.C., Oromí, P. & Hewitt, G.M. (2000) Colonization and diversification: towards a phylogenetic synthesis for the Canary Islands. *Trends in Ecology & Evolution*, **15**, 104–109.
- Kuhl, F.P. & Gardina, C.R. (1982) Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing*, **18**, 236–258.
- López-Martínez, N. & López-Jurado, L.F. (1987) Un nuevo murido gigante del Cuaternario de Gran Canaria *Canariomys tamarani* nov. sp. (Rodentia, Mammalia). *Doñana Acta Vertebrata (Publicación Ocasional)*, **2**, 1–66.
- Lowe, S., Browne, M., Boudjelas, S. & de Poorter, M. (2000) *100 of the world's worst invasive alien species database*. The Invasive Species Specialist Group (ISSG). *Aliens* newsletter, Auckland.
- Masseti, M. (1998) Holocene endemic and anthropogenous wild animals of the mediterranean islands. *Anthropozoologica*, **28**, 3–20.
- Masseti, M. (2002) *Uomini e (non solo) topi. Gli animali domestici e la fauna antropocora*. Firenze University Press, Università degli Studi di Firenze.
- Mederos Martín, A. & Escribano Cobo, G. (2002) *Los aborígenes y la prehistoria de Canarias*. Centro de la Cultura Popular Canaria, La Laguna.
- Musser, G.G. & Carleton, M.D. (2005) Superfamily Muroidea. *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn (ed. by D.E. Wilson and D.M. Reeder), pp. 894–1531. The Johns Hopkins University Press, Baltimore, MD.
- Nogales, M., Rodríguez-Luengo, J.L. & Marrero, P. (2006) Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review*, **36**, 49–65.
- Pergams, O.R. & Ashley, M.V. (2001) Microevolution in island rodents. *Genetica*, **112/113**, 245–256.
- Quammen, D. (1996) *The song of the Dodo. Island biogeography in an age of extinction*. Hutchinson, London.
- Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J. & Weyhenmeyer, C.E. (2004) IntCal04 Terrestrial radiocarbon Age Calibration, 0–26 Cal Kyr BP. *Radiocarbon*, **46**, 1029–1058.
- Renaud, S. (2005) First upper molar and mandible shape of wood mice (*Apodemus sylvaticus*) from northern Germany: ageing, habitat, insularity. *Mammalian Biology*, **70**, 157–170.

- Renaud, S. & Michaux, J.R. (2003) Adaptive latitudinal trends in the mandible shape of *Apodemus* wood mice. *Journal of Biogeography*, **30**, 1617–1628.
- Renaud, S. & Millien, V. (2001) Intra- and interspecific morphological variation in the field mouse species *Apodemus argenteus* and *A. speciosus* in the Japanese archipelago: the role of insular isolation and biogeographic gradients. *Biological Journal of the Linnean Society*, **74**, 557–569.
- Renaud, S., Michaux, J., Jaeger, J.-J. & Auffray, J.-C. (1996) Fourier analysis applied to *Stephanomys* (Rodentia, Muridae) molars: non-progressive evolutionary pattern in a gradual lineage. *Paleobiology*, **22**, 251–261.
- Rohlf, F.J. & Archie, J.W. (1984) A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae). *Systematic Zoology*, **33**, 302–317.
- Vigne, J.-D. (1999) The large “true” Mediterranean as a model for the Holocene human impact on the European vertebrate fauna? Recent data and new reflections. *The Holocene history of the European vertebrate fauna. Modern aspects of research* (ed. by N. Benecke), pp. 295–322. Deutsches Archäologisches Institut, Eurasian-Abteilung, Berlin.
- Vigne, J.-D. & Cucchi, T. (2005) *Premières navigations au Proche-Orient : les informations indirectes de Chypre. Past exploitations of aquatic ecosystems in south-west Asia* (ed. by J. Desse and N. Desse-Berset), *Paléorient*, **31**, 186–194.
- Vigne, J.-D. & Valladas, H. (1996) Small mammal fossil assemblages as indicators of environmental change in northern Corsica during the last 2500 years. *Journal of Archaeological Science*, **23**, 199–215.

BIOSKETCH

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