

Short Communication

Molecular phylogenetics reveals Messinian, Pliocene, and Pleistocene colonizations of islands by North African shrews

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Received 5 September 2007; revised 13 December 2007; accepted 14 December 2007

Available online 25 December 2007

1. Introduction

Since the seminal work of McArthur and Wilson (1967) on the equilibrium theory of island faunas, colonization and extinction events have remained a focus of research; however, these dynamic events are clearly related to continental islands where the colonization probability and species turnover rates are high (Diamond, 1969). On oceanic islands, and even shelf islands, natural colonization events by terrestrial mammals are so exceptional that local evolution and speciation is more rapid than the arrival of new species (Williamson, 1981). This was the case until at least the end of the last Ice Age, before the arrival of humans. This model is also true for most islands in the Mediterranean basin, as well as the Canary Islands (Juan et al., 2000), situated within the Atlantic Ocean approximately 100 km off the coast of Morocco. Introductions occurred either during periods of low sea level that led to the formation of filter bridges that allowed the passage of certain organisms, or by sweepstake routes that enabled a small number of organisms to cross by rafting (Simpson, 1940). Such jump dispersals, followed by bottlenecks, genetic drift, and new selective conditions, led to pronounced morphological changes exemplified by dwarf elephants, dwarf hippos, and giant rodents (Sondaar, 1977). All of these mammals became extinct during periods of climatic change or following the immigration of newcomers, but the apoc-

alyptic end of most island endemics began with the arrival of humans during the early Holocene (Diamond, 1992). According to Sondaar (1977), the famous dwarfing and gigantism on these islands are in part explained by a predator-free environment.

To our knowledge, in regard to mammals, only four Pleistocene island endemic taxa survived the extinction events in the Mediterranean basin: the Cypriot mouse *Mus cypriacus* (Cucchi et al., 2006), the “Cyprian shrew” *Crocidura suaveolens cypriacus* (Dubey et al., 2007a), the Cretan shrew *C. zimmermanni* (Vogel et al., 1986), and possibly the Sicilian shrew *C. sicula* on the Siculo–Maltese archipelago (Vogel et al., 1990). Interestingly, these small mammals have no morphological peculiarities and were therefore regarded as continental forms introduced by humans. The endemic character of the mammals from Cyprus was discovered only very recently thanks to molecular analyses and dating of the split from continental forms by molecular clock analyses (Cucchi et al., 2006; Dubey et al., 2007a). The Cretan shrew was discovered thanks to the derived karyotype of $2n = 34$, not found outside of this island (Vogel, 1986).

In the present study, we focus on the Sicilian shrew *C. sicula* and its relatives on other islands as well as continental Africa. These taxa have a complex history that exemplifies the problem of species assignment on islands. In the 1980s, Kotsakis (1984) discovered a fossil shrew, *Crocidura esuae*, in the Spinagallo cave in Sicily that was considered to be identical to the fossil shrew found in Malta’s Ghar Dalam cave, in both cases associated with dwarf elephants. At that time, the extant shrew of Sicily was assigned by Corbet (1978) to the Greater white-toothed shrews *C. rus-*

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sula, whereas the only extant species on Malta, now restricted to the small island of Gozo, was assigned by Schembri and Schembri (1979) to the lesser white-toothed shrew *C. suaveolens*. The extant shrews were thought to have originated either from Italy or Africa and been introduced by human settlers in the Holocene, as summarized in Fig. 1A.

This view changed when chromosome studies of the extant shrew of Sicily revealed a karyotype of $2n = 36$, previously unknown from the Mediterranean region but identical to that of the shrew from Gozo (Vogel et al., 1990). For this taxon, the oldest available name, *Crocidura sicula* Miller, 1900, was applied, and Hutterer (1990) suggested conspecificity with the fossil *C. esuae*.

The interpretation of an endemic Siculo–Maltese shrew species was subsequently challenged by Sarà (1995). Based on a morphometric study of these shrews and the Canary shrew *C. canariensis*, which all share the same karyotype

(Hutterer et al., 1987), Sarà (1995) concluded that all should be assigned to the Sicilian shrew *C. sicula*, except for the fossil *C. esuae*. This led to a new hypothesis (Fig. 1B) of a late Pleistocene dispersal to the Canary Islands and Sicily over land bridges from an unknown African *C. sicula* population.

The first molecular investigation to be conducted (Vogel et al., 2003) revealed a genetic divergence of Kimura two-parameter distance (K2P) of 14.3% between the shrews of Sicily and those of the Canary Islands, clearly higher than the level of intraspecific populations (Bradley and Baker, 2001). This result led us to suggest a third hypothesis concerning the origin of these island shrews; namely, an African ancestor of both species that is either extinct or survives in an extant species (Fig. 1C). Such a potential ancestor was recently found (Vogel et al., 2006) when a cytotoxic analysis of the Saharan shrew *C. tarfayaensis* revealed an identical karyotype of $2n = 36$. The discovery of this shrew opened the way to a new molecular investigation to test not only the hypothesis of a common African ancestor, but also to determine the period of colonization using the molecular clock approach and to develop a plausible scenario of colonization events.

2. Materials and methods

2.1. Sampling, extraction, and DNA amplification

We analyzed 17 samples of *Crocidura* from nine different species distributed around the Mediterranean basin and the Canary Islands (Table 1), a more distant crocidurine shrew, *Suncus murinus* was used as outgroup. Most of the shrews analyzed in this study are from the IZEA collection (University of Lausanne, Switzerland). The two sequences of *Crocidura suaveolens* were taken from Dubey et al. (2006).

DNA extraction was carried out using a QIAamp DNA Mini Kit (Qiagen). Double-stranded DNA amplifications of cytochrome *b* gene were performed with the primer pairs L14841/C4, C1/C2, C3/H15915, and L14841/H15915 (Irwin et al., 1991; Dubey et al., 2006). Amplification conditions consisted of 35 thermal cycles of 30 s denaturation (60 s for the set L14841/H15915) at 94 °C, 45 s annealing (60 s, L14841/H15915) at 50 °C, and 60 s (120 s, L14841/H15915) extension at 72 °C. For details on DNA purification and cycle sequencing see Dubey et al. (2007a).

2.2. Phylogenetic analyses

Nucleotide sequences of *cyt-b* gene were edited with Sequence Navigator (Parker, 1997) and aligned by eye. Three methods of phylogenetic analyses were carried out using PAUP* version 4.0b10 PPC (Swofford, 1998). Tests were conducted on the total fragments (985 bp), all codon positions were used, and trees were rooted using sequence of *S. murinus*. A neighbour-joining (NJ) tree was constructed using Kimura two-parameter genetic distances (Kimura, 1980). This distance was chosen because it allows

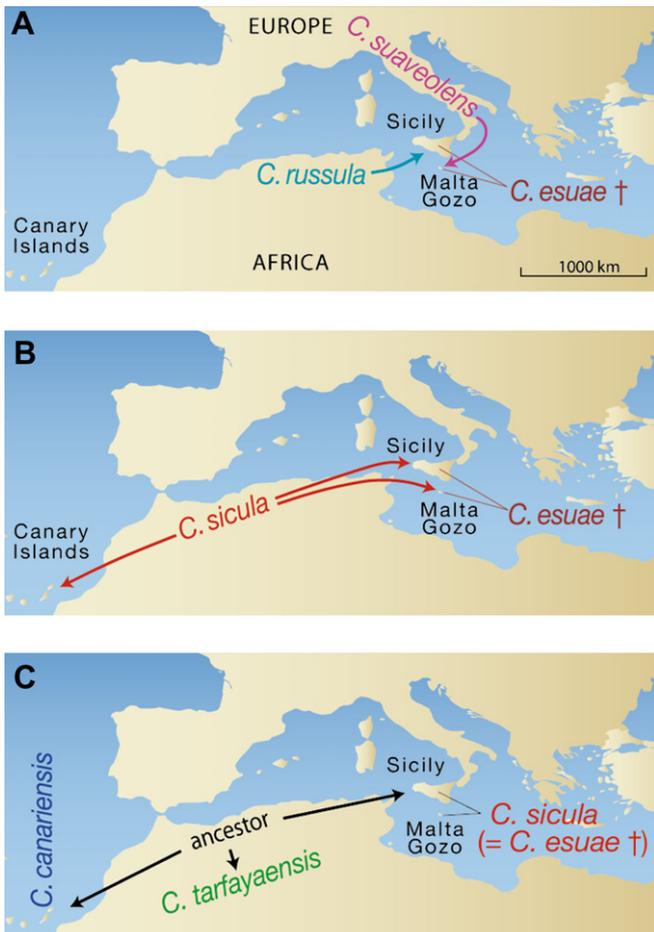


Fig. 1. Hypotheses of the origin of shrews from Sicily, Malta/Gozo, and the Canary Islands. (A) Hypothesis of Kotsakis (1984): the fossil species *C. esuae* was replaced by two introduced species (*C. russula* and *C. suaveolens*). (B) Hypothesis of Sarà (1995): *C. sicula* migrated to the Canary Islands and Sicily from an unknown population in North Africa, replacing the fossil *C. esuae*. (C) Hypothesis of Vogel et al. (2006): *C. sicula* (= *C. esuae*) on Sicily and *C. canariensis* on the Canary Islands are endemic species that evolved from a dispersing North African ancestor that may be related to the recent Saharan shrew *C. tarfayaensis*.

Table 1

Species sequenced and used in the present study (identification number on Fig. 2), collection code, geographic origin of samples, and GenBank accession number

Species	Coll. code	Locality	GenBank
<i>Crocidura canariensis</i> (1)	IZEA 4285	Fuerteventura, Canary Islands, Spain	DQ521042
<i>Crocidura canariensis</i> (2)	LJCC3	Lanzarote, Canary Islands, Spain	DQ975247
<i>Crocidura ichnusae</i>	IZEA 4011	Tunisia	DQ975240
<i>Crocidura leucodon</i>	IZEA 6038	Turkey	DQ975249
<i>Crocidura olivieri</i>	IZEA 3077	Central African Republic	DQ975250
<i>Crocidura russula</i>	IZEA 5936	Spain	DQ975238
<i>Crocidura russula</i>	IZEA 2641	Morocco	DQ975239
<i>Crocidura sicula</i>	IZEA 2943	Sicily, Italy	DQ521040
<i>Crocidura sicula</i>	IZEA 4000	Gozo, Malta	DQ975241
<i>Crocidura suaveolens</i>	IZEA 3191	Spain	AY843491
<i>Crocidura suaveolens</i>	IZEA 7945	Italy	AY843459
<i>Crocidura tarfayensis</i> (1)	IZEA 7807	Morocco	DQ975242
<i>Crocidura tarfayensis</i> (2)	IZEA 7808	Morocco	DQ975243
<i>Crocidura tarfayensis</i> (3)	IZEA 7811	Morocco	DQ975244
<i>Crocidura tarfayensis</i> (4)	IZEA 7809	Morocco	DQ975245
<i>Crocidura tarfayensis</i> (5)	ZFMK 2000.039	Morocco	DQ975246
<i>Crocidura zimmermanni</i>	IZEA 2053	Crete, Greece	DQ521041
<i>Suncus murinus</i>	IZEA V546	India	DQ630386

us to compare our results with others studies. Parsimony analyses (MP) were performed using the following options: heuristic search, stepwise-addition of sequences, 10 replicates of random addition of taxa, and TBR branch swapping (Swofford, 1998); all codon positions were equally weighted. For ML analyses, likelihood ratio tests, implemented with the computer program Modeltest 3.06, were first used to choose the mutation model that best fit the data (36). The GTR+I+G model was selected with base frequencies (A = 0.3024, C = 0.2978, G = 0.1195, T = 0.2804) estimated from the data, an unequal distribution of rates at variable sites ($\alpha = 1.9972$), and six different substitution types (rate [A–C] = 1.8238, rate [A–G] = 12.4629, rate [C–T] = 28.7198, rate [A–T] = 2.0043, rate [C–G] = 0.4372, rate [G–T] = 1.0000). Maximum likelihood analyses were then performed, assuming this model, using the heuristic search option with a stepwise addition of sequences. NJ, MP, and ML results were compared for congruence of tree topologies. Bootstrap support values were obtained with 1000 pseudoreplicates for MP, NJ, and ML analyses, and 10 random replicates of stepwise-addition sequences.

2.3. Molecular clock analyses

The molecular clock hypothesis was tested following Posada and Crandall (1998) calculating the log likelihood score with molecular clock enforced and comparing it with the log likelihood previously obtained without enforcing the molecular clock. In addition, to identify whether there was heterogeneity in the rates of *cyt-b* substitutions among species, relative-rate tests were conducted between each of them, using RR TREE, version 1.0 (Robinson et al., 1998), which improves the test of Wu and Li (1985). Relative-rate tests were performed on the proportions of synonymous

(K_s), non-synonymous (K_a) substitutions. The Bonferroni correction (Rice, 1989) was applied to deal with statistical artifacts created by multiple comparisons.

Estimation of the divergence time from the molecular data was performed according to a calibration developed previously for the Soricidae by Fumagalli et al. (1999), and that allowed fully coherent results in a biogeographic point of view (see, e.g., Vogel et al., 2003; Brändli et al., 2006; Cosson et al., 2005; Dubey et al., 2006, 2007a,b). This calibration is based on an estimate of 20 million years for the split between Crocidurinae and Soricinae shrews, and it was developed considering the cytochrome *b* sequence divergences based on third position transversions, with a rate of 1.36%/Myr (95% confidence interval: 1.08–1.64%/Myr).

3. Results and discussion

For this investigation, based on the sequence of 998 bp of the cytochrome *b* gene, we analyzed the Saharan shrew *C. tarfayaensis* from Morocco, the Sicilian shrew *C. sicula* from Sicily and Gozo, and the Canarian shrew *C. canariensis* from Fuerteventura and Lanzarote. Several other African and three continental European shrew species were included to test possible relationships (see Section 2). The results of this analysis are shown in Fig. 2. The maximum likelihood tree clearly reveals that the $2n = 36$ chromosome group is an independent clade, separate from all other European species.

Relative-rate tests revealed that there were no significant divergences in evolutionary rate between species; and in addition the likelihood ratio test led to acceptance of the molecular clock hypothesis ($\chi^2 = 17.62$, $ddl = 15$, $p = 0.28$).

The first split separated the Sicilian shrew *C. sicula* from the North African ancestor when the species reached the

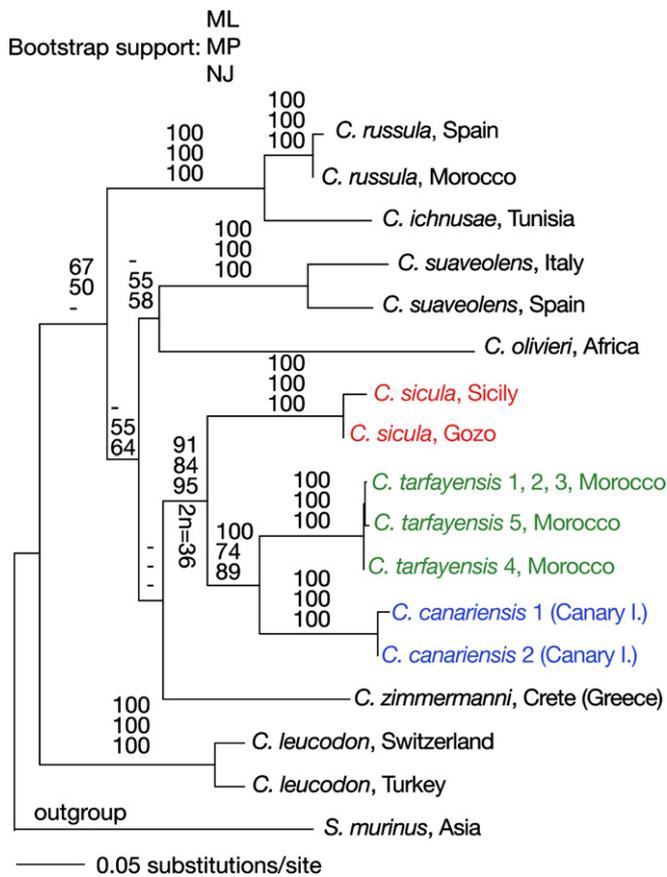


Fig. 2. Maximum likelihood tree of all European and some African *Crocidura* species. The Asian house shrew *Suncus murinus* is used as outgroup. The $2n = 36$ chromosome species cluster together. The Sicilian shrew *C. sicula* split off first at a time estimate that is concordant with the Messinian sea regression. The Canary shrew *C. canariensis* split off during the Pliocene. Bootstrap support from maximum likelihood (ML), maximum parsimony (MP) and neighbour-joining analyses (NJ).

Siculo–Maltese archipelago. The divergence between this branch and the remaining African clade (*C. tarfayensis* and *C. canariensis*), as estimated from the K2P value, is equivalent to 14.5%. The molecular clock approach dates this split at approximately 4.65 Myr B.P. (95% CI: 3.12–6.98). This date is close to the Miocene–Pliocene boundary, and the upper estimate clearly pre-dates this period, characterized by the Messinian salinity crisis that led to the partial evaporation of the Mediterranean Sea and the formation of the most recent land connection between North Africa and continental Europe. At that time, the Siculo–Maltese archipelago was a mountain chain emerging from the partially dry or salt marsh basin characterized by a large “Lago Mare” (Krijgsman et al., 1999). The connection can be compared to a filter bridge (Simpson, 1940) that enables the passage of only a small number of mammals in each direction, from both continental Europe or from Africa.

The divergence between the Sicily and Gozo populations is 1.45%, equivalent to a split at approximately 670,000 yr B.P. (95% CI: 560,000–840,000). This interval lies within a

major cold period (Hunt and Schembri, 1999) during which time a lowering of the sea level created a land passage between Sicily and Malta. It seems most likely that this shrew survived on Sicily for 4 million years because of the complex geomorphological structures that resulted from the high altitudinal gradient of the island; part of this population then dispersed to Malta and Gozo. While remains from the Ghar Dalam cave on Malta testify to the presence of shrews at this site since the Middle Pleistocene, they also show that the population became extinct. This extinction may have resulted from stochastic events in ancient time or more recent modifications of the landscape by humans. The surviving shrew population on Gozo, an island of just 14 km in length, is therefore of great interest from the perspectives of both science and conservation.

A comparison of the Canary and Saharan shrews, *C. canariensis* and *C. tarfayensis*, reveals a different picture. The divergence is about 12%, and the molecular clock approach reveals a split at 2.68 Myr B.P. (95% CI: 1.61–4.30), within the Pliocene. As the Canary Islands were never connected to continental Africa (Steiner et al., 1998), jump dispersal via a natural raft, e.g., a rotten tree trunk with holes must be considered as the most likely mode of colonization. Such a transfer, often inferred from fossil data, has recently been demonstrated for arboreal reptiles during hurricanes (Censky et al., 1998). In regard to the Canary Islands, such transfer is plausible for heterothermic reptiles as Gekkonidae, Lacertidae, and Scincidae, but less probable for shrews with a generally high metabolic rate (Vogel, 1976). However, in contrast to the temperate red-toothed shrews (subfamily Soricinae), the white-toothed shrews (subfamily Crocidurinae) have a rather moderate metabolism. Moreover, they are able to reduce the energy expenditure by torpor during low food availability (Nagel, 1977), especially shrews from desert environment (Sparti, 1990), increasing the probability of a successful transfer. Different to reptiles that dispersed to most of the volcanic islands by rafting (Juan et al., 2000), the shrew remained in the complex of eastern islands Fuerteventura, Lanzarote, Lobos, and Montana Clara that were certainly connected during low sea levels, a fact that is in agreement with the lower probability of a rafting success.

Our new data support the last hypothesis (Fig. 1C), that the island shrews represent two different endemic species whose ancestors reached the islands from North Africa without human assistance. Their precursor survived on the continent as its descendent, the Saharan shrew. These processes are in contrast with the colonization of most other Mediterranean islands by continental species that were passively introduced by humans over the past 12,000 yr, e.g., the North African white-toothed shrew *C. ichnusae* to Sardinia, Pantelleria, and Ibiza (Cosson et al., 2005), and a subspecies of the lesser white-toothed shrew *C. suaveolens gueldenstaedtii* to Crete, Corsica, and Menorca (Dubey et al., 2007a, 2006). A Canary Island population

of the greater white-toothed shrew *C. russula* (originally described as *C. osorio* from Gran Canaria) was possibly introduced from Spain by the Spanish conquistadors (Vogel et al., 2003). In conclusion, shrews represent a highly interesting model organism in terms of illustrating different processes of island colonization.

Acknowledgments

We thank Charlotte Vogel-Gerber for her help in trapping *C. tarfayaensis* and *C. sicula*, P.J. Schembri for his assistance in trapping *C. sicula* on Gozo, Nelly Di Marco for management of the tissue collection, T. Czaka for the map design, and P. Moratal for computer facilities. The Herbette Foundation (Lausanne) provided travel funds.

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