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# Molecular evidence supports recent anthropogenic introduction of the Algerian hedgehog *Atelerix algirus* in Spain, Balearic and Canary islands from North Africa

DOI 10.1515/mammalia-2014-0180

Received December 19, 2014; accepted June 5, 2015; previously published online July 17, 2015

**Abstract:** The Algerian hedgehog, *Atelerix algirus*, is recorded from North Africa, the Balearic, Canary and Maltese islands, and into parts of the Mediterranean coastal regions of Spain. The lack of an archeozoological record in Europe, Balearic, Maltese or Canary Islands has led several authors to postulate recent introductions by humans, but few studies actually investigated this hypothesis. We used both mitochondrial and nuclear genes to test it. To this aim, we widely sampled the Algerian hedgehog in North Africa (Algeria, Morocco and Tunisia), continental Spain (Catalonia), and Balearic and Canary islands. Our mitochondrial and nuclear data are consistent and show low genetic diversity across the geographical range of the Algerian hedgehog. Our results suggest the recent colonisation of Spain, Balearic and Canary Islands by this species (Holocene), probably mediated by humans. Several subspecies, mainly based on pelage variations, have been described either from mainland or island populations, but our data do not show any genetic

discontinuity, suggesting that subspecific recognition may be unwarranted.

**Keywords:** anthropogenic introduction; Erinaceidae; Islands; Mediterranean basin; phylogeography.

## Introduction

The remarkable biodiversity encountered in North Africa comes from three sources: northern Palaeartic, sub-Saharan Africa and arid Palaeartic (Dobson and Wright 2000). Many works have shown that faunal exchanges regularly occurred through the Mediterranean Sea. Geological evidence indicates that Morocco and the Iberian Peninsula had been connected by a land bridge (Brandy and Jaeger 1980, Jaeger et al. 1987, Blondel and Aronson 1999, Krijgsman et al. 1999, Duggen et al. 2003) during the Betic crisis (16–14 Ma) and during the Messinian salinity crisis (5.59–5.33 Ma). The resulting land corridors allowed biotic interchanges between southern Europe and the Maghreb. The strait reopened at the start of the Pliocene, about 5 Ma, causing the refilling of the Mediterranean and the closing of the terrestrial connection between Europe and the Maghreb (Duggen et al. 2003). This event probably accounts for the vicariance observed in many Mediterranean lineages (Cheylan 1991, Blondel and Aronson 1999, Dobson and Wright 2000) and for the genetic differentiation between some Iberian and Maghreb biota (García-Mударra et al. 2009). Additionally, several recent genetic studies showed that crossing the strait of Gibraltar or the strait of Sicily in both senses was possible during the Pleistocene period, either via natural colonisation or via incidental human introduction (Cosson et al. 2005, Juste et al. 2009, Husemann et al. 2014).

The Algerian hedgehog, *Atelerix algirus* (Lereboullet, 1842), is recorded from North Africa (Alegría, Morocco, Tunisia, and North of Libya); in parts of the Mediterranean

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coastal regions of Spain; and the Balearic, Canary and Maltese islands (Hutterer 2005, Masseti 2010). In France, it was reported from the Var department and from La Rochelle (Heim de Balsac 1936, Saint Girons 1969), but it is now extinct (Saint Girons 1984). In continental Spain, it is reported throughout the Mediterranean coast of Catalonia (Girona, Barcelona) via Valencia and Murcia to Andalusia (Malaga, Almeria) (Alcover 2007). In the Balearic Island, it is known from Mallorca, Minorca, Ibiza, Formentera and Cabrera (Alcover et al. 1993, Johnson et al. 2012).

According to Heim de Balsac (1936), the presence of *Atelerix algirus* in North Africa, Spain, France and the Canaries suggest that it is a relic of the Pliocene, when land connections between France, North Africa and the Canaries occurred. Fossils of this species are recorded in North Africa since the Late Pleistocene (Stoetzel 2013). The lack of an archeozoological record in continental Europe, Balearic, Maltese or Canary Islands and the restricted distribution of the Algerian hedgehog in Spain have led several authors to postulate recent introductions by humans (Malec and Storch 1972, Corbet 1988, Dobson 1998, Lapini 1999, Long 2003, Borg 2005, Hutterer 2005, Gippoliti and Amori 2006), but few studies actually investigated this hypothesis. Morales and Rofes (2008) provided unequivocal evidence of the presence of this species in a Bronze Age grave at the site of Biniai Nou in Minorca (Balearic islands). These authors provided circumstantial evidence pointing to the Muslims of Almohad empire as the responsible agents for the introduction of *A. algirus* into Minorca. The introduction of this species in the Canary Islands could have happened in 1892, when a pair of hedgehogs was brought from Morocco to Fuerteventura, from where the species was probably shipped to other islands (Hutterer 1983). The Phoenicians may have introduced the Algerian Hedgehog into Spain, Southern France, and possibly also the Maltese Islands around 1000 BC (Borg 2005).

Genetic data provide powerful tools to infer the geographical origin and colonisation time of a given population. However, few genetic data are available for the Algerian hedgehog. Sanchez et al. (1996) sequenced the *Sry* gene of one specimen from Spain. In a multigene study, Bannikova et al. (2014) investigated the phylogenetic relationships between the species of hedgehogs and gymnures. They showed that *Atelerix algirus* is the sister species of *A. albiventris*. However, only one specimen of *A. algirus* was included in this paper and it came from Gran Canaria Island. In the present study, we widely sampled the Algerian hedgehog in North Africa (Algeria, Morocco and Tunisia), Canary and Balearic islands, and in continental Spain (Catalonia) to infer its phylogeographic

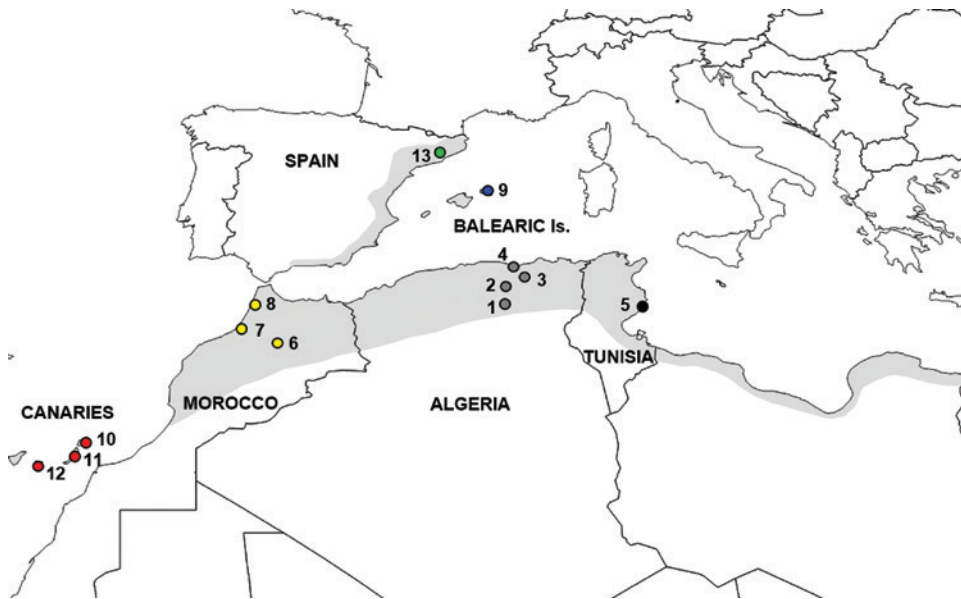
history and the time of colonisation of continental Europe, Balearic and Canary islands. We used both mitochondrial (cytochrome *b*, *Cytb*) and nuclear (beta fibrinogen intron 7, *BFIBR*) genes to answer this question.

## Materials and methods

Available specimens were collected from most of the known distribution of the species (Figure 1, Table 1). Tissue samples were stored in 96% ethanol, and DNA was extracted using the NucleoSpin Tissue Core kit (Macherey-Nagel, Hoerdt, France). The *Cytb* gene was amplified with primers L14724 (Kocher et al. 1989) and H15149 (Irwin et al. 1991), whereas the *BFIBR* gene was amplified using the primers *BFIBR1* and *BFIBR2* (Seddon et al. 2001). The double-stranded PCR products were purified and sequenced at the Genoscope (Ivry/Seine, France). For the final analyses, *Cytb* sequences of 356 bp were retained for 56 individuals (Genbank KP279765 to KP279819), and *BFIBR* sequences of 641 bp were retained for 52 specimens (Genbank KP279820 to KP279871).

Phylogenetic reconstructions were performed on each gene separately to evaluate each signal and to detect any incongruence. Phylogenetic relationships between haplotypes were inferred by constructing a network using the median-joining (MJ) method available in NETWORK v4.500 (Bandelt et al. 1999). This method accounts for the coexistence of ancestral and descendent haplotypes, multifurcations, and reticulate relationships (Posada and Crandall 2001). Prior to this analysis, the existence of heterozygous positions for the nuclear gene fragment was investigated and an input file was constructed from this information using SeqPHASE (Flot 2010). The phase of each haplotype and its reconstruction were carried out using PHASE v.2.1.1 (Stephens et al. 2001, Stephens and Scheet 2005) by running the formerly built input file and by considering the default parameters of the software. The results obtained for two individuals (H66 and MA734) were unclear (i.e. several possible haplotype pairs for each individual with similar probabilities), thus they were removed from all subsequent analyses.

The number of haplotypes, number of polymorphic sites, haplotype diversity, nucleotide diversity and average number of nucleotide differences were calculated using Arlequin 3.5 (Excoffier and Lischer 2010). To estimate haplotype richness while controlling for unequal sample sizes (Leberg 2002), we used rarefaction analysis (Analytic Rarefaction v. 1.4; UGA Stratigraphy Lab website; <http://www.uga.edu>).



**Figure 1:** Map of North Africa and Southern Europe showing the geographical distribution of *Atelerix algirus* (in grey, adapted from Amori et al. 2008) and the sampling localities (circles). Colours refer to the main geographical areas discussed in the text (Algeria, Morocco, Tunisia, continental Spain, Balearic and Canary islands).

## Results

We obtained *Cytb* sequences for 56 specimens. Genetic diversity was low: 12 distinct haplotypes and 20 polymorphic sites were identified. The most common haplotype was recovered in Algeria (23 individuals), Morocco (one individual) and Catalonia (the four sampled individuals; Figure 2). All other haplotypes were found in only one given geographical area: seven haplotypes were unique to Algeria, one haplotype was unique to Tunisia, one haplotype was unique to Morocco, one haplotype was unique to Balearic Islands and one haplotype was unique to the Canaries. Controlling for sample size, the number of *Cytb* haplotypes is significantly greater in Algeria than in continental Spain and Canary Islands. The sample size for Balearic Islands is too small to warrant any conclusion. The mean number of pairwise differences between sequences was 1.830, and it varies from 0.000 (continental Spain, Canary Islands) to 3.000 (Morocco) depending on geographical region (Table 2). Between geographical regions, the mean number of pairwise differences varies from 1.00 to 6.00 (Table 3).

We obtained 100 *BFIBR* sequences after phasing. Genetic diversity was low: 10 distinct haplotypes and 14 polymorphic sites were identified. One haplotype was found in common in the six sampled regions (Algeria, Morocco, Tunisia, Spain, Balearic and Canary islands); one haplotype was found in common in Algeria, Morocco,

Spain and the Canaries; and one haplotype was found in common in Algeria, Morocco and Spain (Figure 2). The seven remaining haplotypes were found only in Algeria. Taking into account sample size, the number of *BFIBR* haplotypes is not significantly different between Algeria, Morocco, Tunisia, continental Spain, Balearic and Canary islands. The mean number of pairwise differences between sequences was 3.914, and it varies from 0.000 (Tunisia, Balearic Islands) to 4.046 (Algeria) depending on geographical region (Table 2). Between geographical regions, the mean number of pairwise differences varies from 0.00 to 4.62 (Table 3).

## Discussion

Our mitochondrial and nuclear data are consistent and show low genetic diversity across the geographical range of the Algerian hedgehog. With both genetic markers, the specimens from Spain always display the same haplotype compared with the specimens from North Africa. With the nuclear marker, the specimens from Balearic and Canary islands are genetically similar to the specimens from North Africa. With the mitochondrial marker, the specimens from both the Balearic and Canary islands display unique haplotypes, but they differ by less than three mutations from the haplotypes of the specimens from North African. A similar, or even greater, level of genetic difference is

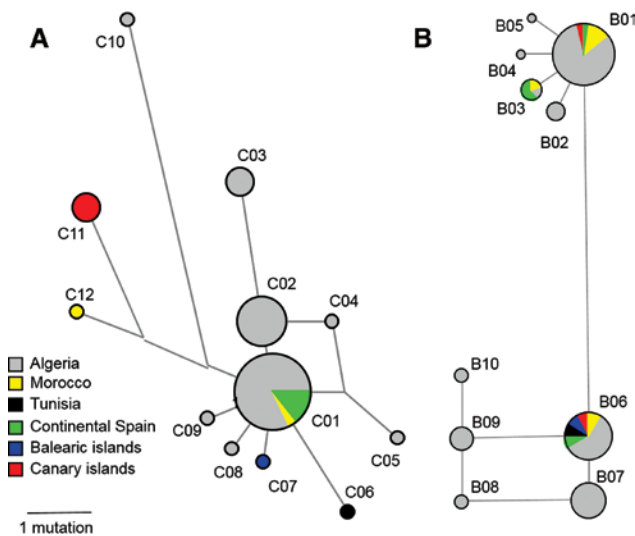
**Table 1:** List of specimens used in this study with geographical origin, haplotype number and Genbank numbers.

Country	Locality name	Locality code	Field number	Cytb Genbank number	Cytb haplotype number	BFIBR Genbank number	BFIBR phased haplotype number
Algeria	M'sila, Ain-Elhedjel	1	H69	KP279808	C02		
	M'sila, Beni-Yelmane	1	H46	KP279792	C02		
	M'sila, Benserour	1	H17	KP279771	C01	KP279828	B01
	M'sila, boukhmissa	1	H60	KP279804	C04	KP279859	B10
	M'sila, Diss	1	H10	KP279769	C02	KP279826	B07
	M'sila, Diss	1	H34	KP279785	C02	KP279843	B07
	M'sila, Djaafra (Msila center)	1	H42	KP279789	C02		
	M'sila, Djebel Thameur – Ain Elmalh	1	H47	KP279793	C01		
	M'sila, Guerf	1	H36	KP279786	C01	KP279844	B01
	M'sila, Hammam Dalaa	1	H27	KP279779	C02	KP279837	B06
	M'sila, Laaouaïz (Ouled Aïdai El Guebala)	1	H41	KP279788	C02	KP279847	B07
	M'sila, M'cif	1	H50	KP279795	C09	KP279852	B06
	M'sila, M'cif	1	H20	KP279773	C01	KP279830	B01,B02
	M'sila, M'cif	1	H26	KP279778	C01	KP279836	B06
	M'sila, M'cif	1	H55	KP279799	C01	KP279856	B01
	M'sila, Msila centre (Djabbanet Lihoud)	1	H38			KP279846	B01,B05
	M'sila, Nouara	1	H16	KP279770	C01	KP279827	B09
	M'sila, Nouara	1	H24			KP279834	B01
	M'sila, Nouara	1	H30	KP279781	C01	KP279839	B01,B02
	M'sila, Ouanougha	1	H31	KP279782	C01	KP279840	B01
	M'sila, Ouanougha	1	H32	KP279783	C01	KP279841	B01,B04
	M'sila, Ouanougha	1	H33	KP279784	C02	KP279842	B01
	M'sila, Oued Chiir	1	H25	KP279777	C05	KP279835	B01
	M'sila, Ouled Derradj	1	H57	KP279801	C01	KP279857	B06
	M'sila, Ouled Mansour	1	H49	KP279794	C10	KP279850	B01
	M'sila, Ouled Mansour	1	H35				
	M'sila, Reserve Naturelle de Mergueb	1	H04	KP279765	C02		
	M'sila, Reserve Naturelle de Mergueb	1	H05	KP279766	C01	KP279851	B01
	M'sila, Reserve Naturelle de Mergueb	1	H08	KP279767	C01	KP279864	B01
	M'sila, Reserve Naturelle de Mergueb	1	H09	KP279768	C01	KP279865	B01,B02
	M'sila, Reserve Naturelle de Mergueb	1	H37	KP279787	C01	KP279845	B09
	M'sila, Selmane	1	H28	KP279780	C01	KP279838	B07
	M'sila, Selmane	1	H44	KP279790	C02	KP279848	B06
	M'sila, Selmane	1	H45	KP279791	C01	KP279849	B07
	Bordj Bouarreridj, Bellimor	2	H21	KP279774	C03	KP279831	B01
	Bordj Bouarreridj, Bellimor	2	H22	KP279775	C03	KP279832	B01,B06
	Bordj Bouarreridj, Bellimor	2	H23	KP279776	C08	KP279833	B01
	Bordj Bouarreridj, Bellimor	2	H59	KP279803	C03	KP279858	B01,B03
	Bordj Bouarreridj, Bellimor	2	H63			KP279861	B07
	Bordj Bouarreridj, Bordj Laghdir	2	H19	KP279772	C03	KP279829	B01,B02
	Bordj Bouarreridj, Hammadia	2	H64	KP279807	C02	KP279862	B06
	Bordj Bouarreridj, Laanasser	2	H54	KP279798	C01	KP279855	B07
	Bordj Bouarreridj, Mansoura	2	H56	KP279800	C01		
Bordj Bouarreridj, Mansoura	2	H61	KP279805	C02	KP279860	B01	
Bordj Bouarreridj, Mgadem	2	H62	KP279806	C01			
Bordj Bouarreridj, Yachir	2	H58	KP279802	C01			
Sétif, Boutaleb	3	H53	KP279797	C01	KP279854	B09	
Sétif, near Zenadia forest	3	H52	KP279796	C01	KP279853	B08	
Bejaïa, Chemini –Djenane	4	H66			KP279863	excluded	
Tunisia	Sfax	5	23/VI/2010	KP279818	C06	KP279823	B06
Morocco	Road between Ifrane and Michlifen	6	MA954			KP279870	B01,B03
	Rabat (market place)	7	IS1	KP279809	C12	KP279866	B07
	Rabat (market place)	7	IS2	KP279810	C01	KP279867	B01
	Merja Zerga	8	MA676			KP279868	B01
	Merja Zerga	8	MA734			KP279869	excluded



Table 1 (continued)

Country	Locality name	Locality code	Field number	<i>Cytb</i> Genbank number	<i>Cytb</i> haplotype number	<i>BFIBR</i> Genbank number	<i>BFIBR</i> phased haplotype number
Balearic Islands	Minorca Island (Menorla)	9	18/07/2001	KP279813	C07	KP279822	B06
Canary Islands	Lanzarote	10	10062606	KP279814	C11	KP279820	B01
	Fuerteventura (La Olivia)	11	10101601	KP279817	C11		
	Fuerteventura (La Olivia)	11	10101602	KP279816	C11	KP279821	B06
	Gran Canaria	12	KF783144	KF783144	C11		
Spain	Catalonia (Collserola Natural Park, Barcelona)	13	CO7110901	KP279811	C01	KP279824	B06
	Catalonia (Collserola Natural Park, Barcelona)	13	CO7992501	KP279812	C01	KP279825	B03
	Catalonia (Collserola Natural Park, Barcelona)	13	CS/2006/391	KP279819	C01		
	Catalonia (Collserola Natural Park, Barcelona)	13	SN 27/7/10	KP279815	C01	KP279871	B01,B03



**Figure 2:** Minimum spanning network of *Atelerix algirus* mtDNA (*Cytb*; A) and nDNA (*BFIBR*; B) haplotypes. Circle sizes are proportional to the number of similar haplotypes observed in the data set. Branch lengths are proportional to the number of mutations between haplotypes. Codes refer to haplotype numbers (“C” for *Cytb* haplotypes, “B” for *BFIBR*-phased haplotypes).

observed between the Algerian or Moroccan haplotypes. Thus, the presence of distinct haplotypes in the Balearic and Canary Islands is more likely due to low sample size than to the accumulation of genetic differences by allopatric diversification. Higher genetic variability is expected in source populations. Because of unequal sample size, it is not always possible to compare the genetic diversity obtained from distinct geographical regions. However, when controlling for sample size, the number of *Cytb* haplotypes is significantly greater in Algeria than in continental Spain and Canary Islands. Our results suggest the recent colonisation of Spain, Balearic and Canary Islands

by this species (Holocene). According to published data, the introduction of *Atelerix algirus* into Minorca occurred during the 13th century (Morales and Rofes 2008), around 1000 BC into continental Spain (Borg 2005), and in 1892 in the Canaries (Hutterer 1983). To confirm these dates of introductions using molecular markers, a greater sample size and more variable genetic markers are needed. The four individuals from Canary Islands (Fuerteventura, Lanzarote and Gran Canaria) share the same mtDNA haplotype. This result supports the hypothesis that a pair of hedgehogs was brought from Morocco to Fuerteventura, which then colonized all Canary Islands (Hutterer 1983). The low *Cytb* genetic diversity observed in Canary Islands is likely due to a founder event and the maternal inheritance of mtDNA, but this hypothesis has to be confirmed using a greater sample size.

The recent anthropogenic introduction of this species in Europe and these islands may be explained by the facts that 1) it is sometimes taken from the wild to be kept as a pet (Alcover 2002, 2007); 2) it is also locally caught and eaten across the Mediterranean region, including the Balearic islands (Alcover 2002, 2007); 3) in Morocco, it is used locally for medical purposes and appears in local witchcraft markets (Bellakhdar 1978, Camps-Fabrer and Peyron 2000); and 4) in the 19th century, it was introduced to the island of Comino (Malta) to control the large cockroach population (Borg 2005).

Several subspecies have been described either from the mainland (*Atelerix a. fallax* from Tunisia, *A. algirus algirus* from Algeria and Tunisia, and *A. algirus lavaudeni* from Morocco) or from islands (*A. algirus vagans* from Minorca, Balearic Islands; *A. algirus caniculus* from Fuerteventura, Canaries; and *A. algirus girbaensis* from Djerba, Tunisia) (Cabrera 1928, Heim de Balsac 1936, Ellerman and Morrison-Scott 1951, Kahmann and Vesmanis 1978). Given

**Table 2:** Diversity estimates of *Atelerix algirus* for each gene (*Cytb* and *BFIBR* intron 7) and each geographical region.

Country	N	S	h	Hd	Pi	K
<i>Cytb</i> gene						
All specimens	56	20	12	0.704±0.054	0.00514±0.00091	1.830
Algeria	44	13	8	0.656±0.058	0.00371±0.00839	1.321
Morocco	2	3	2	1.000±0.500	0.00843±0.00421	3.000
Tunisia	1					
Continental Spain	4	0	1			0.000
Balearic Islands	1					
Canary Islands	4	0	1			0.000
<i>BFIBR</i> gene						
All specimens	100	14	10	0.753±0.030	0.00611±0.00342	3.914
Algeria	78	14	10	0.756±0.035	0.00631±0.00353	4.046
Morocco	8	7	8	0.607±0.164	0.00441±0.00296	2.821
Tunisia	2	0	1			0.000
Continental Spain	6	7	3	0.733±0.155	0.00595±0.00402	3.800
Balearic Islands	2	0	1			0.000
Canary Islands	4	6	2	0.667±0.204	0.00626±0.00470	4.000

Number of sequences (N), number of polymorphic sites (S), number of haplotypes (h), haplotype diversity (Hd), nucleotide diversity (Pi), and average number of nucleotide differences (k) are given.

**Table 3:** Average number of pairwise differences between populations of *Atelerix algirus* from distinct geographical regions.

	Algeria	Morocco	Tunisia	Continental Spain	Balearic Islands	Canary Islands
Algeria		2.29	2.82	0.82	1.82	2.29
Morocco	3.66		3.50	1.50	2.50	3.50
Tunisia	3.65	4.62		2.00	3.00	6.00
Continental Spain	4.04	3.00	4.50		1.00	4.00
Balearic Islands	3.65	4.62	0.00	4.50		5.00
Canary Islands	3.57	3.12	3.00	3.50	3.00	

Above diagonal: *Cytb* gene (356 bp). Below diagonal: *BFIBR* gene (641 bp).

that the differential diagnosis is mainly based on pelage variations (hairs, spines), the validity of these subspecies has been regularly questioned (Corbet 1988, Hutterer 2005, Happold 2013). Our data do not show any genetic discontinuity between the Algerian, Moroccan, Tunisian, Spanish, Balearic or Canarian populations, suggesting that subspecific recognition may be unwarranted. To further investigate the taxonomy of this species and its phylogeographic history, increasing the sample size from diverse parts of its distribution and increasing the number of genetic markers would be useful.

**Acknowledgments:** This work was funded by the ANR projects PEX04-MOHMIE. Molecular analyses were supported by the Service de Systématique Moléculaire of the French National Museum of Natural History (UMS 2700, Paris, France) and the network “Bibliothèque du Vivant” funded by the CNRS, the Muséum National d’Histoire Naturelle, the INRA, and the CEA (Genoscope). In the field, we

benefited from the help of A. Lalis, E. Stoetzel, A. Delapré, C. Denys, S. Cahill and F. Llimona. MK thanks particularly Prof. I. Doadrio and Dr. F. Alda from Spain for their help. The authors wish to thank all those who provided samples for this study in Algeria, Morocco, Tunisia and Spain.

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