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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

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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 Palaearctic, sub-Saharan Africa and arid Palaearctic (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 (Alegeria, 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>).

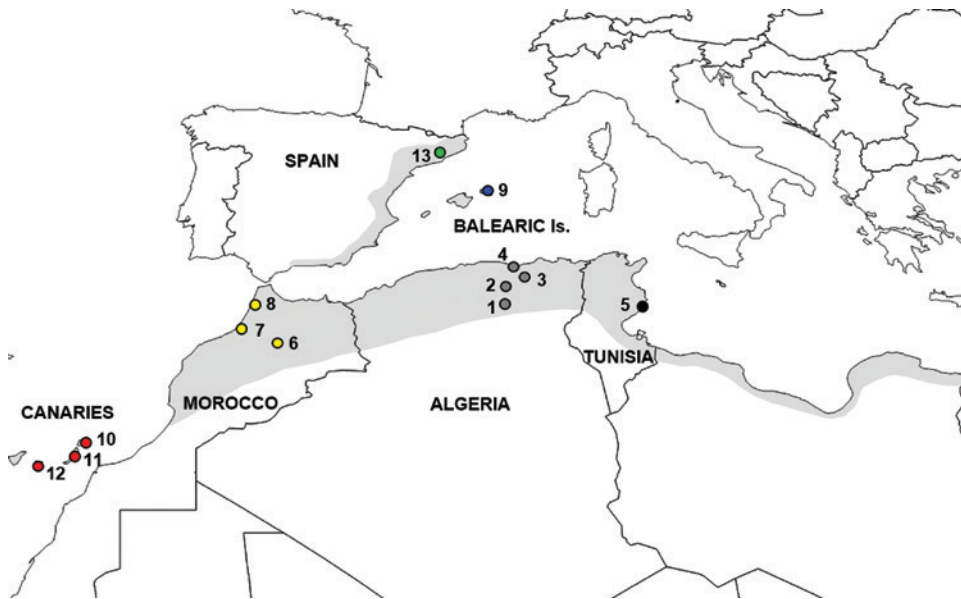


Figure 1: Map of North Africa and Southern Europe showing the geographical distribution of *Atelerix algirus* (in grey, adapted from Amori et al. 2008) and the sampling localities (circles). Colours refer to the main geographical areas discussed in the text (Algeria, Morocco, Tunisia, continental Spain,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

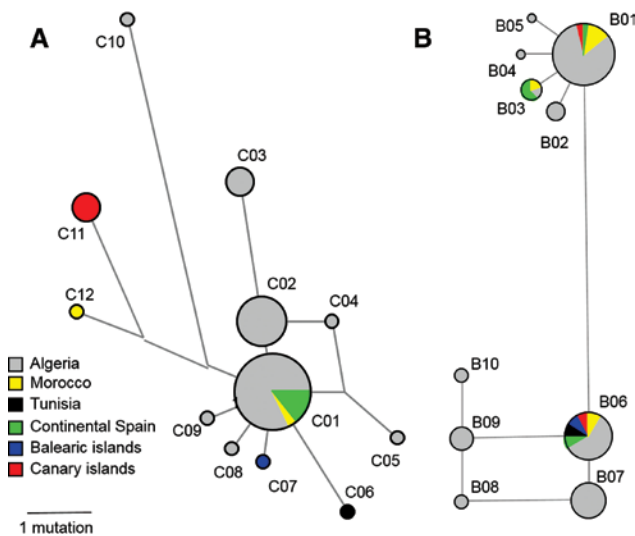


Figure 2: Minimum spanning network of *Atelerix algirus* mtDNA (*Cytb*; A) and nDNA (*BFIBR*; B) haplotypes. Circle sizes are proportional to the number of similar haplotypes observed in the data set. Branch lengths are proportional to the number of mutations between haplotypes. Codes refer to haplotype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

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