



Phylogeographic analyses of western Palearctic *Scaurus* (Coleoptera: Tenebrionidae) reveal undetected taxonomic substructure along the pre-Saharan Atlantic Coast of western Africa

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<https://zoobank.org/4CAF4C53-004E-4EE0-B502-7242A1BA2660>

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Abstract

Phylogeography stands as a key tool to explore evolutionary patterns and processes, playing a crucial role in delimiting evolutionary units. Identifying these units is essential for providing robust taxonomic decisions. In this study, we present a comprehensive phylogeographical framework of *Scaurus uncinus* (Forster, 1771) and *Scaurus gigas* Walz, 1835 across the Iberian Peninsula and North-western Africa, where they are widely co-distributed, coexisting in several localities on both sides of Strait of Gibraltar. Our results show that the Strait of Gibraltar did not act as a geographical barrier for these species, revealing shared mitochondrial haplotypes and nuclear alleles between populations on both sides. However, the Souss Valley in Morocco appears to have historically served as a significant geographical barrier within the *S. gigas* lineage, leading to the divergence of two morphologically distinct sublineages, one to the north (*S. gigas*) and the other to the south (*S. ferrerii* stat. nov.). In addition, we point out a case of cytonuclear discordance between *S. uncinus* and *S. gigas* in the southwest corner of the Iberian Peninsula, suggesting the occurrence of an ancient event of genetic introgression between the two species.

Keywords

Allele networks, cyto-nuclear discordances gene flow, genetic isolation, haplotype networks, introgression, mitochondrial DNA

1. Introduction

Understanding the patterns and processes underlying the origin and distribution of lineages, both at intra- and supra-specific levels, is fundamental for testing taxonomic hypotheses (Szymura and Barton 1986; Babik et al. 2005; Dufresnes and Martínez-Solano 2020; Sánchez-Vialas et al. 2020, 2021; Kamiński et al. 2021; Sainz-Escudero et al. 2022). In this context, phylogenetic and phylogeographic analyses have become key tools

for delimiting evolutionary units, contribute to resolving long-standing taxonomic problems (Mas-Peinado et al. 2021; Sainz-Escudero et al. 2021; Cuesta-Segura et al. 2023).

Complex evolutionary dynamics, encompassing hybridization among morphologically similar species or lineages have usually driven to intense taxonomic debates (Dufresnes et al. 2020; Doniol-Valcroze et al. 2021). Gene

flow across well-defined species can determine different outcomes along the speciation continuum, including reinforcement (strengthening preexisting reproductive isolating mechanisms between lineages) (Servedio and Noor 2003; Pfenning 2016), melting pots (Dinis et al. 2019), lineage fusion (Taylor et al. 2006), instant speciation (Ramsey and Schemske 1998; Gonçalves and Brito 2020), and introgression (Zieliński et al. 2013; Racimo et al. 2015). Within this context, the understanding of these processes is required to perform solid taxonomic revisions.

The extend of hybrids zones and the fate of the parental lineages depends on the strength of the barriers to gene flow (Dufresnes et al. 2020). In this sense, restricted and localized introgression is consistent with strong selection against hybrids, which also is of paramount importance to determine the taxonomic status of the evolving lineages (Dufresnes et al. 2020). The hallmark of gene flow between closely related species can be noticed as cyto-nuclear discordances (Wielstra and Arntzen 2020). This phenomenon is well-documented in regions of climatic instability, where range shifts promote secondary contact and lineages admixture (Hewitt 1999, 2004). This is the case of the western Palearctic, where cyclic climatic oscillations during the Pleistocene had a significant influence on the genetic diversity and distribution of the local biota (Hewitt 2004; Gómez and Lunt 2006). The integration of phylogeographic hypotheses and congruence analysis enables more accurate taxonomic investigations of morphologically difficult to interpret groups.

Scaurus Fabricius, 1775 (Coleoptera: Tenebrionidae) is a group of thermophilic darkling beetles comprised by 25 species widespread through the Mediterranean basin, with extensions into the Atlantic and Saharan regions (Escalera 1914; Labrique 2009, 2020; Iwan and Löbl 2020; Nabozhenko et al. 2020). Some species of this genus exhibit partially overlapping distributions, making them an excellent system for comparative phylogeographic studies. This applies to *Scaurus uncinus* (Forster, 1771) and *S. gigas* Walther, 1835, two species with partially sympatric distributions across both sides of the Gibraltar Strait (Cartagena et al. 2002; Cartagena and Galante 2005; Español 1957, 1960, 1963; Labrique 1995a, 1995b). The former species extends over the western Mediterranean basin and the Atlantic coast of Morocco, whereas the latter, *S. gigas*, is restricted to the Atlantic coastal plains from the Oued Draa in Morocco to the southwestern corner of the Iberian Peninsula (Español 1960; Labrique 2004). Although no seasonal differences have been identified between these species, habitat segregation may be occurring; *S. gigas* inhabits sandy coastal areas and does not venture into inland regions, whereas *S. uncinus* occupies a broader range of open habitats and is rarer in coastal plains (Español 1960; López-Pérez 2010). Idiosyncratic patterns of distribution across the Gibraltar Strait have been reported in ecologically similar species of Tenebrionoidea, such as in *Pimelia* Fabricius, 1775, in which for some species the Strait of Gibraltar act as a geographical barrier but clearly not for others (Mas-Peinado et al. 2021). However, whether this barrier accounts for phylogeographical structuration in *Scaurus* is unknown.

The genus *Scaurus* is characterized by a conserved general morphology, which resulted in a complex taxonomic history for several species, including *S. uncinus* and *S. gigas* (see Labrique 2004). Whereas *S. uncinus* presents a relatively uniform morphology across most of its distribution, the southern Moroccan populations of *S. gigas* are diagnosable from other conspecifics (Español 1943, 1960). These populations were initially classified as subspecies, named *Scaurus uncinus ferrerii* Español, 1943, based on specimens from Sidi Ifni, but were later transferred as a synonym of *S. gigas* (Labrique 2004). Currently, *S. gigas* encompasses two additional synonyms from northern Morocco: *Scaurus hespericus* (Solier, 1838) (Type locality: Tanger, Mahon and Gibraltar) and *Scaurus maroccanus* (Fairmaire, 1875) (Type locality: Mogador). Despite their partly overlapping geographic ranges on either sides of the Gibraltar Strait, no comparative phylogeographic studies have been conducted between the species pair *S. uncinus* and *S. gigas*, and consequently, their evolutionary history remains enigmatic. Given these shortfalls, a revision of the diversity and distribution of *S. uncinus* and *S. gigas* across most of their range is needed.

In this work, we perform comparative phylogeographic analyses by combining mitochondrial and nuclear gene fragments of *S. uncinus* and *S. gigas* sampled over an extensive area that covers most of their respective distribution ranges. We aim to explore (1) the intraspecific patterns of mitochondrial and nuclear genetic variation in both species, (2) the existence of shared phylogeographic patterns and barriers to gene flow, (3) the strength of the reproductive barriers between these pairs of species, and (4) the nature of the morphological differentiation among the populations of *S. gigas*.

2. Materials and methods

2.1. DNA extraction, sequencing, and sequence alignment

Thirty-seven specimens of *S. gigas* (N=14), *S. ferrerii* (N=3), and *S. uncinus* (N=20) from the Iberian Peninsula and Morocco were preserved in 96° ethanol at 6°C for molecular DNA analyses. All specimens were injected with 96° ethanol before preservation. The studied specimens have been deposited in the entomological collection of the Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain.

Genomic DNA was extracted from leg tissue using the Qiagen DNeasy commercial kit. PCR was used to amplify fragments of the cytochrome B (Cyt *b*) (30 specimens) and the nuclear internal transcribed spacer (ITS2) (33 specimens) genes. Although attempts were made to amplify genetic material from all 37 specimens, complete success was not achieved across all specimens. The Cyt *b* was amplified using the set of primers CB-J-10933/CB-N-11367 (Kergoat et al. 2014) and CB-3/CB-4 (Barra-

clough et al. 1999), whereas the ITS2 was amplified using the set of primers CAS28sB1d and CAS5p8sFt (Ji et al. 2003). PCRs were performed in 25 μ l, including 23 μ l of the PCR products (15.6 μ l of H₂O, 2.5 μ l of a reaction buffer with MgCl₂ [2 mM], 1 μ l of dNTP [10 mM], 2.5 μ l of MgCl₂ [50 mM], 0.5 μ l of each primer [10 mM], and 0.2 μ l of Taq polymerase [5U/mL]) and 2 μ l of DNA. PCR conditions for Cyt *b* with the set of primers CB-J-10933/CB-N-11367 were as follows: 3 min at 94°C, followed by 40 cycles of denaturation at 94°C for 1 min, annealing at 56°C for 1 min and extension at 72°C for 1 min, with a final single extra extension step at 72°C for 10 min; and with the set of primers CB-3 and CB-4: 3 min at 94°C, followed by 5 cycles of denaturation at 92°C for 1 min, annealing at 38°C for 1 min and extension at 72°C for 1 min, followed by 40 cycles of denaturation at 92°C for 1 min, annealing at 48°C for 1 min and extension at 72°C for 1 min, with a final single extra extension step at 72°C for 10 min. For ITS2 PCR conditions were: 5 min at 96°C, followed by 40 cycles of denaturation at 94°C for 1 min, annealing at 48°C for 1 min, and extension at 72°C for 1 min, with a final single extra extension step at 72°C for 10 min. PCR products were checked in a 1.5% agarose gel and the products of expected length were purified

and directly sequenced at Macrogen Inc. (Macrogen Europe, Madrid, Spain).

2.2. Haplotype and allelic networks

Sequences were collapsed into haplotypes using ALTER (Glez-Peña et al. 2010). Haplotype (Cyt *b*) and allele (ITS2) networks were built using a minimum spanning network (Bandelt et al. 1999) and Farris's maximum-parsimony (MP plotted in Pop Art (Leigh and Bryant 2015).

3. Results

The studied populations of *Scaurus gigas* from the Iberian Peninsula and North Africa are represented by 12 Cyt *b* haplotypes, three are only found in the Iberian Peninsula, eight exclusively in Morocco, and a single one is shared at both sides of the Strait of Gibraltar (Fig. 1; Table 1). The studied populations from Aglou and Deghaimis (Morocco) present two haplotypes separated between each

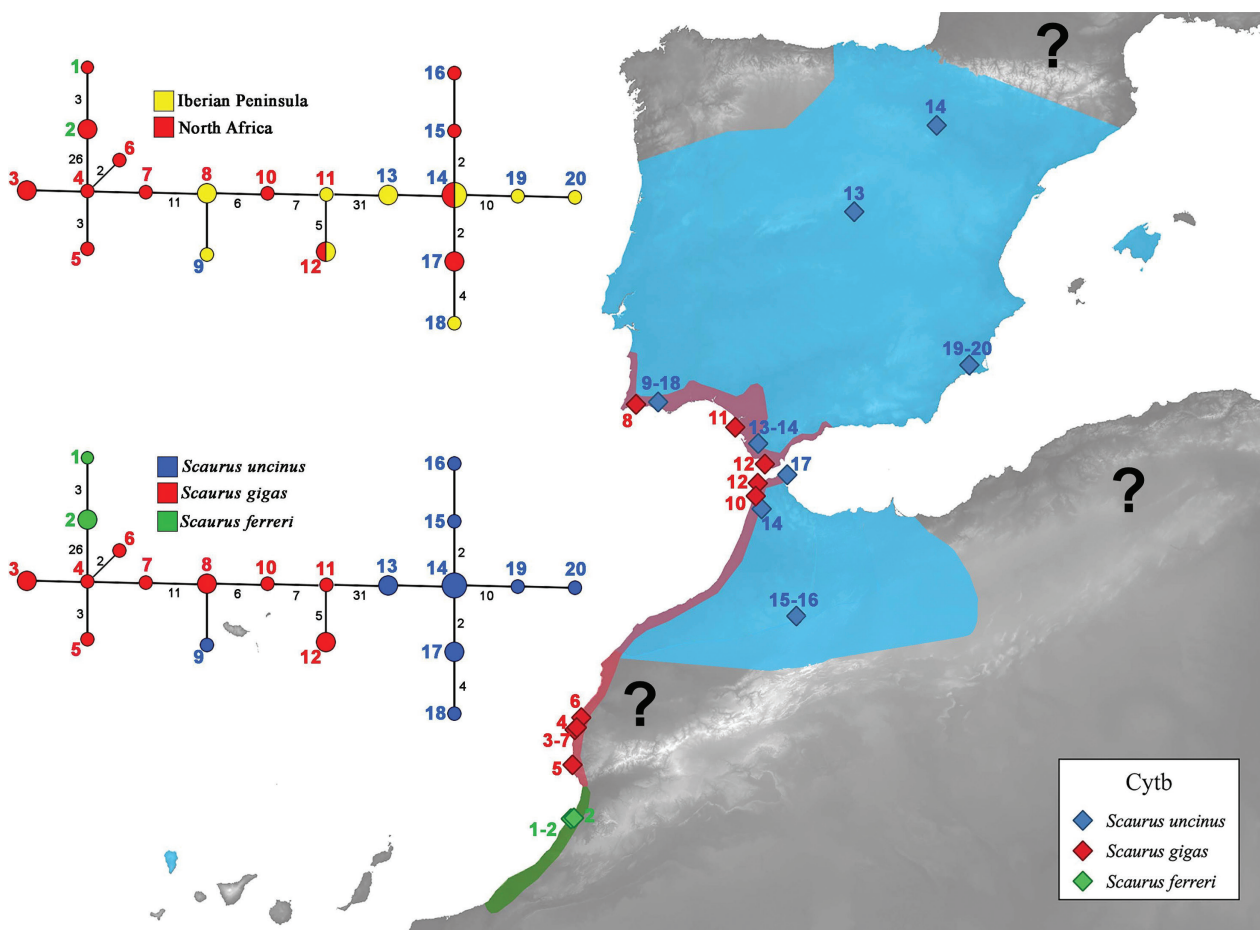


Figure 1. Haplotype network based on Cyt *b* haplotypes for *Scaurus gigas* (Waltl, 1835) (red), *Scaurus uncinus* (Forster, 1771) (blue), and *Scaurus ferreri* Español, 1960 (green). Inferred intermediate haplotypes are counted with black numbers. Colors correspond to the geographic origin of the specimens. The size of the circles indicates the relative frequency of sequences belonging to a particular allele. The presence of *S. uncinus* outside the blue shaded area requires confirmation because it is easy to be confused with other species of similar morphology and the records are old and imprecise.

Table 1. Species identities, collecting localities, voucher numbers and GenBank accession numbers for the samples analyzed in this study.

Code	Species	Locality	Coordinates	Haplotype (Cyt <i>b</i>)	Cyt <i>b</i> Genbank code	Allele (ITS2)	ITS2 Genbank code
CDAS0047	<i>Scaurus gigas</i>	Morocco: Essaouira: Ouassane – Sidi Kaouki	31°22'48"N, 9°47'37"W	4	P0438088	1	PQ435559
CDAS0048	<i>Scaurus gigas</i>	Morocco: Essaouira: Ouassane – Sidi Kaouki	31°22'48"N, 9°47'37"W	6	P0438089	1	PQ435560
CDAS0050	<i>Scaurus gigas</i>	Portugal: Faro: Lagos: Meia Praia	37°06'59"N, 8°39'08"W	8	P0438082	3	PQ435566
CDAS0051	<i>Scaurus gigas</i>	Portugal: Faro: Lagos: Meia Praia	37°06'59"N, 8°39'08"W	8	P0438083	3	PQ435567
CDAS0112	<i>Scaurus gigas</i>	Spain: Cádiz: Chipiona	36°44'12"N, 6°25'45"W	11	P0438085	—	—
CDAS0114	<i>Scaurus gigas</i>	Spain: Cádiz: Playa de Bolonia	36°5'17"N, 5°46'21"W	12	P0438086	3	P0435568
CDAS0115	<i>Scaurus gigas</i>	Morocco: Tanger: Cap Espartel	35°45'5"N, 5°55'56"W	12	P0438087	—	—
CDAS0117	<i>Scaurus gigas</i>	Morocco: Tnine Chtouka (Tnine-des-Ghtouka)	33°18'5"N, 8°9'18"W	—	—	3	PQ435569
CDAS0118	<i>Scaurus gigas</i>	Morocco: between Diet and Larache	35°31'34"N, 5°58'42"W	10	P0438084	—	—
CDAS0119	<i>Scaurus gigas</i>	Morocco: Road Essaouira-Moulay Bouzerktoun	31°35'46"N, 9°39'48"W	3	P0438090	1	P0435561
CDAS0120	<i>Scaurus gigas</i>	Morocco: 4 km S El Ghazoua	31°25'09"N, 9°45'10"W	3	P0438091	1	P0435562
CDAS0121	<i>Scaurus gigas</i>	Morocco: 4 km S El Ghazoua	31°25'09"N, 9°45'10"W	7	P0438092	1	PQ435563
CDAS0124	<i>Scaurus gigas</i>	Morocco: 3 km SW Afra (Imsouane)	30°45'52"N, 9°49'16"W	5	P0438093	2	PQ435564
CDAS0125	<i>Scaurus gigas</i>	Morocco: 3 km SW Afra (Imsouane)	30°45'52"N, 9°49'16"W	—	—	2	P0435565
CDAS0129	<i>Scaurus ferreri</i>	Morocco: Aglou Beach	29°49'05"N, 9°49'31"W	1	P0438094	4	PQ435570
CDAS0130	<i>Scaurus ferreri</i>	Morocco: Aglou Beach	29°49'05"N, 9°49'31"W	2	P0438095	4	PQ435571
CDAS0133	<i>Scaurus ferreri</i>	Morocco: Deghaimis	29°49'59"N, 9°45'55"W	2	PQ438096	4	P0435572
CDAS0001	<i>Scaurus uncinus</i>	Spain: Cadiz: Medina Sidonia	36°26'59"N, 5°55'8"W	13	P0438097	5	P0435573
CDAS0002	<i>Scaurus uncinus</i>	Spain: Cadiz: Medina Sidonia	36°26'59"N, 5°55'8"W	14	P0438104	5	P0435574
CDAS0006	<i>Scaurus uncinus</i>	Spain: Madrid: Sanchinarro, Valde-fuentes	40°30'07"N, 3°38'33"W	13	P0438099	5	P0435575
CDAS0007	<i>Scaurus uncinus</i>	Spain: Madrid: Sanchinarro, Valde-fuentes	40°30'07"N, 3°38'33"W	13	P0438098	6	P0435581
CDAS0008	<i>Scaurus uncinus</i>	Spain: Murcia: Fuente Álamo de Murcia	37°43'12"N, 1°08'02"W	19	P0438109	5	P0435576
CDAS0009	<i>Scaurus uncinus</i>	Spain: Murcia: Fuente Álamo de Murcia	37°43'12"N, 1°08'02"W	20	PQ438110	8	P0435584
CDAS0013	<i>Scaurus uncinus</i>	Spain: Navarra: Ablitas	41°57'43"N, 1°36'12"W	—	—	5	P0435577
CDAS0014	<i>Scaurus uncinus</i>	Spain: Navarra: Ablitas	41°57'43"N, 1°36'12"W	14	P0438105	9	P0435585
CDAS0017	<i>Scaurus uncinus</i>	Morocco: E of Ifrane	33°28'38"N, 5°01'39"W	—	—	10	P0435586
CDAS0018	<i>Scaurus uncinus</i>	Morocco: E of Ifrane	33°28'38"N, 5°01'39"W	—	—	10	P0435587
CDAS0024	<i>Scaurus uncinus</i>	Morocco: Tanger	35°17'58"N, 5°51'02"W	14	P0438101	7	P0435582
CDAS0025	<i>Scaurus uncinus</i>	Morocco: Tanger	35°17'58"N, 5°51'02"W	14	P0438100	7	PQ435583
CDAS0027	<i>Scaurus uncinus</i>	Portugal: Faro: Loulé: Lombada	37°09'59"N, 8°09'30"W	9	P0438081	5	P0435578
CDAS0028	<i>Scaurus uncinus</i>	Portugal: Faro: Loulé: Lombada	37°09'59"N, 8°09'30"W	18	P0438106	5	PQ435579

Code	Species	Locality	Coordinates	Haplotype (Cyt <i>b</i>)	Cyt <i>b</i> Genbank code	Allele (ITS2)	ITS2 Genbank code
CDAS0029	<i>Scaurus uncinus</i>	Morocco: 15 km S-SW Timahdite	33°24'20"N, 5°07'17"W	15	P0438107	—	—
CDAS0030	<i>Scaurus uncinus</i>	Morocco: 15 km S-SW Timahdite	33°24'20"N, 5°07'17"W	16	P0438108	10	PQ435588
CDAS0109	<i>Scaurus uncinus</i>	Spain: Ceuta: Cala Desnarigado, Monte Hacho	35°53'45"N, 5°16'54"W	17	P0438102	5	P0435580
CDAS0110	<i>Scaurus uncinus</i>	Spain: Ceuta: Cala Desnarigado, Monte Hacho	35°53'45"N, 5°16'54"W	17	P0438103	10	PQ435589
CDAS0092	<i>Scaurus uncinus</i>	Morocco: El Hajeb	33°42'10"N, 5°21'30"W	—	—	11	PQ435591
CDAS0093	<i>Scaurus uncinus</i>	Morocco: El Hajeb	33°42'10"N, 5°21'30"W	—	—	10	P0435590

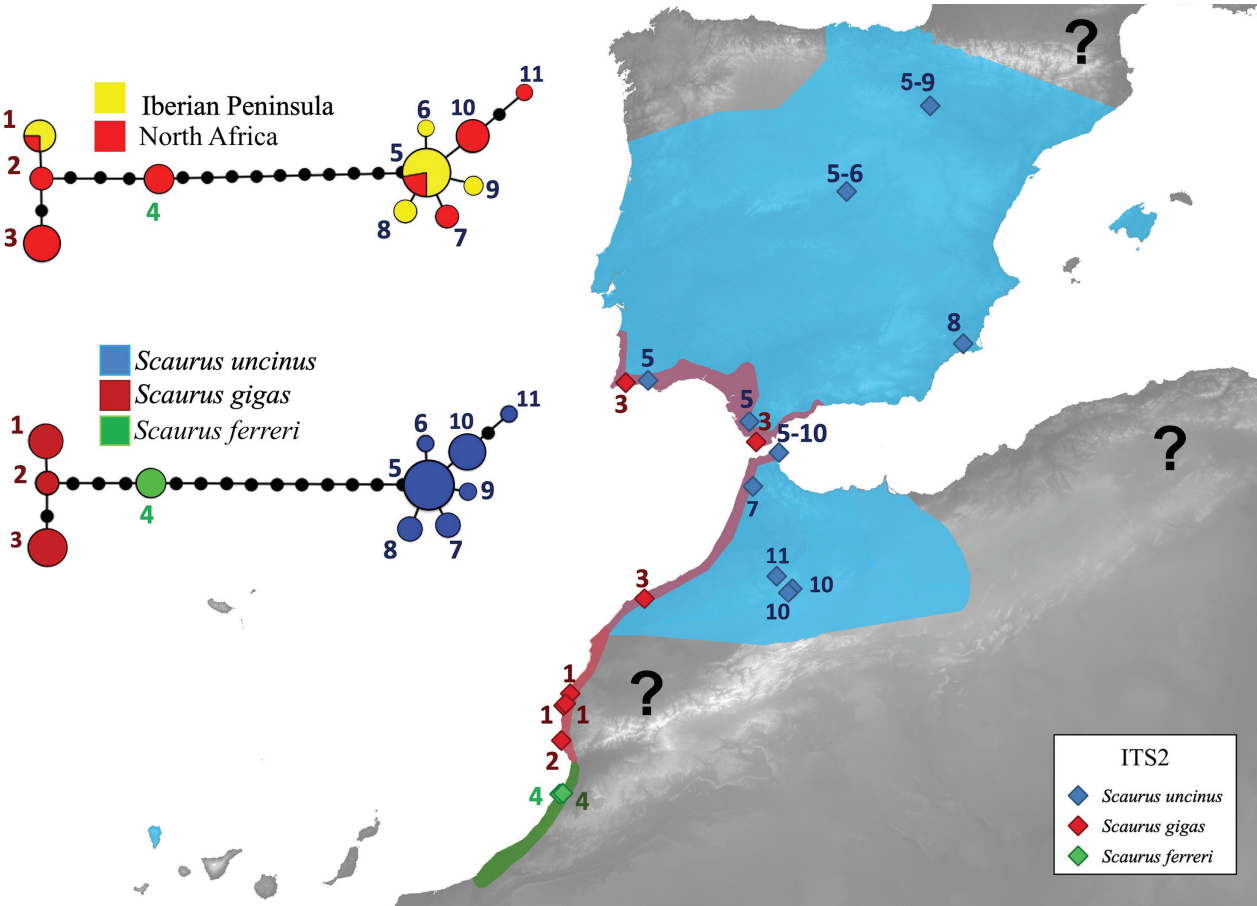


Figure 2. Allelic network based on partial sequences of the nuclear second Internal Transcribed Spacer (ITS2) for *Scaurus gigas* (Waltl, 1835) (red), *Scaurus uncinus* (Forster, 1771) (blue), and *Scaurus ferrerii* Español, 1960 (green). Inferred intermediate alleles are represented by small black circles. Colors correspond to the geographic origin of the specimens. The size of the circles indicates the relative frequency of sequences belonging to a particular allele.

other by 4-point mutations, but they are notably distant (26-point mutations) from all other haplotypes.

The studied populations of *Scaurus uncinus* presented eight Cyt *b* haplotypes. This species shows lower haplotype diversity than *S. gigas*. Four haplotypes are only found in the Iberian Peninsula, three only in Morocco, and one is shared across the Strait of Gibraltar. The studied population from Murcia (Spain) is separated by 10 mutations from the closest haplotype (Fig. 1).

Allele networks based on ITS2 for the studied populations of *S. gigas* (15 specimens) and *S. uncinus* (20 spec-

imens) were represented by four and seven alleles, respectively (Fig. 2). The studied populations of *S. gigas* present one allele shared between North African and Iberian populations. All the other alleles are only present in Africa. The studied populations from Aglou and Deghaimis (Morocco) present a single allele separated by four-point mutations from the rest of the Iberian and African haplotypes (Fig. 2).

Scaurus uncinus, shows a higher allelic diversity than *S. gigas*, with seven ITS2 alleles observed. The most common allele is present both in the Iberian Peninsula,

where it is widespread (at Faro, Cádiz, and Madrid), and in North Africa (at Ceuta). Also, three alleles are observed in North Africa and another three different alleles in the Iberian Peninsula. A single specimen morphologically identified as *S. uncinus* (CDAS0027, See Table 1) has mitochondrial DNA of *S. gigas* being represented by the Cyt *b* haplotype number 9 (Fig. 1; Table 1) and with nuclear DNA in concordance with its morphology being characterized by the ITS2 allele number 5 (Fig. 2; Table 1).

4. Discussion

The Strait of Gibraltar, located between northwestern Africa and southwestern Europe, has acted as a geographical barrier for dispersion in different groups of small vertebrates and arthropods (Busack et al. 1985; Mas-Peinado et al. 2021; Sánchez-Vialas et al. 2020), although in some other cases it had no effect at all (Gutiérrez-Rodríguez et al. 2017; Mas-Peinado et al. 2022). The effect of the Strait and its evolutionary consequences are highly variable even for different species within the same genus (Mas-Peinado et al. 2021, 2022). The phylogeographic pattern shown by *S. uncinus* and *S. gigas* agree with those species that have been able to disperse across this marine strait, such as other tenebrionids like species of the subgenera *Amblyptera* Solier, 1836 and *Amblypteraca* Mas-Peinado et al. 2018 of *Pimelia* (Mas-Peinado et al. 2022). The studied molecular markers of *S. uncinus* and *S. gigas* present shared haplotypes and alleles between the Iberian Peninsula and northern Morocco (Figs 1, 2).

The large degree of genetic structure found in the *S. gigas* lineage indicates a long history of geographic isolation and diversification in the African continent. This pattern is reversed in *S. uncinus*, which presents a pattern of subtle genetic structuring only among the European populations. The main nuclear allele of *S. uncinus* is widespread over the central and southwestern region of the Iberian Peninsula, but it is also present in northern Morocco. This allelic distribution could be related to a rapid range expansion into the African continent (Recuero and García-París 2011; Rodríguez-Flores et al. 2017; Cox et al. 2019). These data support the existence of recent intraspecific migration and gene flow through the Strait of Gibraltar for both species. However, the direction of the colonization seems to be different in each taxon. High levels of haplotypic diversity and internal recent speciation processes in the *S. gigas* lineage occur in the African continent suggesting that colonization of Europe took place from Africa; while in the *S. uncinus* lineage larger haplotypic diversity and geographic structuring occur within the European populations suggesting the opposite pattern of colonization, from Europe to Africa.

Scaurus gigas has its meridional limit at the surroundings of the Draa valley in Morocco (Español 1960). Populations of *S. gigas* from the Draa valley to Cabo Cantín (= Cabo Beddouza, 35 km North of Safi) were described

by Español (1943) with subspecific status as *S. uncinus ferrerii* (type locality: Sidi Ifni), morphologically characterized by presenting a poorly marked to absent dorsal carina in the anterior half of the elytra, which is well marked in the northern populations. Español (1943) ascription of these populations to *S. uncinus* was a result of an historical nomenclatural confusion stemming from early misidentifications. This confusion led to what is now recognized as *S. gigas* being incorrectly identified as *S. uncinus*, and *S. punctatus* being assigned to what is currently known as *S. uncinus* (Labrique 2004). During Labrique's (2004) reassessment of the taxonomy of these species, *S. uncinus ferrerii* was included in the synonymy of *S. gigas* (Labrique 2004; Iwan and Löbl 2020).

However, our results reveal the presence of a distinct haplotypic and nuclear lineage, closely related to *S. gigas*, found at the western foothills of the Anti-Atlas Mountains, south of the Souss Valley, specifically at Aglou Beach and Deghaimis. This population exhibits a morphology consistent with the type series of *S. u. ferrerii* housed at the Museu de Ciències Naturals of Barcelona, confirming its alignment with specimens from Aglou and Deghaimis. The Aglou Beach population is located approximately 57 km north of the type locality of *S. g. ferrerii*, well within the geographic range outlined by Español (1943) for the southern subspecies (Fig. 4F). The phylogeographic structure of the clade *Scaurus gigas* – *S. ferrerii* in Morocco is likely derived from a latitudinal vicariant process of differentiation thought the Atlantic coast of Morocco, marked and more diverse in the South, and followed by a more recent northward expansion to the Iberian Peninsula, where populations are genetically more homogeneous (Figs 1, 2). Within this framework, it is noteworthy that in the southern distribution range of *S. gigas* – *S. ferrerii* clade, there are no obvious current geographic barriers to dispersal that could prevent gene flow between populations located at both sides of the Souss Valley. Some studies suggest orography as the key factor influencing the maintenance of fine patterns of allopatric lineage structuration (Habel et al. 2012). However, *S. gigas* – *S. ferrerii* are coastal species that do not occur far from the coastline, what makes difficult to infer if orography (Anti-Atlas) is accounting for their differentiation. The coastal area of the Souss Valley primarily comprises fluvial terraces with aeolian dunes (Bhiry and Occhietti 2004), flanked by the High Atlas Mountains to the North by and the Anti-Atlas to the South. Over time, this region has undergone significant environmental changes since the Miocene, including uplifted mountains and shifting environmental conditions (Aït Hssaine 1994; Bhiry and Occhietti 2004). These dynamic geological and ecological factors may have potentially promoted speciation among the reported lineages of *Scaurus*. A plausible similar pattern is evidenced by geckos of the genus *Saurodactylus* Fitzinger, 1843 and lizards of the *Acanthodactylus pardalis* species group. In the case of *Saurodactylus*, two lineages arised allopatrically (now species), which contact in the Souss valley without signs of genetic admixing (Rosado et al. 2017), while for the *Acanthodactylus pardalis* species group, the Anti-Atlas establishes a

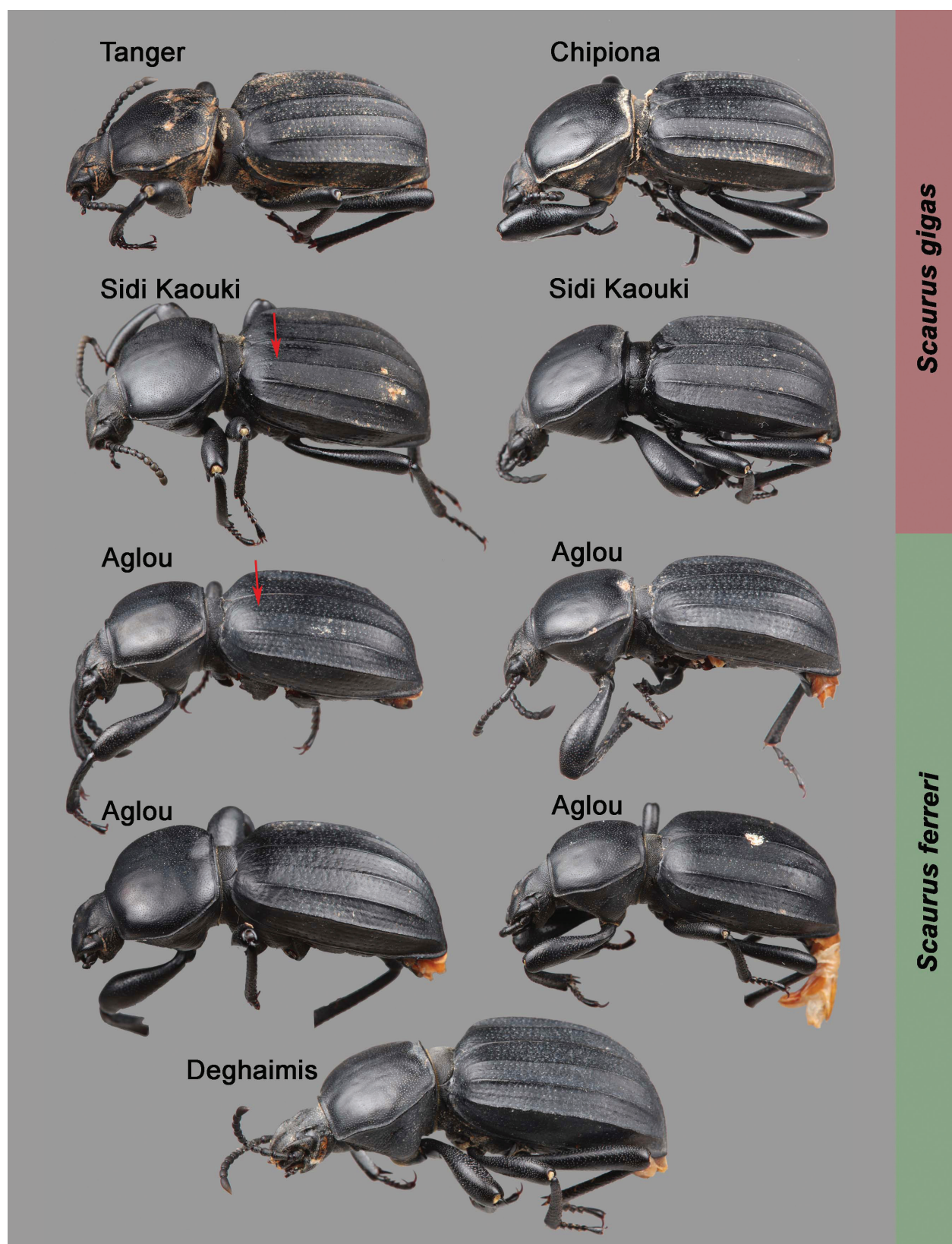


Figure 3. Morphological differences between *S. gigas* (Tanger, Chipiona and Sidi Kaouki) and *S. ferrerii* (Aglou and Deghaimis) (see Table 1 for locality details). Note the poorly marked carina on the anterior elytral region in *S. ferrerii*, which are relatively well-marked in *S. gigas* (indicated by a red arrow in one selected specimen for each species).

significant distribution gap between two sister species, one found in the Souss Valley, in the north of the Anti-Atlas, and the other to the South (Tamar et al. 2017). In our sampling we found strict concordance between nu-

clear and mtDNA markers depicting an isolated lineage south to the Souss Valley with no shared nuclear alleles between populations belonging to distinct mitochondrial populations in *S. gigas* – *S. ferrerii*.



Figure 4. Live specimens and typical habitat of *S. gigas* (a–c) and *S. ferreri* (d–f). Specimens photographed are from (a) Meia Praia, Lagos (Portugal), (b) Chipiona, Cádiz (Spain), (d) Aglou Plage (Morocco) and (e) Deghaimis (Morocco). Landscape images represent (c) the northernmost range of *S. gigas* (near Sines, Portugal) and (f) one of the northern locations of *S. ferreri* at Aglou Plage (Morocco).

Although, our sampling across the Souss valley is very limited to test for the existence of complete reproductive isolation between the two lineages, the concordance between morphology (Figs 3, 4) and molecular markers made us considered them differentiated enough as to represent two independent evolutionary units. We, therefore, propose here the formal recognition of the southernmost populations of the *S. gigas* lineage, to be part of an independent species, and therefore revalidating the name *Scaurus ferreri* Español, 1943 stat. nov. for these populations (<https://zoobank.org/C3150EA6-EE3D-447D-BB50-D22D80F4DF2C>).

As expected by their morphological distinctiveness (Español 1943, 1960), genetic admixture between *S. gigas* and *S. uncinus* was almost absent across their contact

zone. However, we observed a striking case of cyto-nuclear discordance in a single specimen morphologically identified as *S. uncinus* from Faro, southern Portugal. This specimen has a Cyt *b* haplotype of *S. gigas*, but its nuclear ITS2 allele as well as its morphology are within the variability of *S. uncinus*. This pattern of cyto-nuclear discordance observed in a single specimen, agrees with a possible hybrid origin for the specimen (Doniol-Vacroze et al. 2021). The low frequency of hybrids ($n=1/30$) across a wide potential area of sympatry (southwestern Atlantic coast of Europe and northwestern Atlantic coast of Africa), suggests that reproductive barriers between *S. gigas* and *S. uncinus* are strong, but not complete enough to prevent single episodes of hybridization (Dufresnes et al. 2020).

Transcontinental intraspecific patterns of colonization appear to be much common than previously expected between Africa and Europe for relatively large, flightless, xeric-adapted, species of terrestrial arthropods as darkling beetles (Condamine et al. 2013; Sánchez-Vialas et al. 2021; Mas-Peinado et al. 2018, 2022; Tinaut and Ruano 2021). Their low ability for dispersal is likely counteracted by large population densities and a strong survival ability in hostile environments. When darkling-beetle populations are located in coastal areas, as it is the case of the species of *Scaurus* studied here, they might be passively transported during exceptional climate disruptions (strong storms and tornados) or catastrophic volcanic episodes (ending in tsunamis) as it has been considered for other species as frogs (*Hyla meridionalis* Boettger, 1874) (Recuero et al. 2007) or tenebrionid beetles (*Archaeoglenes* Broun, 1893, *Amblyptera* Mas-Peinado, Buckley, Ruiz & García-París, 2018) (Iwan et al. 2015; Mas-Peinado et al. 2022). While other representatives of Tenebrionoidea use complex strategies for dispersal, as blister beetles with larval phoresy (Sánchez-Vialas et al. 2021), darkling beetles seem to rely on passive dispersal favored by episodic events or even human accidental transport, as it seems likely the case for some populations of *S. uncinus*, resulting from heavy maritime transport from the Iberian coast to the Spanish city of Ceuta in northern Africa.

5. Declarations

Conflict of interest. The authors declare no conflict of interest.

Data availability statement. The molecular data newly generated for this study is available in GenBank. Accession numbers P0438082–P0438110 for Cyt *b* and PQ435559–PQ435590 for ITS2 sequences.

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