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Phylogeography of *Psammodromus algirus* (Linnaeus, 1758) in Morocco

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Abstract. Currently, two subspecies of *Psammodromus algirus* are typically considered in Morocco — *P. algirus algirus* and *P. algirus nollii* –, while a third form “*ketamensis*” is generally identified as a morphotype. However, this classification is based on colouration differences, and has not been assessed using genetic data, as the previously conducted biogeographic studies included only specimens from the range of *P. algirus algirus*. In order to better assess phylogeographic patterns within the species we sequenced a nuclear and a mitochondrial marker from Moroccan individuals, including samples from within the “*nollii*” range, and combined this with previously published data, predominantly from the Iberian Peninsula. No genetic evidence to support the separation of the Moroccan *P. algirus* in two distinct subspecies was found. Unlike most other studies of reptiles from this region, the identified diversity appears to have little or no corresponding geographical structuring, possibly due to the generalist nature of the species.

Keywords. Lacertidae, Morocco, Maghreb, phylogeny, speciation, morphotype

Introduction

Psammodromus Fitzinger, 1826 is a genus of European and North African lacertids, with six described species, three of which are known to inhabit Morocco: *P. algirus* (Linnaeus, 1758), widespread through the country, *P. blanci* (Lataste, 1880), present only to the East, and *P. microdactylus* (Boettger, 1881), an elusive species endemic to Morocco (Bons and Geniez, 1996; Mendes et al., 2017).

Regarding the former, *Psammodromus algirus* inhabits most of Iberia and characteristically Mediterranean regions of the Maghreb. In Morocco, besides covering the Mediterranean coast, it is also found on the northern slopes of the High and Middle Atlas — where it can reach up to 2,600 meters —, the Rif region, in locations dotting the area between the Atlas Mountains and the Atlantic coast, and in eastern Morocco, between the Middle Atlas and the Algerian border (Bons and Geniez, 1996). Within its Moroccan range, two subspecies are typically considered: *P. algirus algirus* (Linnaeus, 1758) and *P. algirus nollii* Fischer, 1887. The former covers most of the range, while the latter is found in its easternmost interior part, across the Hauts-Plateaux, mainly in the province of Taourirt and on the southern slopes of the Middle Atlas, between the provinces of Khenifra and Errachidia. Distinction between the two is based on *P. algirus nollii* presenting an extra pair of dorsal lines. Individuals of the two subspecies with intermediate phenotypes have also been reported (Bons and Geniez, 1996). A third monochromatic subspecies was also described, *P. algirus ketamensis* Galán, 1931, from the Rif mountains, but this is now generally considered a morphotype of *P. algirus algirus* (Pasteur and Bons, 1960; Bons and Geniez, 1996).

Various studies have assessed phylogeographic patterns within *P. algirus*. Busack and Lawson (2006) analysed mitochondrial DNA and allozyme data from *P. algirus* from Spain and five Moroccan regions, three in the Rif, one in the Middle Atlas, and one in the High Atlas, and proposed that the lizards had evolved in Southern Morocco and expanded northward. In the same year, however, Carranza et al. (2006) suggested that the species had instead emerged in Iberia and invaded North Africa after the opening of the Strait of Gibraltar.

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They analysed data from partial sequences from the mitochondrial cytochrome b, 12S rRNA and 16S rRNA from Iberian and North African *P. algirus*, reporting the existence of two lineages within Iberia — Eastern and Western — that had split around 3.6 Ma, and that North African samples weakly formed a group within the Western lineage — with Tunisian samples distinct from the Moroccan ones — having split from their Iberian counterparts only 1.9 Ma. Verdú-Ricoy et al. (2010) later revisited the phylogeography of *P. algirus*, corroborating the existence of the two lineages proposed and further splitting the western one into three clades: the African, the Iberian Northwestern, and the Iberian Southwestern, obtaining strong statistical support for these groupings. Mendes et al. (2017) assessed relationships across the Strait of Gibraltar within the genus, performing ancestral range analysis to confirm the origin of each lineage. Regarding *P. algirus*, they identified the species as having its origin in the Iberian Peninsula, and that a dispersal to North Africa occurred around 1.4 MYA. The other African taxa, *P. microdactylus* and *P. blanci*, both have an African origin from a now extinct common ancestor that would have come to North Africa from the Iberian Peninsula around 10 MYA.

Despite these earlier studies, within *P. algirus*, patterns of genetic diversity across Morocco remained largely unassessed, and in particular the "*nollii*" range was essentially unsampled. This is critical, since many reptile species show a pattern of deep divergence between specimens in Eastern Morocco and those to the West of the Atlas Mountains, including species within the genera *Saurodactylus*, *Podarcis* and *Trogonophis* (Kaliontzopoulou et al., 2011; Rosado et al., 2017; Salvi et al., 2018).

With the present study, we therefore intended to improve the current coverage of genetic data for the species across Morocco to determine phylogeographic patterns for the species in the country, using both mitochondrial and nuclear DNA sequences, and to compare our results to patterns recovered from other reptiles across this region. At the same time, by including individuals from the *P. algirus nollii* range, we plan to re-evaluate support for this subspecies.

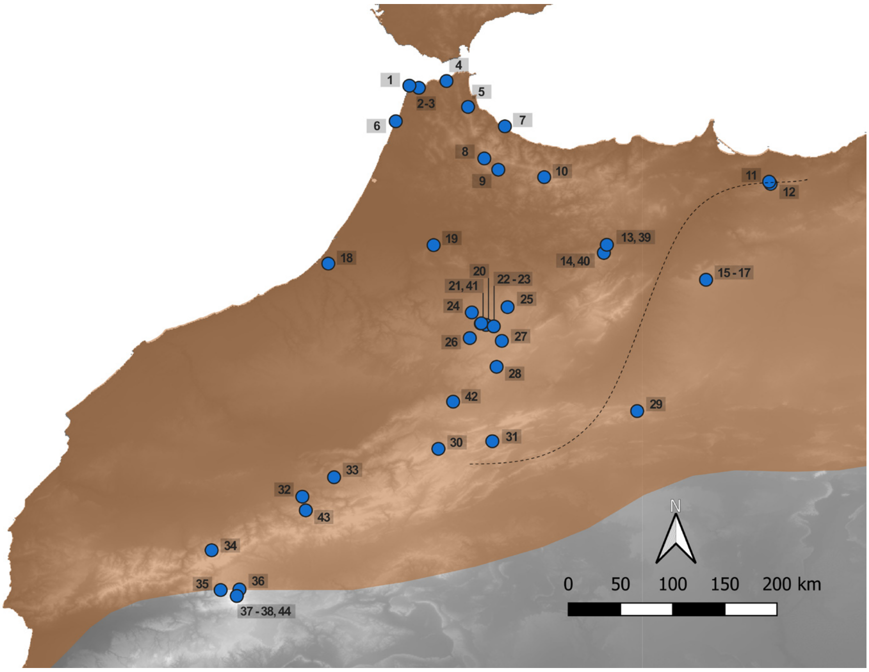

Figure 1. Map of sampling locations for Morocco. Numbers relate to partial ND4 phylogeny (1-38; Fig. 2) and partial MC1R haplotype network (6-11, 14-17, 19, 20, 22-25, 27-31, 33, 35-37, 39-44; Fig. 3). Light brown shade represents the species distribution according to IUCN (Mateo et al., 2009), and the dotted line marks the border between *Psammodromus algirus algirus* and *P. a. nollii* distribution ranges, approximately following the Moulouya river valley area.

Table 1. Location data of all newly sequenced samples included in this work. The Number relates the map of sampling locations (Fig. 1), with an asterisk marking samples from within the "*nollii*" range. One sample (DB11922) did not have precise coordinates, and is therefore not included.

Sample	Number	Country	Locality	Latitude	Longitude
DB90	42	Morocco	Khenifra province	32.6620	-5.4994
DB143	30	Morocco	Errachidia province	32.1964	-5.6429
DB441	43	Morocco	Azilal province	31.5892	-6.9369
DB929	18	Morocco	Oulad Yakoub, Sale Al Jadida province	34.0249	-6.7171
DB943	20	Morocco	Azrou, Ifrane province	33.4191	-5.17841
DB951	19	Morocco	Sidi Kacem province	34.2073	-5.6895
DB 1624	31	Morocco	Tazarine, Errachidia province	32.2714	-5.1170
DB 2357	24	Morocco	Ifrane province	33.5427	-5.3169
DB 2389	29*	Morocco	Figuig province	32.5691	-3.7043
DB 3767	8	Morocco	Bab Taza, Chefchaouen province	35.0626	-5.1951
DB3770	14	Morocco	Taza province	34.1305	-4.0292
DB3771	10	Morocco	Tlata Ketama, Al Hoceima province	34.8782	-4.6109
DB3774	23	Morocco	Mischliffen, Ifrane province	33.4054	-5.1033
DB3985	22	Morocco	Mischliffen, Ifrane province	33.4054	-5.1033
DB4068	11*	Morocco	Berkane province	34.8333	-2.4167
DB4235	40	Morocco	Taza province	34.1305	-4.0292
DB9364	36	Morocco	Amassine, Ouarzazate province	30.8081	-7.5837
DB14454	15*	Morocco	Taourirt Province	33.8653	-3.0324
DB14455	16*	Morocco	Taourirt Province	33.8653	-3.0324
DB14457	17*	Morocco	Taourirt Province	33.8653	-3.0324
DB15506	25	Morocco	Ifrane province	33.5954	-4.9684
DB15549	9	Morocco	Chefchaouen province	34.9520	-5.0585
DB15559	7	Morocco	Chefchaouen province	35.3796	-4.9947
DB23812	37	Morocco	Taroudant province	30.7439	-7.6096
DB24246	35	Morocco	Taroudant province	30.8022	-7.7674
DB25246	33	Morocco	Azilal Province	31.9159	-6.6609
DB25444	27	Morocco	Ifrane province	33.2618	-5.0244
JH1	6	Morocco	Assilah, Tangier-Assilah Prefecture	35.4298	-6.0591
JH5	28	Morocco	Ifrane province	33.0059	-5.0752

Material and Methods

A total of 31 individuals were sequenced, with 4 belonging to *P. algirus nollii* (samples 15, 16, 17, and 29) — based on distribution and visual identification in the field — 2 found in an area where both subspecies and intermediates are recorded (samples 11 and 12), and the remainder to *P. algirus algirus* from across the range in Morocco (Tab. 1; Fig. 1). A sample was included from the "*ketamensis*" type locality of Ketama (sample 10), but no confirmation of morphotype was available. Samples consisted of tail-tip muscle, stored in 96% ethanol.

A standard high-salt method was employed for total DNA extraction (Sambrook et al., 1989). Two molecular markers were selected for analysis: partial NADH dehydrogenase subunit 4 (ND4) mitochondrial gene, and partial melanocortin 1 receptor (MC1R) nuclear gene. Amplification conditions followed Arévalo et al. (1994) for the ND4 partial gene, and Pinho et al. (2010) for the MC1R gene region, with reagent concentrations following manufacturer indications for the polymerases — 5x HOT FIREPol® Blend Master Mix (Solis BioDyne) for the ND4, GoTaq®G2 Flexi DNA Polymerase (Promega) for the MC1R. PCR products were sent to a commercial company (GENEWIZ) for purification and sequencing.

Obtained sequences were complemented with sequences retrieved from GenBank and provided by other authors upon request, bringing the total of analysed samples to 392 for partial ND4 and 44 (88 sequences) for partial MC1R; GenBank sequences from *Psammodromus hispanicus* Fitzinger, 1826 were used as outgroup. For both markers, sequences were aligned, manually revised and trimmed to the same length — to 652 bp for partial ND4, and to 562 bp for partial MC1R — using Geneious® v4.8.5 (Biomatters). Gblocks (Castresana, 2000) was used to determine poorly aligned positions and divergent regions, though none were identified.

For the ND4 data, Bayesian inference (BI) and maximum likelihood (ML) approaches were used to estimate a phylogeny. For the BI, the most appropriate model of molecular evolution was defined with the AIC, using PartitionFinder2 (Lanfear et al., 2017) and the phylogenetic analyses implemented with MrBayes v3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). BI was performed with the GTR+G+I model, using random starting trees, run for 8×10^6 generations, and sampled every 1,000 generations. A 25% burn-in was applied to the obtained trees. Remaining data was used to estimate posterior nodal probabilities and produce a summary phylogeny. Two separate replicates were performed and compared to check for local optima (Huelsenbeck and Bollback, 2001). The ML approach was executed with MEGA X v10.0.5, both for defining the most appropriate model of molecular evolution with the AIC and producing a phylogeny. The chosen model was the TN93+G+I and a phylogenetic tree was inferred using a Nearest-Neighbor-Interchange heuristic method, with 500 bootstrap replications used to assess reliability. Again, two replicas were performed.

For the MC1R data, haplotype estimation was performed using the built-in Phase tool from DnaSP v5.10 (Librado and Rozas, 2009). A phylogenetic network using statistical parsimony was built with TCS v1.21 (Clement et al., 2000) and visualised in tcsBU (Santos et al., 2016). New sequences were submitted to GenBank (MW358039–MW358080).

Results

Our estimate of a phylogeny based on partial ND4 (Fig. 2) is congruent with the eastern and western lineage division for *P. algirus*, with North African samples falling in the western lineage, as expected. Within this lineage, the three subdivisions identified by Verdú-Ricoy et al. (2010) are also observed, clustering the African clade and the Iberian northwestern and southwestern clades. Within the African clade, the specimen from Tunisia is sister-taxon to the remaining Moroccan samples. Within Morocco there is considerable diversity, up to 2.34%. However, there is no clear phylogeographic structure, and in particular samples from the *P. algirus nollii* range do not form a clade.

For the haplotype network from partial MC1R (Fig. 3), 15 haplotypes were identified for Morocco, with two common haplotypes. Iberian individuals clearly demonstrated the eastern and western clade division based on the MC1R marker. Only five haplotypes were identified, although sampling was much more limited. The most divergent haplotypes within Iberian populations were separated by 19 nucleotide changes — for comparative purposes, the closest *P. algirus* haplotypes to *P. hispanicus* are separated by only 5 nucleotide changes to the East and West Iberian clades, respectively.

For Moroccan individuals, no association was found between their genetic diversity and geographical distribution, in either nuclear or mitochondrial DNA.

Discussion

The lack of coherency between phylogeny and geographical distribution for Moroccan *P. algirus* was unexpected, as many other widespread reptiles across this region exhibit clear patterns of population structuring (Kaliontzopoulou et al., 2011; Barata et al., 2012a,b). Indeed, the Moulouya River valley region, which approximately separates the two Moroccan subspecies, often coincides with phylogeographic breaks in reptiles (Beddek et al., 2018). In the case of *P. algirus*, not only is there no break at this point, but there is no clear phylogeographic structure at all. For *P. algirus*, the observed situation could be due to the species being a generalist (Moreno-Rueda et al., 2018), thriving in low shrub habitats independently of their actual floristic composition (Diaz and Carrascal, 1991) while being capable of shifting between habitats during their seasonal availability (Martín and López, 1998), and furthermore not having its distribution highly affected by many of the mesoclimates within the Moroccan landscape or by constrains from competition with other lacertid species (Diaz and Carrascal, 1991). Juveniles are also able to survive in inappropriate habitats for the species, improving their mobility between populations (Martín and López, 1998). In this way, there may be even greater movement of individuals across the species range, limiting breaks in gene-flow that over time could lead to phylogeographic structuring.

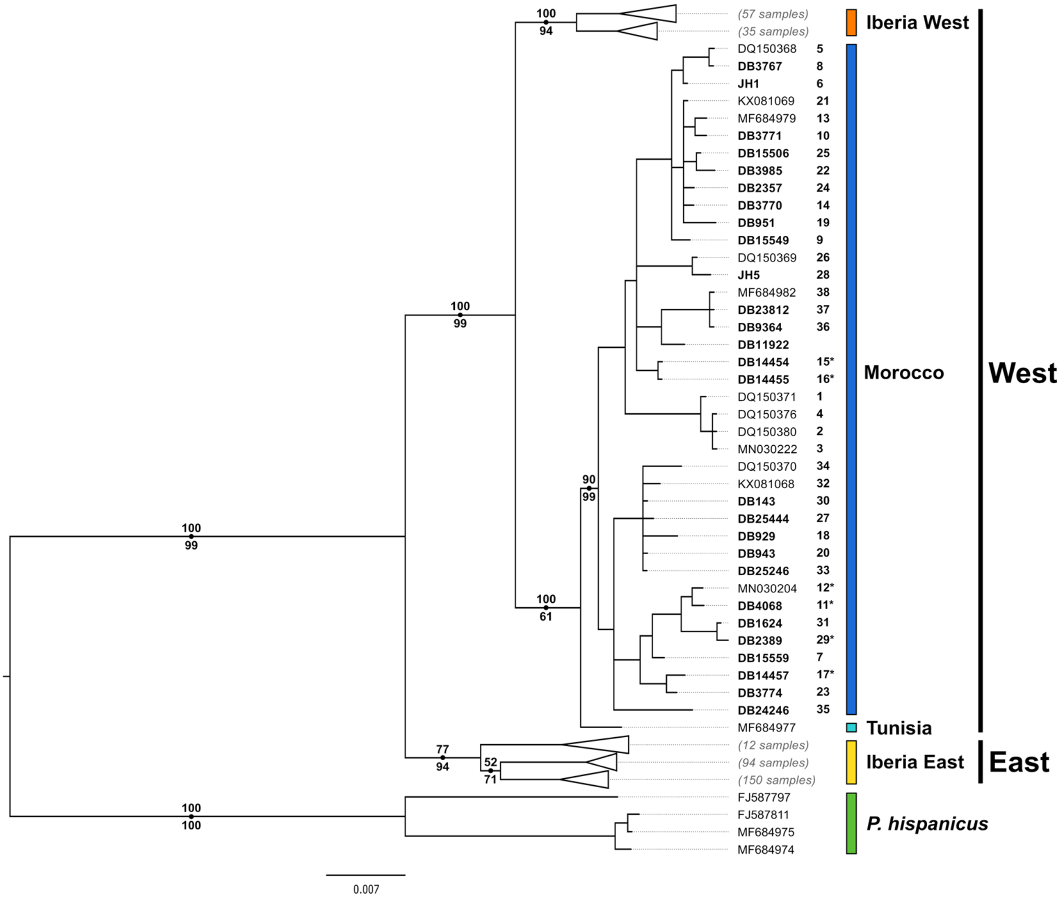

Figure 2. Obtained estimate of a phylogeny for *Psammodromus algirus*, derived from BI with partial ND4 sequences. BI posterior probabilities and ML Bootstrap values are indicated respectively above and under relevant nodes. Samples in bold correspond to samples sequenced on purpose for this study. Numbering relates the map of sampling locations (Fig. 1), with an asterisk marking samples from within the "*nollii*" range. Colours relate to partial MC1R haplotype network (Fig. 3). Iberian clades are collapsed according to the lineages defined by Diaz et al. (2017) for ease of representation, with the number of samples within each indicated next to it. The tree was rooted with *P. hispanicus.*

Samples from the "*nollii*" range (samples 11, 12, 15, 16, 17, and 29) show no evidence of being distinct based on either marker, nor did the specimen from the type locality of "*ketamensis*" (sample 10). Similar instances where identified colour morphotypes did not correspond with distinct genetic lineages have already been observed in this region, for example, the snake *Psammophis schokari* (Forskål, 1775) exhibits three colour morphotypes throughout its North African range although these do not reflect the species' evolutionary history, but rather local adaptations to the environment (Rato et al., 2007). Within Iberian *P. algirus*, Díaz et al. (2017) also suggested that the phenomena of adaptation for crypsis could be masking their phylogeographic structure, working both to promote divergence within clades, but also admixture between them. It is not clear if the two morphotypes come into contact in Morocco, but given the complex patterns observed in the Iberian Peninsula, this would be interesting to assess if possible.

The lack of observed genetic differentiation for the supposed *P. algirus nollii* individuals for the ND4 gene, alongside the evidence regarding striped versus unstriped forms of *P. algirus* from the Iberian Peninsula, indicate that these phenotypes do not reflect evolutionary history. Naming geographical variation within species is

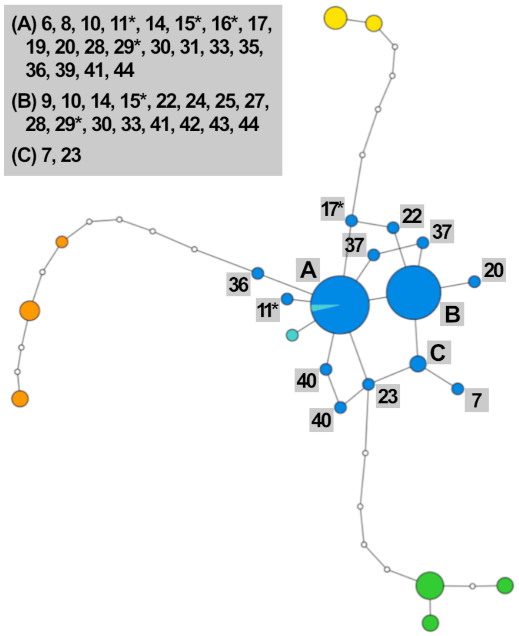

Figure 3. Haplotype network for *Psammodromus algirus* from partial MC1R sequences. Four haplogroups can be identified, three for *P. algirus*: North African — Moroccan (blue) and Tunisian (cyan) — Iberian West (orange), Iberian East (yellow); and one for *P. hispanicus* (green). Numbering relates to the map of sampling locations (Fig. 1), with an asterisk marking samples from within the "*nollii*" range; colours relate to partial ND4 phylogeny (Fig. 2).

complex and often controversial (recently reviewed in Hillis, 2020). Certainly *P. algirus* encompasses notable genetic and morphological variation, but the current subspecific taxonomy does not reflect this and therefore warrants revision.

Although this work provides greatly improved phylogenetic coverage for the Moroccan region, the countries of Algeria and Tunisia are still poorly sampled. The single Tunisian sample formed a sister-taxon to the Moroccan clade using the mitochondrial DNA marker as previously found (Carranza et al., 2006), albeit with a shallow divergence, and without evidence of differentiation based on the nuclear marker assessed for the first time in this study. In a comparative study of the region, Beddek et al. (2018) identified two major biogeographic breaks: one along the Moulouya river valley and another in Kabylia in Central Algeria. Sampling in this second region might help identify the distribution limits of Moroccan and Tunisian lineages.

Within Morocco, no clear phylogeographic structure was observed, unlike in almost all other studies of lacertid lizards from the region to date. We hypothesise that this is associated with habitat usage and dispersal ability, which enables greater levels of gene-flow between populations relative to most other similar species, however additional studies of more generalist species across the region are needed to further assess this hypothesis.

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