



## The role of climatic cycles and trans-Saharan migration corridors in species diversification: Biogeography of *Psammophis schokari* group in North Africa



Duarte Vasconcelos Gonçalves<sup>a,b,c,\*</sup>, Fernando Martínez-Freiría<sup>a</sup>, Pierre-André Crochet<sup>d</sup>, Philippe Geniez<sup>e</sup>, Salvador Carranza<sup>c</sup>, José Carlos Brito<sup>a,b</sup>

<sup>a</sup> CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal

<sup>b</sup> Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Rua Campo Alegre, 4169-007 Porto, Portugal

<sup>c</sup> Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37-49, E-08003 Barcelona, Spain

<sup>d</sup> CNRS-UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive, 1919 route de Mende, F-34293 Montpellier-Cedex 5, France

<sup>e</sup> EPHE, PSL Research University, CNRS, UM, SupAgro, IND, INRA, UMR 5175 CEFE, 34293 Montpellier, France

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### ABSTRACT

Highlands, hydrographic systems and coastal areas have been hypothesised to form corridors across the hyperarid Sahara desert in North Africa, allowing dispersal and gene flow for non-xeric species. Here we aim to provide a genetic test for the trans-Saharan corridor model, and predict the location and stability of ecological corridors, by combining phylogeography and palaeoclimatic modelling. The model was the *Psammophis schokari* (Schokari sand racer) group, fast-moving and widely distributed generalist colubrids occurring mostly in arid and semiarid scrublands. We combined dated phylogenies of mitochondrial and nuclear markers with palaeoclimatic modelling. For the phylogeographic analysis, we used 75 samples of *P. schokari* and *P. aegyptius*, and Bayesian and Maximum-Likelihood methods. For the ecological models, we used Maxent over the distribution of *P. schokari* and West African lineages. Models were projected to past conditions (mid Holocene, Last Glacial Maximum and Last Inter-Glacial) to infer climatic stable areas. Climatic stability was predicted to be mostly restricted to coastal areas and not spatially continuous. A putative temporary trans-Saharan corridor was identified in Eastern Sahara, with a more stable one along the Atlantic coast. Six parapatric lineages were identified within *P. schokari*, four occurring in North Africa. These likely diverged during the Pliocene. The Tamanrasset River might have been a vicariant agent. African lineages may have experienced further subsequent diversification during the late Pleistocene. The main *P. schokari* refugia were probably located along the northern margins of the Sahara, allowing its North-to-South colonization. Trans-Saharan corridors seem to have played a role in *P. schokari* biogeography, allowing colonization of central Saharan mountains and Sahel. Some might have worked as refugia, and even the most stable corridors may have sections working as filters, depending on each climatic phase. We expect the use of trans-Saharan corridors to decrease for more mesic species or with less dispersal capabilities.

### 1. Introduction

Numerous geological and climatic events have affected the geographic and biological diversity of North Africa in the last few million years (Le Houérou, 1997; Fabre, 2005). Geological events include the opening of the Mediterranean to the Atlantic 7–9 million years ago (Ma), the subsequent closure 6 Ma and re-opening 5.3 Ma (MSC, Krijgsman et al., 1999), recurrent episodes of desiccation and refilling in the Red Sea area (Girdler, 1991; Bosworth et al., 2005), marine transgressions (Tawadros, 2011), or the Atlas mountains uplift (de

Jong, 1998). These had climatic repercussions, but the most wide-ranging climatic event was a shift from tropical to arid environments around mid-Miocene (Zachos et al., 2001) that eventually led to the appearance of the Sahara desert between 7 Ma and 2.5 Ma (Schuster et al., 2006; Swezey, 2009). Arid and humid conditions then alternated during the last few million years, causing a series of expansions and contractions of climatic zones (Le Houérou, 1992; Swezey, 2009) that largely determined current biodiversity patterns (Brito et al., 2014).

Diversification due to humid-arid cycles has been explained through genome rearrangements (Dobigny et al., 2005), adaptation to novel

\* Corresponding author at: CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal.

E-mail address: [duartenvg@gmail.com](mailto:duartenvg@gmail.com) (D.V. Gonçalves).

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habitats (Boratynski et al., 2012; Carranza et al., 2002; Guillaumet et al., 2008) or, most commonly, divergence in allopatry (Brito et al., 2014). While during humid phases, the hyper-arid regions were reduced and probably isolated, in arid phases the mesic species were pushed towards coastal areas and mountains (Le Houérou, 1992; Messerli and Winiger, 1992). This resulted in disjoint distributions and allopatric diversification, currently best observed in mesic species, for example Mediterranean-Sahel separations (e.g. Gonçalves et al., 2012; Guillaumet et al., 2008), isolated populations in highlands (Geniez and Arnold, 2006; Metallinou et al., 2015), rock pools (Brito et al., 2011a; Vale et al., 2015) or desert-border refugia (Dobigny et al., 2013). Arid phases conversely allowed range expansions of xeric taxa (Arnold et al., 2008; Kissling et al., 2016; Leaché et al., 2017; Pook et al., 2009), later broken during humid phases (Metallinou et al., 2015; Pook et al., 2009).

Landscape features modulate gene flow (Brown and Lomolino, 1998). Depending on climatic-cycle phase and species' ecological requirements, a geographic feature can constitute a barrier to gene flow, an ecological corridor (connecting two larger similar areas), a filter bridge (or barrier, a more selective connection), or a refugium (where a species survives during unfavourable periods). Lake Chad, for instance, has been identified as a refugium (Granjon and Dobigny, 2003) or a corridor connecting the Sahel to the Tibesti (Drake et al., 2011; Dumont, 1982) for mesic taxa and a vicariant barrier for xeric ones (Pook et al., 2009; Metallinou et al., 2015). Mountains, presently working as biodiversity hotspots and refugia for mesic species (Brito et al., 2014, 2011a; Vale et al., 2015), likely constitute barriers for lowland or xeric species. Lastly, mountains, coastal areas and hydrographic systems can be linked, forming ecological corridors for mesic species. Several areas likely to constitute North-South oriented ecological corridors have been proposed (Dumont, 1982); these geographic features are hereby referred to as trans-Saharan corridors (tS-corridors), to avoid confusion with the ecological corridor feature. They include the more transitory river drainages from central Sahara Mountains (Drake et al., 2011), or the more stable (thus possibly refugia for some species) Red Sea, Nile River or Atlantic Sahara (Brito et al., 2014). However, these have been proposed based on ecological/geological data and species' distributions, and no genetic-level assessments have been conducted so far.

Our goal is to provide a genetic assessment of the validity of the tS-corridor model. For that, since most speciation events far predate the last humid/arid shift, data on the distribution of intraspecific genetic variability is required. While many mesic taxa may use the corridors during the humid phases, only those with high mobility and more adaptations to xeric environments are expected to do so during arid phases. Mesic-xeric species with broad ecological spectrum are thus expected to make more use of tS-corridors. We have selected the *Psammophis schokari* (Schokari sand racer) group in North Africa as a model since it is widely distributed in North Africa, occurring mostly in arid and semiarid habitats; it presents a continuous distribution along the Atlantic coast, thus apparently making use of this tS-corridor (Fig. 1). These snakes are large and mobile animals with likely good dispersal abilities. Thus, we do not expect limited dispersal or narrow distribution to restrict its use of ecologically suitable corridors. Previous work on *P. schokari* (Rato et al., 2007) identified several lineages but no conclusions were drawn regarding trans-Saharan dispersal.

Here we propose to model the species' potential distribution in different climatic phases to assess the suitability of candidate tS-corridors as ecological corridors for *Psammophis*, thus allowing us to build clear hypothesis on the persistence of gene flow along tS-corridors for mesic species during the past climatic cycles. The general aim of this study is to assess the role of corridors in trans-Saharan dispersal, with particular focus on the Atlantic Sahara tS-corridor, in an integrative framework joining phylogeography and palaeoclimatic modelling. Using *P. schokari*, we aim to answer the questions: (1) where are the areas with higher climatic stability throughout the species range and

particularly West Africa and where are the potential dispersal routes across the Sahara?; (2) how is the genetic variability spatially structured?. By combining results from these two sections, we expect to find phylogeographic patterns coherent with refugia close to the Mediterranean coast and in the Saharan mountains, and tS-corridors connecting them.

## 2. Material and methods

### 2.1. Sampling and study areas

The snake genus *Psammophis* includes 34 diurnal fast-moving species occurring mostly throughout tropical Africa, with some species reaching the Middle East and South-Central Asia (Sindaco et al., 2013; Uetz and Hošek, 2016). *Psammophis schokari* (FORSKÅL, 1775), commonly known as Schokari sand racer, is a common colubrid occurring from West Africa to India (Fig. 1), mostly in desert and xeric scrublands, marginally in sandy habitats in dry Mediterranean zones (Kelly et al., 2008; Schleich et al., 1996; Sindaco et al., 2013). Its sister species *Psammophis aegyptius* MARX, 1958, commonly known as Egyptian sand snake, is a typical Saharan species renowned for inhabiting even the driest areas of the eastern Sahara (Baha El Din, 2006).

We used 68 samples of *P. schokari* covering a representative part of the species distribution, particularly in West Africa (Table S1; Fig. 1). Seven samples of *P. aegyptius* were also included. For the phylogenetic analyses (see below), outgroups and other species of *Psammophis* were selected based mostly on Kelly et al. (2008). Additional *P. schokari* sequences were retrieved from GenBank. Two datasets were assembled: dataset 1, used to evaluate the phylogenetic relationships and placement within the genus of the *P. schokari* and *P. aegyptius* lineages; and dataset 2, used to date the divergence events among the lineages. Dataset 1 included all *P. schokari* and *P. aegyptius*, eleven *Psammophis* species representative of the diversity of the genus, and six outgroups (Table S1). Dataset 2 included eleven *P. schokari* and two *P. aegyptius* specimens representative of intraspecific lineages, plus representatives of other species spanning the *Psammophis* genus and the superfamily Colubroidea, plus *Achrocordus granulatus* as outgroup, in line with previous works (Table S1; see also Section 2.5).

For ecological models, a total of 748 observations (Figs. S3 and S4) were collected from fieldwork ( $n = 244$ ), museum collections ( $n = 110$ ) and bibliography ( $n = 394$ ). These observations were used to create two datasets: (i) Global, with 629 records at five arc-minute resolution ( $\sim 10 \times 10$  km); and (ii) Regional (Northwest Africa), with 379 records at 30 arc-second resolution ( $\sim 1 \times 1$  km). A 150 km buffer around minimum convex polygons including each dataset was used to delimit two corresponding study areas (see Section 2.6). All spatial analyses were conducted in ESRI ArcGIS 10. In order to reduce bias from uneven sampling, and to geographically and environmentally homogenize datasets (Merow et al., 2013), localities were randomly removed from clusters of species occurrence (e.g. Martínez-Freiria et al., 2015). The nearest-neighbour (NN) index (ArcGIS 10) was used as assessment. Low clustered distributions were obtained for both global ( $z$ -score =  $-19.67$ ; NN-ratio = 0.478) and regional ( $z$ -score =  $-11.57$ ; NN-ratio = 0.599) datasets, keeping 388 and 225 records, respectively (Table 2).

### 2.2. Climatic variables

Nineteen variables for current climatic conditions at 30 arc-second resolution ( $\sim 1 \times 1$  km) were downloaded from WorldClim ([www.worldclim.org](http://www.worldclim.org); Hijmans et al., 2005). Variables were clipped to each study area (Global and Regional) and, for the Global dataset, upsampled to five arc-minutes ( $\sim 10 \times 10$  km). After visual inspection, five variables were excluded due to the presence of spatial artefacts. The remaining 14 variables (Table S2) were considered for ecological models. Bivariate correlations among the 14 variables were tested within Global

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