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Some like it hot: Past and present phylogeography of a desert dwelling gecko across the Arabian Peninsula

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Abstract

Aim: Deserts represent dynamic ecosystems that support communities of endemic and specialised species. We analysed the role of present and past climatic conditions in shaping the distribution of the widespread *Bunopus* geckos in the Arabian and south-west Asian deserts. We studied their phylogeographic and demographic history to test whether the *Bunopus* geckos colonised Arabia from Asia or, vice versa, Asia from Arabia and to identify migration corridors that have historically enabled the dispersal of *Bunopus* geckos.

Location: The Middle East, especially the Arabian Peninsula.

Taxon: Genus *Bunopus* (Squamata; Gekkonidae).

Methods: We generated sequence data for four genes and performed maximum likelihood, Bayesian inference and time-calibrated phylogenetic analyses and ancestral area reconstruction to infer the phylogenetic and biogeographic history of the genus. We modelled the species' distribution and projected it to several past time periods spanning from mid-Pliocene to the present. We analysed contemporary landscape connectivity across the peninsula to identify dispersal corridors that enable migration and promote gene flow among *Bunopus* populations in Arabia.

Results: *Bunopus* is formed by deeply divergent lineages that correspond to up to eight candidate species. The genus originated in southwest Asia and dispersed to Arabia in the late Miocene. The Arabian populations were stable through most of their history in terms of size and distribution extent. Major corridors for contemporary *Bunopus* dispersal stretch along the eastern Arabian coasts from where they cross through the peninsula to the northern Red Sea coasts.

Main Conclusions: The evolutionary history of *Bunopus* was substantially influenced by paleoenvironmental conditions. The generalist habits and ground-dwelling lifestyle enabled the geckos to colonise most of the arid regions of southwest Asia, with Arabia being colonised from the Iranian Plateau in the late Miocene. The distribution extent of *Bunopus* responded to the past climatic and habitat oscillations; the range

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was fragmented during moist climatic phases, and it expanded in times of increased aridity. The genus requires taxonomic revision to formally assess its diversity. Based on the results obtained in this study, *Crossobamon orientalis* is reassigned to *Bunopus*.

KEYWORDS

biogeography, *Bunopus*, *Crossobamon*, Gekkonidae, Middle East, palearctic naked-toed geckos, paleodistribution, quaternary oscillations

1 | INTRODUCTION

Past climatic oscillations have played a crucial role in shaping the current distribution of biodiversity worldwide. In contrast to the temperate biomes that were characterised by recurrent warm-to-cold climate shifts during the Quaternary, subtropical deserts have experienced alternations of humid and arid conditions (Glennie, 2020; Hesse et al., 2004). Arid deserts have received considerably less attention from biodiversity researchers compared to other ecosystems (Durant et al., 2012), and our understanding of the effects of past climatic fluctuations on their biota remains rather incomplete (Douglas et al., 2006; Pepper & Keogh, 2021).

The Arabian Peninsula is an isolated subcontinent that was historically part of Africa, from which it drifted away to the northeast after their split in the mid-Oligocene to Early Miocene (Bosworth et al., 2005). The peninsula is rimmed by mountains that run along the seas which flank Arabia from the west, south and east. The Arabian interior is dominated by basalt flows and salty plains, but most notably by sand and gravel deserts with the Rub' Al Khali sand sea (also called the Empty Quarter) being the dominant feature (Edgell, 2006). The extent of these deserts was, however, not stable throughout the history of Arabia as it responded to fluctuating climatic conditions. The climate of Arabia is believed to have been humid with well-developed systems of seasonal river valleys (termed wadis) that drained the peninsula during the Late Pleistocene and Early Pliocene (Anton, 1984; Dabbagh et al., 2020). At that time, these deserts were covered by open savanna woodlands and the giant sand dunes in southern Arabia were interspaced with lakes and swamps (Edgell, 2006; McClure, 1976; Vincent, 2008). During the Quaternary, the climate of Arabia fluctuated regularly between hyper-arid (similar to those of today) and humid that was characterised by increased precipitation and the reactivation of river and lake systems in the interior (Breeze et al., 2015; Dinies et al., 2015). This generated a complex spatial and temporal mosaic of habitats that likely impacted the population dynamics of the desert dwelling biota and provided windows of opportunity for dispersal for animals and hominins (Parker, 2010; Stimpson et al., 2016).

The mountains of Arabia have been shown to support unique diversity of squamates with exceptional levels of endemism and as such have received considerable scientific attention (Carranza et al., 2016; Carranza & Arnold, 2012; Garcia-Porta et al., 2017; Metallinou et al., 2015; Šmíd et al., 2013, 2017). By contrast, the fauna of the inland deserts has been overlooked until relatively recently (Metallinou et al., 2012; Pola et al., 2021; Šmíd et al., 2021). The phylogeographic histories of widespread fauna may reveal how past climatic oscillations have affected the whole peninsular faunal assemblage.

Geckos of the genus *Bunopus* Blanford, 1874 are habitat generalists that inhabit a broad range of habitats throughout Arabia and the Iranian Plateau, ranging from southern Israel in the west to central Pakistan in the east (Sindaco & Jeremčenko, 2008; Šmíd et al., 2014, 2021). Their ground-dwelling habits in combination with their widespread distribution and high local population densities make them a suitable model for studying present and past dispersal dynamics in these hyper-arid environments. Two to three species of *Bunopus* are currently recognised, *B. crassicauda*, *B. tuberculatus* and presumably also *B. blanfordii*. While the first is endemic to Iran, the second occupies the rest of the genus' range including the entire Arabian Peninsula. The status of the third species, *B. blanfordii*, remains questionable, and the species is often considered a synonym of *B. tuberculatus* (see Bauer et al., 2013). The apparent uniformity of *B. tuberculatus* across its range was first doubted by Červenka et al. (2008) and later on by Khosravani et al. (2017), who found cryptic diversity within the species indicating that it likely represents a species complex. Nonetheless, the status of the populations occurring in the Arabian Peninsula has not been thoroughly investigated.

In this study, we analyse the role of present and past climatic conditions in shaping the distribution of a widespread generalist species in the Arabian deserts. We analyse sequence data of two mitochondrial and two nuclear markers to untangle the phylogenetic and phylogeographic history of the *Bunopus* species and populations across the entire distribution of the genus range. We use the genetic data and a dense sampling from throughout the Arabian Peninsula to infer the demographic history of the Arabian populations since the Pliocene to the present. Finally, we apply species distribution modelling to identify the extent of suitable habitats for *Bunopus* in Arabia in the present and in the past. The integration of the genetic and spatial results allows us to analyse the connectivity of landscapes across the peninsula and its role in the migration of this broad-ranging genus. This ultimately leads to the identification of dispersal corridors that enable migration and promote gene flow among *Bunopus* populations in Arabia.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling and outgroup selection

Tissue samples included in this study originated from targeted field trips of the authors and colleagues. They were supplemented by samples obtained from museum voucher specimens from the following collections: Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK); Museum of Vertebrate Zoology, Berkeley,

USA (MVZ); CEFE – EPHE/CNRS collection of the Biogeography and Ecology of the Vertebrates team, Montpellier, France (BEV); California Academy of Sciences, San Francisco, USA (CAS); Steinhardt Museum of Natural History at Tel Aviv University, Israel (TAU.R); National Museum Prague, Czech Republic (NMP); Institute of Evolutionary Biology, Barcelona, Spain (IBE); Daniel Jablonski's field collection housed at Comenius University, Bratislava, Slovakia (DJ). We assembled a total of 88 samples covering densely the Arabian part of the genus range. We retrieved sequences for 93 additional samples from the GenBank and BOLD (www.boldsystems.com) databases. The final dataset included 174 ingroup samples from across the entire range of the genus (Figure 1). We adopted the code system proposed by Khosravani et al. (2017) for the undescribed candidate species (*Bunopus* sp. 1–5).

As for the outgroup taxa, there are disputes with regards to what gecko genus is the closest relative to *Bunopus*. Numerous molecular phylogenetic studies showed a sister relationship between *Crossobamon* and *Bunopus* (Bauer et al., 2013; de Pous et al., 2016; Gamble et al., 2012; Machado et al., 2019, 2021; Metallinou et al., 2012). However, other studies recovered *Crossobamon* to be nested within *Bunopus* (Agarwal et al., 2014; Pyron et al., 2013; Zheng & Wiens, 2016), making the latter paraphyletic. The phylogenetic position of the two genera with respect to each other remains disputed and using only *Crossobamon* as the outgroup for the phylogenetic analyses might affect the results. We therefore used samples of both known *Crossobamon* species, *C. eversmanni* and *C. orientalis*, that cover broadly their ranges, but we also included more distant taxa *Agamura persica* and *Trachydactylus spatulurus* to root the tree.

2.2 | DNA extraction, amplification and sequence analysis

Genomic DNA was extracted from ethanol-preserved tissue samples using Tissue Genomic DNA Mini Kit (Geneaid) following the manufacturer's instructions. We PCR-amplified up to four genetic markers: two mitochondrial (mtDNA): the 12S rRNA (12S) and the cytochrome c oxidase subunit 1 (COI), and two nuclear (nDNA): the recombination activating gene 2 (RAG2) and the oocyte maturation factor MOS (*c-mos*). The PCR products were purified using EXOSAP-IT® PCR Product Cleanup Reagent (Thermo Fisher Scientific) and were Sanger-sequenced in both directions in Macrogen Europe (Amsterdam, the Netherlands). Primers, their sequences and PCR conditions are provided in Table S1.

Raw sequence data were inspected and contigs assembled using Geneious R11 (Kearse et al., 2012). Heterozygous positions in the nuclear markers were identified by the Heterozygote Plugin and were coded according to the IUPAC ambiguity codes. Sequences of each genetic marker were aligned independently by MAFFT (Katoh et al., 2019) using the default auto strategy for all genes except the 12S, where the Q-INS-i strategy that considers the secondary structure of RNA was applied. For the 12S alignment, we used Gblocks (Castresana, 2000) to trim poorly aligned regions with gaps. Sequences of protein-coding genes were translated into amino acids and no stop codons were detected. Samples used in this study are listed in Table S2.

The final concatenated alignment of the four markers was 1842 base pairs (bp) long – 378 bp of 12S (after Gblocks trimming), 663 bp of COI, 408 bp of RAG2 and 393 bp of *c-mos*.

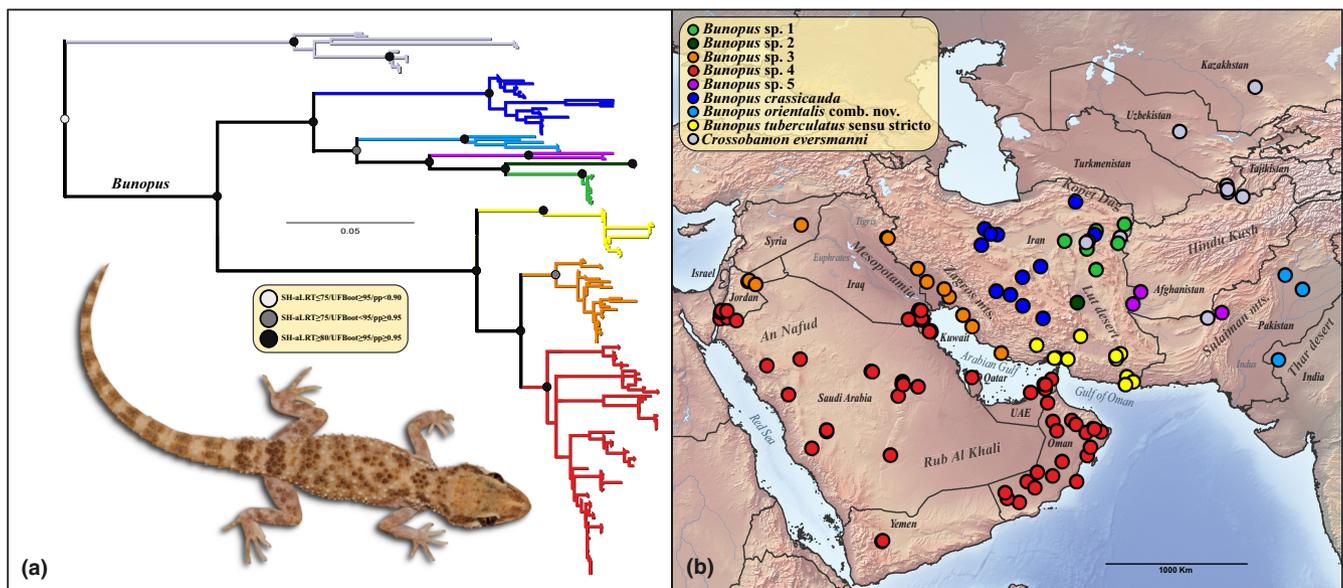


FIGURE 1 (a) Maximum likelihood phylogenetic tree reconstructed from the concatenated dataset of 12S, COI, RAG2 and *c-mos* genes (1842 bp). The tree was rooted using *Trachydactylus spatulurus* and *Agamura persica* (not shown in the figure). Support values (SH-aLRT/UFBoot/pp) are indicated by the circles at nodes with colours explained in the legend under the tree. Colours of tree branches match those of the sampled sites in (b). (b) Map showing the geographical sampling across the Middle East. Complete trees with original ML and BI support values are provided as Figures S1, S2, respectively. Taxon names correspond to changes proposed in this study. Specimen depicted is an individual photographed in south Jordan (Photo: Lukáš Pola).

2.3 | Phylogenetic and nuclear network analyses

We performed maximum likelihood (ML) and Bayesian inference (BI) analyses using the concatenated dataset of the four markers. The ML was carried out in IQ-TREE (Nguyen et al., 2015) using its online web interface W-IQ-TREE (Trifinopoulos et al., 2016). The dataset was partitioned by gene with models selected automatically by ModelFinder (Kalyaanamoorthy et al., 2017) as implemented in IQ-TREE. Branch support was assessed by the Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al., 2010) and the Ultrafast bootstrap approximation algorithm (UFBoot; Minh et al., 2013), both with 1000 replicates.

The BI was performed using BEAST v.2.5.2 (Bouckaert et al., 2019). The dataset was again partitioned by gene, site and clock models were unlinked across partitions. We applied the reversible-jump based method for best model selection with four gamma-distributed rate categories (Bouckaert et al., 2013). The relaxed lognormal clock model was applied to each partition. We used the coalescent constant population tree prior with a $1/X$ population size prior. Lognormal prior distributions were selected for the clock parameter priors (uclMean), with the mean=0.1 and standard deviation=1.25. Rate variation across lineages (uclStdev) of each partition was estimated using an exponential prior distribution (mean=0.5). The analysis ran three times for 5×10^7 generations through the CIPRES Science Gateway (Miller et al., 2010) with trees and parameters sampled every 2×10^4 generations. Tracer v.1.7.1 (Rambaut et al., 2018) was used to check the effective sample size of all parameters and to ensure that stationarity and convergence had been reached. Tree files were then combined using LogCombiner after discarding 10% of the posterior trees as burn-in. The maximum clade credibility tree was identified using TreeAnnotator. Nodes that received SH-aLRT ≥ 80 , UFBoot ≥ 95 in the ML analysis, and Bayesian posterior probability (pp) ≥ 0.95 were considered strongly supported.

Inter- and intraspecific relationships were inspected by reconstructing haplotype networks of the nuclear loci. To resolve the heterozygous single nucleotide polymorphisms, the alignments of RAG2 and *c-mos* were phased using the PHASE algorithm (Stephens et al., 2001) as implemented in DnaSP v.6 (Rozas et al., 2017) with probability threshold set to 0.7. Prior to phasing, we excluded several shorter sequences and the outgroups to avoid misleading results. Haplotype networks were constructed from the phased alignments using the TCS algorithm (Clement et al., 2000; Templeton et al., 1992) implemented in PopART (Leigh & Bryant, 2015).

2.4 | Estimation of divergence times

We calibrated the phylogeny with the substitution rate of the 12S gene estimated by Carranza and Arnold (2012), with the mean clock rate of 0.00755 and standard deviation of 0.00247. Similar approach has proven useful when calibrating trees of other gekkonid taxa in

the region (Carranza & Arnold, 2012; de Pous et al., 2016; Machado et al., 2021). The analysis was run in BEAST through CIPRES with parameters and priors as described above. The only difference was that we applied the Yule tree prior that assumes a constant lineage birth rate with sampling limited to one sample per lineage. The described and candidate species of *Bunopus* and all the outgroup species were thus represented by one sample each. Only the Arabian candidate species, *Bunopus* sp. 4, was represented by four samples to be able to estimate divergence times between the major geographic lineages as recovered by the ML and BI analyses (see Results below). The analysis ran three times for 3×10^7 generations and was sampled every 3000 generations.

2.5 | Ancestral area reconstruction

To infer the biogeographical history and ancestral ranges of *Bunopus*, we used the R package 'BioGeoBEARS' (Matzke, 2013). We used the calibrated tree as input and pruned the outgroup species prior to the analysis. We also retained only one tip for the *Bunopus* sp. 4 candidate species. We defined three biogeographic areas based on the geological history of the region (Popov et al., 2004): (i) Arabia, for the Arabian Peninsula including the desert in southern Jordan; (ii) Mesopotamia, for the lowlands along the Euphrates and Tigris Rivers; (iii) mainland Asia east of the Zagros Mountains in Iran. We assigned each tip to one or more of these areas based on the current distribution of that lineage. We restricted the maximum number of areas in which ancestral nodes could occur to two and performed ancestral reconstructions using the three models available in BioGeoBEARS: Dispersal-Extinction-Cladogenesis (DEC; Ree & Smith, 2008), DIVALIKE (Ronquist, 1997) and BAYAREA (Landis et al., 2013). We examined the plausibility of the results of each model empirically and we also assessed the fit of the models by the Akaike information criterion corrected for sample size (AICc; Akaike, 1973). The + J parameter that is implemented in BioGeoBEARS and allows including founder-event speciation (jump-dispersal; Matzke, 2014; Ree & Sanmartín, 2018) was not included in the models.

2.6 | Inferring the demographic history

To estimate population size changes through time, we used Extended Bayesian Skyline Plots (EBSP) using BEAST v.2.5.2 (Heled & Drummond, 2008). Since the focus of the study lies on the Arabian populations of *Bunopus*, we pruned the dataset for this analysis to only include samples of the candidate species from Arabia, *Bunopus* sp. 4, of which there were 83. The BEAST settings followed those described above for the BI analysis. The average number of population changes was modelled with a Poisson prior distribution. The analysis ran three times for 2×10^8 generations, and 10% of the posterior parameter values were discarded as burn-in.

2.7 | Modelling potential distribution in the present and in the past

We compiled a database of available distribution records by searching published literature, museum catalogues, public databases (e.g., GBIF) and gathering field observations. In total, we assembled 1314 records of *Bunopus* representing 920 unique localities. We thinned the dataset using the 'spThin R' package (Aiello-Lammens et al., 2015) to reduce possible model bias resulting from high concentrations of distribution records from thoroughly explored areas (e.g., the UAE, Oman; Carranza et al., 2018, 2021; Burriel-Carranza et al., 2019). We used a radius of a minimum of 50 km to separate any two records and run the thinning ten times, which produced ten different and randomly sampled datasets of 161 records. Since we focus in this study on the Arabian populations of *Bunopus*, we only used records of the clade containing *Bunopus tuberculatus* sensu stricto and the candidate species *Bunopus* sp. 3 and sp. 4. We pooled records of these three lineages together for the modelling purposes. The reasoning was that although they show a certain degree of genetic differentiation, it is mostly in the mitochondrial DNA and only in a limited way in the nuclear DNA, and with our current knowledge, it cannot be ruled out that the three lineages represent a single species. The species and candidate species from the Iranian Plateau were not included in the modelling since their environmental niches may differ from those of the Arabian clade and because they were not the primary aim of this study.

Nineteen bioclimatic variables were downloaded from CHELSA (Karger et al., 2017) at the resolution of 2.5 arc-minutes and cropped to the study area. BIO8, BIO9 and BIO18 were excluded because they showed spatial artefacts and BIO14 because it showed no variation across the study area. In addition to the bioclimatic layers, we used layers for elevation and slope. To be able to project habitat suitability in the past when sea level was different from today, we created a layer of elevation that also contained negative values for areas below the sea level (bathymetry data downloaded from GEBCO; <https://www.gebco.net>). We tested for collinearity between the layers using ENMTools (Warren et al., 2010) and of those with correlation over 0.75 we retained only the more biologically meaningful ones (Elith & Leathwick, 2009). The final set contained these variables: elevation, slope, mean diurnal air temperature range (BIO2), temperature seasonality (BIO4), mean daily mean air temperatures of the coldest quarter (BIO11), precipitation seasonality (BIO15), mean monthly precipitation amount of the wettest quarter (BIO16), and mean monthly precipitation amount of the driest quarter (BIO17).

We used Maxent 3.3 (Phillips et al., 2006) to develop the species distribution model and to assess the importance of each variable. Ten model replicates with the cross-validate resampling method were run for each of the ten input datasets, using 10,000 background sample points and with 5000 maximum iterations. The area under the curve (AUC) was assumed as a measure of individual model fit. The final model of potential distribution was averaged over the ten

replicates. To test whether the models performed better than random, we generated 100 null models, each for a set of 161 records randomly generated within the study area and with settings similar to the models based on real data.

To assess the dynamics and stability of the *Bunopus* distribution in Arabia, we projected the model to past periods, ranging from the late Holocene to mid-Pliocene. We downloaded bioclimatic layers for the following past periods: late Holocene (4.2–0.3 thousand years ago [ka]); Pleistocene/early Holocene (12.9–11.7 ka); late Pleistocene (14.7–12.9 ka); Pleistocene – Last Glacial Maximum (LGM; ca. 21 ka); Pleistocene – Last Interglacial (LIG; ca. 130 ka); mid-Pleistocene (ca. 787 ka); and mid-Pliocene (ca. 3.3 Ma). Spatial data were obtained from www.Paleoclim.org (Brown et al., 2018), with the original sources being Dolan et al. (2015), Fordham et al. (2017) and Otto-Bliesner et al. (2006). The elevation and slope layers were also included in the paleo projections. The elevation was manually adjusted for each of the past time periods to reflect the sea level difference at that time compared to the present. For projections to the mid-Pleistocene and mid-Pliocene, mean diurnal air temperature range was excluded as it was not available for those time periods. The paleo projections were run ten times each with the final model averaged over the ten runs. Input layer and parameter details of the distribution modelling are reported in an ODMAP protocol file (Zurell et al., 2020) in the Supplementary Material.

2.8 | Identifying contemporary dispersal corridors

We analysed contemporary spatial connectivity of the *Bunopus* populations across the Arabian Peninsula, Mesopotamia and coastal Iran by visualising least-cost corridors (LCC; Chan et al., 2011) among the genetically sampled localities using SDMtoolbox (Brown, 2014) in ArcGIS 10.3 (ESRI, 2011). The contemporary distribution model was inverted to create the friction layer for the calculation. We assigned sampled sites to genetic groups based on the results of the phylogenetic analyses (see below). We tested three different assignment schemes as follows: (i) all sites of the three lineages – *B. tuberculatus*, *Bunopus* sp. 3, and *Bunopus* sp. 4 – were pooled together; (ii) samples were assigned to the three lineages, which were treated as distinct evolutionary entities; and (iii) the three lineages were treated as separate groups, and samples of *Bunopus* sp. 4 were further divided to five groups based on the intraspecific structure of the phylogeny. The percentage of least-cost path value was used to select the LCC with the high, mid and low cut-off values being respectively 5, 2 and 1.

2.9 | Spatial analysis of population structure

We assessed the genetic structure of the Arabian populations of *Bunopus* and identified spatial genetic neighbourhoods using the 'MEMGENE' R package (Galpern et al., 2014). MEMGENE regresses

Moran's Eigenvector Maps (MEM), it is variables describing patterns of positive and negative spatial autocorrelation, against genetic distances to detect genetic structure and visualises spatial components of genetic dissimilarity among individuals (Galpern et al., 2014). Based on the results of the phylogenetic analyses (see below) we included in this analysis only samples and localities of the candidate species *Bunopus* sp. 4. We calculated pairwise genetic distances between all samples on the ML tree using the Geneious software. Forward selection of positive and negative MEM eigenvectors against genetic distance added eigenvectors to a regression model until they ceased to improve model fit. Principal component scores of the predicted values are defined as Memgene variables and we used those with the highest R^2 values to produce maps of the spatial patterns of genetic relationships.

We also visualised the correlation between the geographic and genetic distances. We used functions from the 'MASS' (Venables & Ripley, 2002) and 'adeigenet' (Jombart & Ahmed, 2011) packages to create a kernel density plot of *Bunopus* records in Arabia to highlight regions of increased point density in the plot. We calculated linear geographical distances between sampled sites using the 'raster' R package (Hijmans et al., 2014) and correlated them with the genetic distances calculated above. In addition to the Euclidean (straight) distances, we also calculated least-cost path distances between all pairs of points using the corridor layer identified in section 2.8 as a cost layer and correlated this distance matrix with the genetic distances. We are aware that the correlation between genetic and geographic distances does not account for spatial autocorrelation, we however find it useful for visualising the relationships between the variables.

3 | RESULTS

For this study, we generated 351 new sequences for 110 samples of the total of 202 samples used in the analyses. Sampling completeness (i.e., all four gene sequences available per sample) was 79.8% for the samples newly sequenced in this study and 55.6% with the GenBank and BOLD sequences included.

3.1 | Phylogenetic analyses

Both ML and BI analyses resulted in almost identical topologies in most nodes. According to the results (Figure 1; Figures S1, S2), a strongly supported clade that contained all *Bunopus* species and *Crossobamon orientalis* was recovered in all analyses (SH-aLRT = 98.9/UFBoot = 100/pp = 1.00, support values are given in this order hereafter). It was formed by two strongly supported sister clades: Iranian (96.4/100/1.00) and Arabian (100/100/1.00). The Iranian clade consists of species occurring on the Iranian plateau and further East and North: *Bunopus crassicauda*, the candidate species *Bunopus* sp. 1, *Bunopus* sp. 2 and *Bunopus* sp. 5, and also *Crossobamon orientalis* from Pakistan and India. The relationships within this clade

were only partially resolved. *Bunopus crassicauda* was inferred to be sister to the remaining species, but the topology was only partially supported (78.3/92/1.00). The Arabian clade is formed by *Bunopus tuberculatus* sensu stricto from southern Iran, and the candidate species *Bunopus* sp. 3 from Mesopotamia and *Bunopus* sp. 4 from the Arabian Peninsula, with *B. tuberculatus* sensu stricto being strongly supported as sister to the remaining two (88.3/96/1.00). The phylogenetic position of *C. evermanni* differed between the resulting trees. In the ML tree, it was supported as sister to the whole *Bunopus* clade (98.9/100), in the BI tree it was sister to *Agamura persica*, although with low support.

In light of the paraphyly of the genus *Crossobamon* recovered in both ML and BI analyses, we run additional analysis to test whether the genus is significantly non-monophyletic. We constrained the topology of the tree and forced the two *Crossobamon* species to form a clade. We used the approximately unbiased (AU), the Shimodaira-Hasegawa (SH) and the Kishino-Hasegawa (KH) tests to compare this enforced topology with the unconstrained tree. Per-site log likelihoods were calculated in raxmlGUI v.1.5 (Silvestro & Michalak, 2012) and *p*-values were calculated using CONSEL v.0.1 (Shimodaira & Hasegawa, 2001). The results indicate that the monophyly of *Crossobamon* can be significantly rejected (AU: 0.001; SH: 0.002; KH: 0.002).

The haplotype networks (Figure 2) show a certain degree of allele sharing between the *Bunopus* species, including *Crossobamon orientalis*, in both nuclear markers. The only species that have all alleles private (i.e., not shared with other species) are *Crossobamon evermanni*, *Bunopus crassicauda* and *Bunopus* sp. 1. All the other species share alleles of one or both nuclear markers with some other species. Within the Arabian clade, *B. tuberculatus* sensu stricto possesses unique haplotypes in RAG2, and all the three species of that clade share one common allele in c-mos.

3.2 | Estimation of divergence times

The initial split within the genus that separated the Iranian (including *C. orientalis*), and the Arabian clades was estimated to take place 14.0 million years ago (Ma) (highest posterior density interval [HPD]: 10.8–17.6 Ma; Figure 3). The crown diversification within the Iranian clade was estimated to have occurred 10.3 Ma (HPD: 7.8–13.1) and within the Arabian clade 5.8 Ma (HPD: 4.2–7.8). The split between the candidate species *Bunopus* sp. 3 and sp. 4 was estimated to 3.4 Ma (HPD: 2.4–4.6).

3.3 | Ancestral area reconstruction

The results of the biogeographic reconstruction were largely congruent between the tested biogeographic models. DIVALIKE was the most plausible of the models (Table S3) and we therefore present only the results based on this model (Figure 3). The origin of the Iranian clade was unequivocally inferred to be Asian (marginal

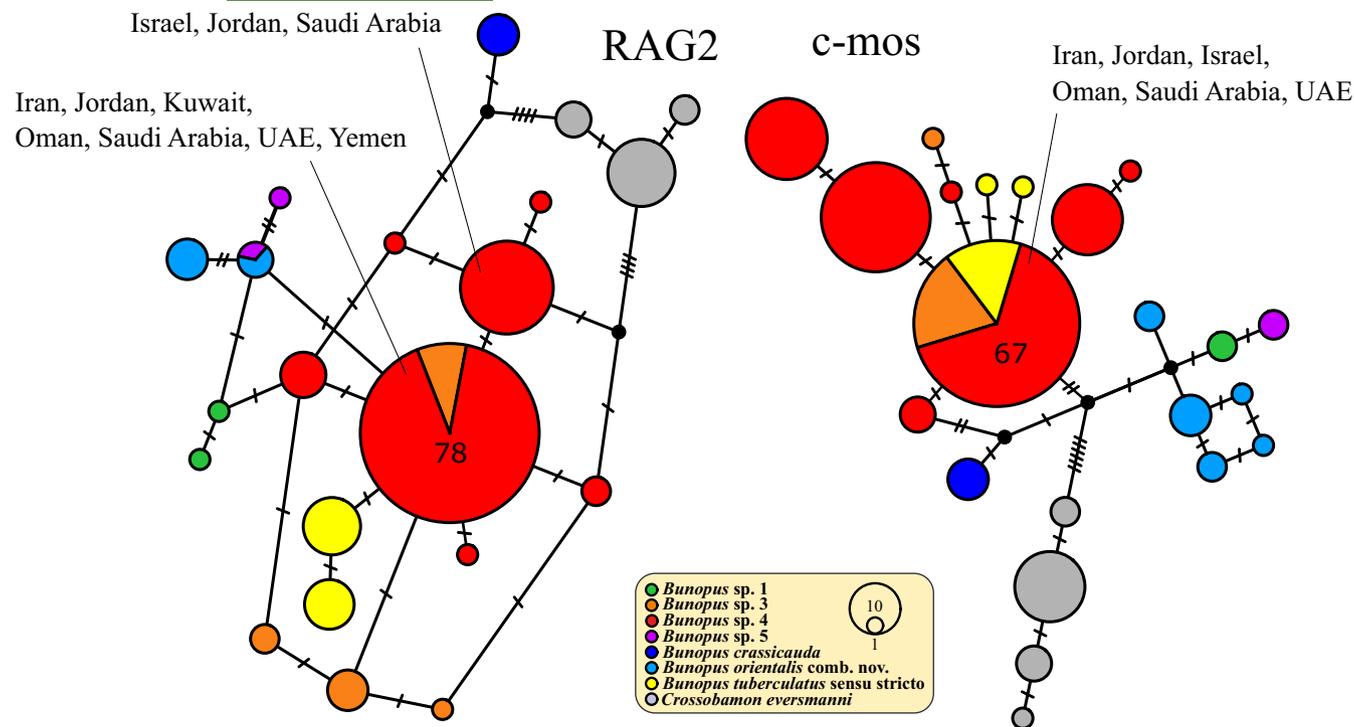


FIGURE 2 Haplotype networks of the RAG2 and c-mos nuclear markers. Circle size is proportional to the number of samples that share that allele. Transverse bars on the connecting lines indicate the number of mutational steps between alleles. Colours correspond to those in Figure 1. Taxon names correspond to changes proposed in this study.

probability 100% in DEC and DIVALIKE, 92.6% in BAYAREA). The Arabian clade was inferred to have originated either in Asia or in Mesopotamia (89.7% in DEC, 98% in DIVALIKE, 61.7% in BAYAREA). The biogeographic origin of the crown *Bunopus* clade (including *C. orientalis*) was not resolved with certainty; the DEC model supported an unresolved Asian or Mesopotamian origin (60.3%) while DIVALIKE and BAYAREA only Asian origin (66.7% and 57.7%, respectively).

3.4 | Inferring the demographic history

The reconstruction of the demographic history of the Arabian populations shows a stable population trend since the split between *Bunopus* sp. 3 and sp. 4 at 3.4Ma until about 200ka (Figure 3). At that time the population size started decreasing considerably, which continued until after the LIG (ca. 130ka). At about 80ka, the trend turned, and the population increased almost to the pre-drop level.

3.5 | Present and past potential distribution

Mean AUC for the present ranged between 0.744 and 0.768, with the mean being 0.759. The consistency of the AUC values across the models along with extremely low standard deviation values of all runs (0.055–0.06; mean=0.057) implies model stability regardless of the

input data. The models performed significantly better than the null models (AUC: 0.586–0.688; mean=0.637). The AUC values of the models would be categorised as 'fair' according to standard criteria for distribution model evaluation (Araújo et al., 2005). It should however be noted that it has been shown that predictive models of generalist species with broad environmental niches, such as *Bunopus*, achieve lower AUC values compared to habitat specialists (Connor et al., 2018). The most important environmental predictors were the elevation (contribution 48.6%–54.6%; mean=50.8%), precipitation seasonality (contribution 13.9%–19.4%; mean=17.6%), temperature seasonality (contribution 7.2%–10.0%; mean=8.5%) and mean diurnal air temperature range (contribution 6.3%–9.8%; mean=8.0%).

The predictive model based on the present environmental conditions showed that large parts of eastern Arabia, coastal western Arabia and coastal Iran support habitat that is suitable for *Bunopus* (Figure 4). The suitable habitat covers most of Oman and the UAE except the Hajar and Dhofar Mountains and regions adjoining the Rub' al Khali Desert. It extends along the Arabian Gulf through Qatar and Kuwait to southwestern Iran and then further along the Gulf to south-eastern coastal Iran. There is a narrow band of suitable habitat along the Red Sea coast in northwestern Arabia. It connects to the eastern part of the suitable habitat through a longitudinal belt that crosses central Arabia. Interestingly, most of southern Arabia (Yemen and southwestern Saudi Arabia including the Rub' Al Khali Desert) and northern Arabia (the An-Nafud Desert) were not found to be suitable for *Bunopus*.

Projections to past climatic conditions showed that eastern Arabia and most of the Arabian Gulf coast have harboured suitable habitat

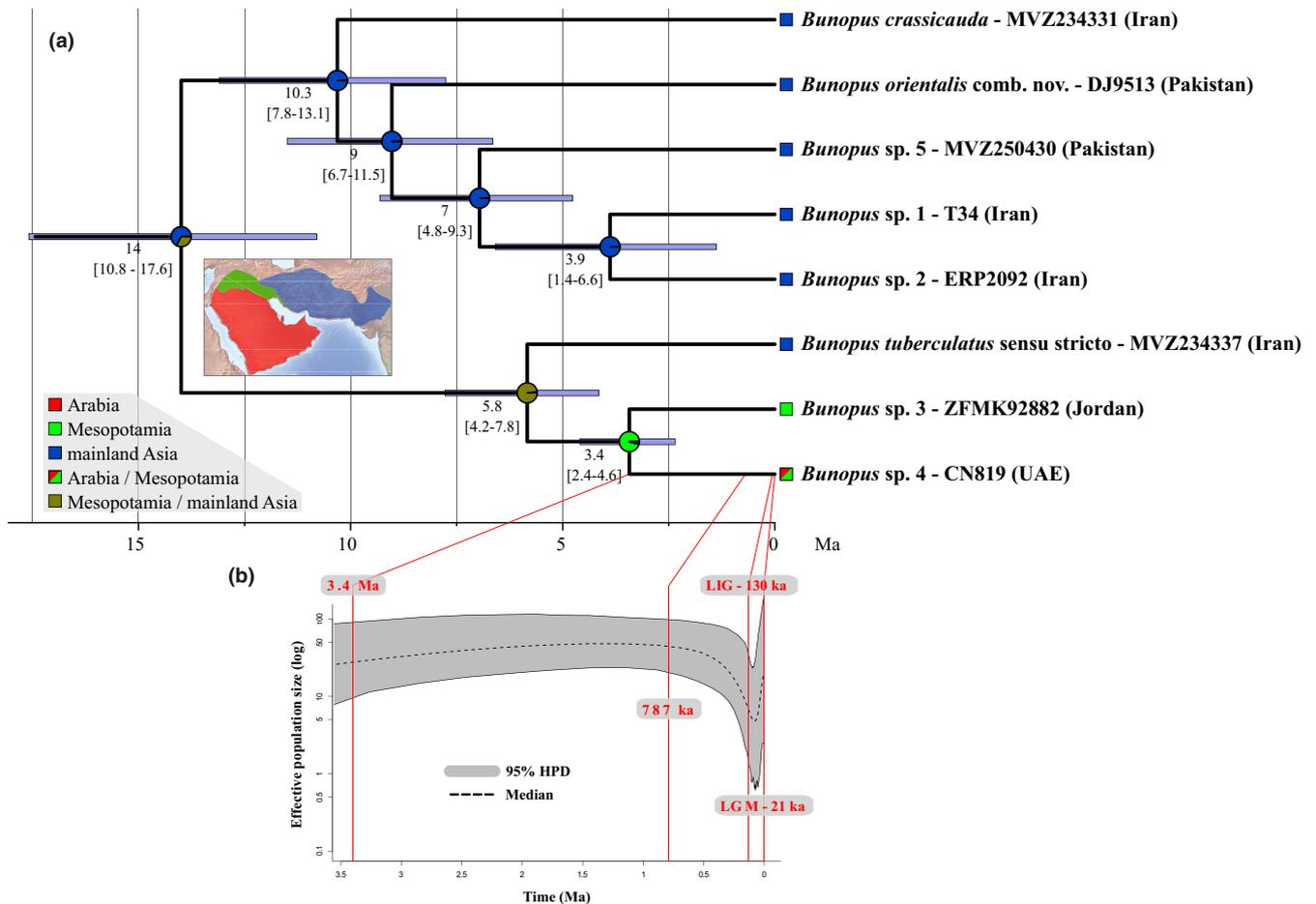


FIGURE 3 (a) Time-calibrated tree and ancestral area reconstruction of *Bunopus*. All nodes were supported with posterior probabilities higher than ≥ 0.95 . Mean age estimates for the branching events are provided below each node with the 95% HPD interval in brackets and also indicated with the blue horizontal bars. The biogeographic areas defined for the analyses are in the inset map. Pie charts at the nodes show the probability of each ancestral area. (b) Extended Bayesian Skyline Plot showing the temporal dynamics of the effective population size of the Arabian populations (*Bunopus* sp. 4) since its split from its sister lineage, *Bunopus* sp. 3. Taxon names correspond to changes proposed in this study.

throughout the past (Figure 4). The extent of suitable habitat was very similar in mid-Pliocene (3.3 Ma) and mid-Pleistocene (ca. 787 ka). It retreated during the LIG (ca. 130 ka) and covered only central Oman and southern coasts of the Arabian Gulf. This habitat reduction was followed by a subsequent north-westerly expansion along and into the desiccated Arabian Gulf during the LGM (ca. 21 ka). During the LGM (ca. 21 ka), the western Arabian coast was also suitable, but its extent has since been retreating. In the late Pleistocene (14.7–12.9 ka) and early Holocene (12.9–11.7 ka), the range expanded and covered most of eastern Arabia, including the inland deserts which, however, became unsuitable again in the late Holocene (4.2–0.3 ka).

3.6 | Dispersal corridors

The dispersal corridors inferred for the three schemes showed congruent spatial patterns (Figure S3). Most of lowland Oman and the coastal UAE are suitable for the dispersal of *Bunopus*,

and the main migration corridor stretches from there along the Arabian Gulf coast through Qatar and Saudi Arabia to Kuwait, from where it continues across central Arabia in a broad, longitudinal belt all the way to the Red Sea coast. The northern part of the Saudi Red Sea coast from around the city of Jeddah to the border with Jordan also promotes *Bunopus* population connectivity. The isolated populations in Yemen and southern Saudi Arabia are connected by dispersal routes to the southern Oman and Arabian Gulf populations, some of which run across the Rub' Al Khali sands (Figure 5).

3.7 | Spatial analysis of population structure

The proportion of overall genetic variance explained by spatial patterns was high (adjusted $R^2=0.586$). The first three MEMGENE variables explained nearly 90% of the total variance (MEMGENE1=0.549; MEMGENE2=0.210; MEMGENE3=0.139).

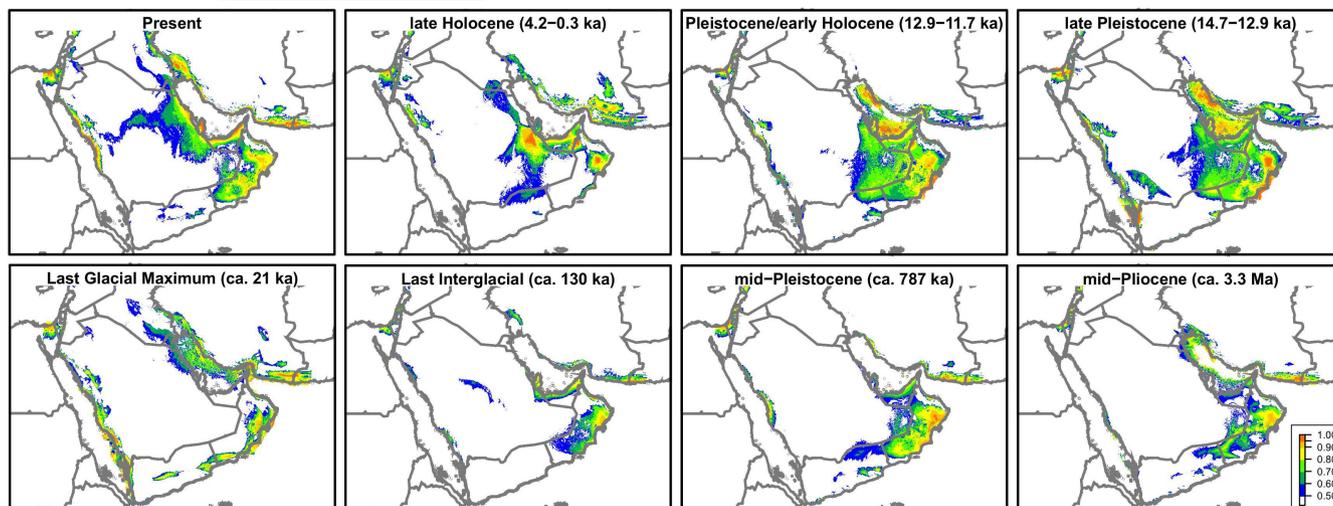


FIGURE 4 Contemporary habitat suitability model of *Bunopus* in the Arabian Peninsula (upper left panel; based on pooled records of *B. tuberculatus* sensu stricto, *Bunopus* sp. 3 and *Bunopus* sp. 4), and habitat suitability models projected to different past time periods as indicated on top of each panel. Warmer colours denote higher probability of presence. Note that the Arabian Gulf dried out during the Quaternary sea-level low stands and the seabed provided a suitable habitat for *Bunopus*.

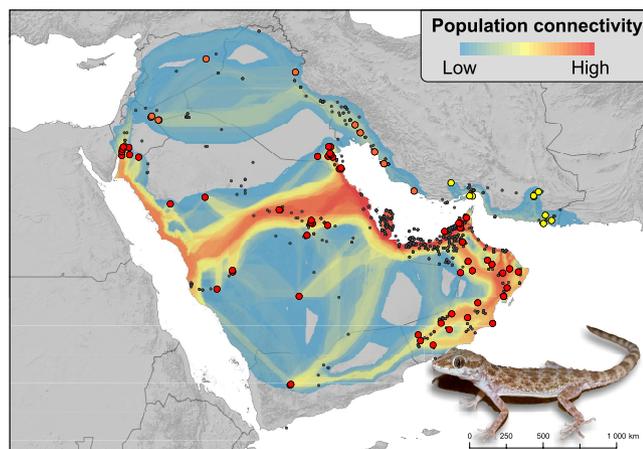


FIGURE 5 Contemporary dispersal corridors for the *Bunopus* geckos across the Arabian Peninsula. Large and coloured dots show sampled localities with colours corresponding to different lineages within *Bunopus* and matching the colours used in Figures 1, 2. Only the Arabian clade that consists of *B. tuberculatus* sensu stricto, *Bunopus* sp. 3 and sp. 4 was included in this analysis. Black dots indicate distribution records that were used for developing the potential distribution model. The population connectivity visualises landscape corridors that enable dispersal and promote gene flow between *Bunopus* populations. Specimen depicted in an individual from south Israel (Photo: Doubravka Velenská).

The first axis (MEMGENE1) showed a significant genetic structure that separates the northwestern Arabian *Bunopus* populations from the rest of the peninsula (Figure 6). Curiously, a sample from Qatar showed genetic affinity to the northwestern populations. The second axis (MEMGENE2) supported the division of eastern Arabian populations from the rest.

The plot of the relationship of the genetic and geographic distances showed a non-linear pattern of several structured

populations, some of which were close both geographically and genetically (Figure 6). Interestingly, the plot of the correlation between the genetic and geographic distances did not change regardless of whether we used the Euclidean distances or distances calculated as least-cost paths through the dispersal corridors. We therefore show only the latter plot. Most between-sample comparisons were separated by a geographic distance between 1000 and 2000 km and a genetic distance of about 0.05 estimated substitutions per site, which is consistent with the results of the phylogenetic analyses that indicated the presence of several clades within *Bunopus* sp. 4.

4 | DISCUSSION

4.1 | Diversification within *Bunopus*

According to our estimates of the evolutionary history of *Bunopus*, the crown diversification took place in the mid-Miocene, about 14 Ma (confidence interval: 10.8–17.6 Ma) and resulted in the split between the Iranian and Arabian clades. The Iranian clade subsequently and gradually diversified into up to five lineages that may correspond to five distinct species (Khosravani et al., 2017). The Arabian clade radiated considerably later at 5.8 Ma (4.2–7.8 Ma) and gave rise to the lineages occurring around the Arabian Gulf and in the Arabian Peninsula. This clade contains *B. tuberculatus* sensu stricto from southern Iran and two candidate species, a Mesopotamian one that is referred to as *Bunopus* sp. 3, and one that is widespread in Arabia (*Bunopus* sp. 4). Our results that are based on a broad geographic and genetic sampling support the findings of Khosravani et al. (2017), who found that Iran supports several genetically distinct lineages within *Bunopus* presumably representing cryptic species. Our results show that the differentiation of the Iranian clade is older and deeper than that in the Arabian clade, and that it is quite

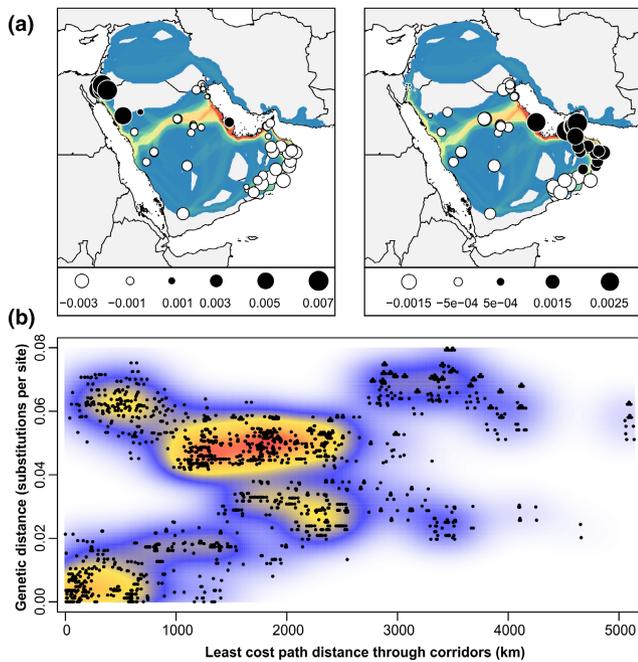


FIGURE 6 (a) Results of the spatial analysis of population structure conducted in MEMGENE. A total of 82 genotyped localities were used for the analysis. Circles of similar size and colour indicate individuals with similar scores along the first (left) and second (right) MEMGENE axes (large black and large white circles describe opposite extremes). The heatmap in the background shows the dispersal corridors for *Bunopus* across Arabia. (b) Plot of genetic distances against distances calculated as least-cost paths connecting all pairs of sampled localities among the Arabian populations of the *Bunopus* geckos. Warmer colours indicate higher densities of points. Note the large cluster of points at the genetic distance of about 0.05, which indicates the presence of several shallow phylogenetic lineages within the species.

likely that at least some of the candidate species will warrant formal taxonomic recognition.

The three lineages of the Arabian clade show clear differentiation at the mitochondrial level but a certain overlap in the nuclear markers (Figures 1, 2). It may be a result of their relatively recent split that simply did not provide enough time for the slowly evolving nuclear genes to differentiate. Alternatively, it could be caused by events of introgression. This remains to be tested with a broader sampling of genomic loci (e.g., SNPs; work in progress). The broad distribution of *Bunopus* in Arabia provides suitable grounds for comparison with other widespread Arabian genera. Most previous studies of other pan-Arabian squamates have uncovered cryptic diversity present across the peninsula and concluded that the diversity of species is in fact much higher than had been previously thought. These findings often resulted in descriptions of new microendemic species, with geckos being the most taxonomically dynamic group of reptiles in this respect (e.g., Carranza et al., 2016; Machado et al., 2019; Simó-Riudalbas et al., 2017, 2018; Šmíd et al., 2013, 2015, 2017, 2023; Tamar et al., 2019; Vasconcelos & Carranza, 2014). *Bunopus*, however, shows a completely different pattern. The results of our phylogenetic analyses imply that, despite the broad distribution

of *Bunopus* sp. 4 lineage, it harbours only low genetic diversity in Arabia.

4.2 | Biogeographic and demographic history

The biogeographic reconstructions together with the time-calibrated analysis indicate that *Bunopus* originated in mainland Asia in the mid-Miocene (Figure 3). All species of the Iranian clade are confined to the Iranian Plateau and adjoining parts of mainland Asia and do not seem to ever have expanded anywhere else. On the other hand, the Arabian clade was estimated to have dispersed from the Iranian Plateau to the Arabian Peninsula during the Pliocene/Pleistocene. At that time, the two landmasses were connected by a continental land bridge (Popov et al., 2004), which likely facilitated biotic interchange between Arabia and mainland Asia (Badiane et al., 2014; Simó-Riudalbas et al., 2019; Tamar et al., 2018; Tamar et al., 2021).

The colonisation of the Arabian Peninsula was a very successful one indeed. The historical range reconstruction shows that *Bunopus* managed to disperse from Mesopotamia in the north throughout the Arabian Peninsula to its eastern- and southernmost margins (Figure 3). The facts that the distribution of *Bunopus* spans across the entire Arabia and that its genetic structure throughout the peninsula is rather shallow point to the present distribution of *Bunopus* sp. 4 being a result of rapid dispersal with ongoing gene flow. This is further supported by the spatial patterns of genetic data that shows genetic homogeneity across most of the Arabian Peninsula (Figure 6). Interestingly, the process of range expansion does not seem to have been associated with expanding population size which was inferred here to have been stable since its split from the Mesopotamian lineage until about 250ka when it dropped substantially (Figure 3). After the decline, the population however returned rapidly to its original size. This drop may also be discernible in the projections of the predictive distribution model to past climatic conditions that indicate range contraction at the time of the Last Interglacial (130ka). At that time, Arabia underwent a predominantly moist climatic phase that was interwoven with short windows of semi-arid to arid conditions (Edgell, 2006; Vincent, 2008) which might have resulted in habitat fragmentation and subsequent population isolation. Since the Last Interglacial, however, the conditions became generally more arid again and *Bunopus* started repopulating Arabia. The considerable range expansion in the latest Pleistocene to early Holocene may be linked with the hyper-aridification of Arabia and the expansion of sand dunes at that time (Vincent, 2008). It is worth noting that the seabed of what is today the shallow Arabian Gulf presented suitable habitat for *Bunopus* during the glacial sea-level drops and likely formed a corridor for migration between the Iranian and Arabian populations (Lambeck, 1996). Taken together, the dynamic system of pulsating habitats that oscillated in response to the changing climatic conditions between humid and hyper-arid seems to have played a crucial role in shaping the present and past distribution of the desert adapted *Bunopus* geckos in Arabia.

4.3 | Dispersal across Arabia

The past distribution models imply that the range of *Bunopus* sp. 4 oscillated substantially according to the prevailing climatic conditions in Arabia. For example, most of eastern Arabia seemed to have supported suitable conditions for *Bunopus* continuously since the mid-Pliocene, while central Arabia became inhabitable only very recently in the late Holocene (Figure 4). The uninterrupted presence of *Bunopus* sp. 4 in eastern Arabia might have been allowed by the absence of dispersal barriers in the region. Most of the region is and has been suitable for the geckos since the mid-Pliocene, with only the massif of the Hajar Mountains always presenting an insurmountable barrier for this lowland-dwelling species. The continuous presence of *Bunopus* in eastern Arabia also likely explains the genetic homogeneity of local populations along the second MEMGENE axis (Figure 6).

Based on the suitable habitat models, the strongest environmental predictor of the genus' distribution in Arabia is the elevation. *Bunopus* rarely occurs above 500m in Arabia (Šmíd et al., 2021) and it is thus not present in the mountain ranges that rim the peninsula: the Hajar Mountains in the east, Dhofar in the south, and the Asir and Hejaz Mountains in the west. This may be paralleled in the lineages of the Iranian clade of *Bunopus* that inhabit the uplifted Iranian Plateau. Although we did not include them in the distribution modelling, it is obvious from the available distribution data that they also avoid high-elevation regions such as the Zagros Mountains in the southwest of Iran (Šmíd et al., 2014). Whether the Iranian and Arabian *Bunopus* lineages show some differences in the environmental niches they occupy should be addressed in a separate study.

The wide belt of suitable habitat that stretches longitudinally across Arabia from the Arabian Gulf to the Red Sea constitutes the dominant contemporary dispersal corridor for *Bunopus* (Figure 5). By connecting the eastern and western margins of the peninsula it enables longitudinal migration between geographically disparate regions with subsequent population connectivity and genetic homogenisation over this vast territory (Figure 6). This corridor turns northwards at the Red Sea coast and runs to Jordan and thus provides connection between the southern Jordanian and Israeli populations with the central Arabian ones. Of note is the origin of the isolated Yemeni populations. Although they are geographically closer to those from southern Saudi Arabia, they more likely originated from southern Oman to which they are also genetically most similar. Such a biogeographic route also conforms to the general distributional patterns in the area (de Pous et al., 2016; Machado et al., 2019; Sindaco et al., 2018).

It should be stressed that although the distribution models performed well for such a broadly distributed and generalist taxon, there were still regions where *Bunopus* was not predicted to occur despite the presence of records in these areas. For example, several distribution records are available from northern Saudi Arabia, but the region was not found suitable for the geckos. If these places

are truly suboptimal for *Bunopus* and the existing distribution points represent sinking populations or if the predicted absence is caused by the scarcity of data is at the moment uncertain. The latter possibility seems very plausible. However, our field experience has taught us that *Bunopus* population densities vary considerably across Arabia and that while in some regions it is the most abundant reptile species (e.g., in central Saudi Arabia around the city of Riyadh), in other seemingly suitable desert habitats it is extremely rare (e.g., southwestern Arabia). Hence, until more field work is conducted in northern Arabia, we prefer not to draw conclusions on the predicted absence of *Bunopus* in these places.

4.4 | Taxonomic account

The results of all phylogenetic analyses conducted for this study support the paraphyly of *Bunopus* with *Crossobamon orientalis* being nested within *Bunopus*. Similar results have been confirmed in some previous studies, which were however always based on much sparser taxon sampling (Agarwal et al., 2014; Pyron et al., 2013; Zheng & Wiens, 2016). The genus *Crossobamon* currently contains two species – *C. evermanni* and *C. orientalis*. The phylogenetic position of the former species in the tree of Khosravani et al. (2017) remained unresolved, and the monophyly of *Bunopus* was not supported. Our sampling of *C. evermanni* covered broadly the distribution of the species and our phylogenetic results enable us to infer its position with more confidence. In summary, the results of all our analyses indicate that the genus *Bunopus* is paraphyletic with respect to *C. orientalis* and the genus *Crossobamon* is polyphyletic.

Crossobamon evermanni (Wiegmann, 1834) is the type species of the genus *Crossobamon* Boettger, 1888 and as such retains its generic name. To resolve the above issue of para- and polyphyly, we propose to reassign *Crossobamon orientalis* to the genus *Bunopus*, the new combination being *Bunopus orientalis* comb. nov. (Blanford, 1876) that should be used from now on. A detailed list of chresonyms is available in the Supplementary Information. The cryptic diversity within the genus *Bunopus* (Červenka et al., 2008; Khosravani et al., 2017) as well as the status of the enigmatic *B. blanfordii* (Bauer et al., 2013) remain a task for future taxonomic investigation. Besides the polyphyly of *Crossobamon* found in our study we also noted deep genetic divergences within *C. evermanni* throughout its range, suggesting possible cryptic diversity.

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CONFLICT OF INTEREST STATEMENT

As authors of this manuscript, we declare no conflict of interest in connection with this paper.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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BIOSKETCH

Author contributions: Lukáš Pola and Jiří Šmíd conceived the project; Lukáš Pola, Pierre-André Crochet, Philippe Geniez, Mohammed Shobrak, Salem Busais, Daniel Jablonski, Rafaqat Masroor, Timur Abduraupov, Salvador Carranza and Jiří Šmíd conducted field work to collect distribution data and samples for genetic analysis; Lukáš Pola collected data from the literature for spatial analyses; Lukáš Pola did laboratory work and DNA sequence analysis; Lukáš Pola and Jiří Šmíd conducted phylogenetic analyses; Jiří Šmíd analysed the spatial data; Lukáš Pola and Jiří Šmíd led the writing with contributions from all authors.

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Lukáš Pola is a herpetologist interested in biogeography, evolutionary history and systematics of the Middle Eastern squamate reptiles. This study was a part of his PhD project at Faculty of Science, Charles University focused on the evolution, biogeography and systematics of the Palearctic naked-toed geckos.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Supplementary Information

Some like it hot: Past and present phylogeography of a desert dwelling gecko across the Arabian Peninsula

Lukáš Pola, Pierre-André Crochet, Philippe Geniez, Mohammed Shobrak, Salem Busais, Daniel Jablonski, Rifaqat Masroor, Timur Abduraupov, Salvador Carranza, Jiří Šmíd

Generic reassignment of *Crossobamon orientalis* to the genus *Bunopus*

As described in the main text of this article, we herewith use genetic data to reassign *Crossobamon orientalis* to the genus *Bunopus*, with the new combination of the name being *Bunopus orientalis* **comb. nov.** (Blanford, 1876). Below here we provide a detailed list of chresonyms, it is taxon names under which the species has appeared in the published literature. Museum acronyms used in the text below are as follows: ZSI - Zoological Survey of India, Kolkata, India; BMNH - British Museum of Natural History, London, the United Kingdom (currently NHMUK, National History Museum, UK).

Chresonymy list

Bunopus orientalis **comb. nov.** (Blanford, 1876)

Stenodactylus orientalis Blanford, 1876. Syntypes (3): ZSI R 5589 from ‘hills west of Shikárpur district’, the ZSI label says ‘Hills of Larkana, Sind’; BMNH 1946.8.23.37 from ‘Near Rohri’; BMNH 1946.8.23.50 from ‘Rhorī, India’ [today’s Sindh Province, in southern Pakistan]

Stenodactylus orientalis in: Murray (1884); Boulenger (1885, 1890); Anderson (1898); Annandale (1906); Smith (1935); Minton (1962, 1966); Das (1966); Mertens (1969); Werner (1976); Sharma and Vazirani (1977); Biswas & Sanyal (1977); Khan (1980, 1985); Murthy (1990); Tikader and Sharma (1992); Sharma (2002)

Stenodactylus dunstervillei: Murray (1884). Type (1): BMNH 1946.8.23.26 from ‘Halla, Sind’

Crossobamon orientalis in: Kluge (1967, 1991, 1993); Khan (2002, 2004, 2006); Szczerbak (1986); Szczerbak & Golubev (1996); Das (1998, 1999); Anderson (1999); Iffat (2006); Feng et al. (2007); Baig et al. (2008); Sindaco & Jeremčenko (2008); Agarwal et al. (2009, 2013, 2014, 2015); Venugopal (2010); Rais et al. (2011, 2013); Fujita & Papenfuss (2011); Khan et al. (2012); Masroor (2012); Gamble et al. (2012); Metallinou et al. (2012); Bauer (2013); Bauer et al. (2013); Solanki et al. (2015); De Pous et al. (2016); Aengals et al. (2018); Machado et al. (2019, 2021); Uetz et al. (2019); Kumawat and Purohit (2020); Ali et al. (2021)

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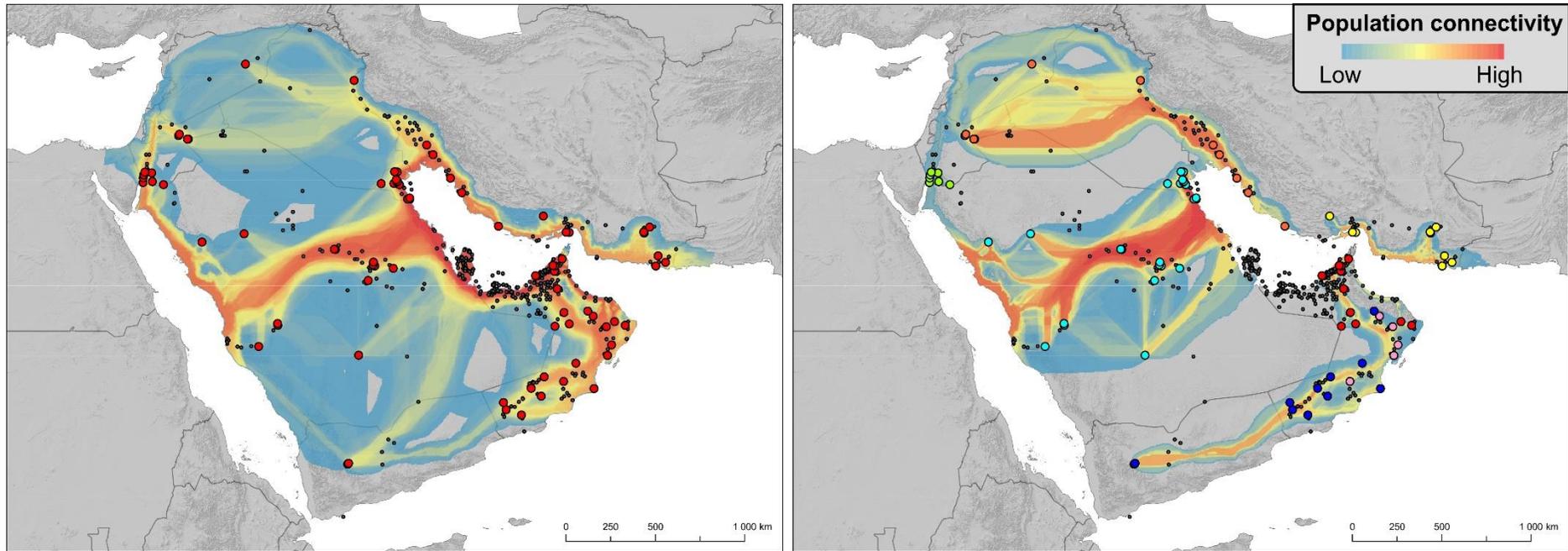
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Figure S3. Contemporary dispersal corridors for the *Bunopus* geckos based on the alternative assignments of sampled sites to genetic groups as indicated by the colors of the circles: all sites of the three lineages - *B. tuberculatus* sensu stricto, *Bunopus* sp. 3, and *Bunopus* sp. 4 - pooled together (left); the three lineages treated as separate groups and samples of *Bunopus* sp. 4 further divided to five groups based on the intraspecific structure of the phylogeny (right).



Supplementary Tables

Table S1. Genetic markers with primers used for their amplification and sequencing. Table shows information on primer orientation (F – forward, R – reverse), primer sequences (5' to 3'), original reference, length of amplified fragment (bp – base pairs) and PCR conditions.

Marker	Primer name	Orientation	Primer sequence	Reference	Amplicon length	PCR conditions
12S	12Sa	F	AAACTGGGATTAGATACCCCACTAT	Kocher et al., 1989	394-397 bp	94°C (5'), 35x [94° (30"), 48° (45"), 72° (1')], 72° (5')
	12Sb	R	GAGGGTGACGGGCGGTGTGT			
COI	ReptCOI-F	F	TNTTMTCAACNAACCACAAAGA	Nagy et al., 2012	664 bp	94° (4'), 36x [94° (40"), 49° (40"), 72° (80")], 72° (10')
	ReptCOI-R	R	ACTTCTGGRTGKCCAAARAATCA			
c-mos	FU-F	F	TTTGGTTCKGTCTACAAGGCTAC	Gamble et al., 2008	394 bp	94° (5'), 35x [94° (30"), 53° (45"), 72° (1')], 72° (10')
	FU-R	R	AGGGAACATCCAAAGTCTCCAAT			
RAG2	PY1-F	F	CCCTGAGTTTGGATGCTGTACTT	Gamble et al., 2008	410 bp	94° (5'), 35x [94° (30"), 53° (45"), 72° (1')], 72° (10')
	PY1-R	R	AACTGCCTRTTGTCCCCTGGTAT			

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Table S2. Samples used in this study including information on voucher, country of origin, GPS coordinates (datum WGS84), and GenBank accession numbers for the two mitochondrial and two nuclear genes. Accession numbers of sequences generated for this study are highlighted in bold. Accession numbers of COI sequences downloaded from the BOLD database (<https://boldsystems.org/>) are indicated by italics. Taxon names correspond to changes proposed in this study.

Species	Voucher code	Tissue sample	Country	Latitude	Longitude	12S	COI	RAG2	cmos
<i>Agamura persica</i>		JIR456	Iran	33.2596169	51.8064119	PP377711	PP375999		PP353840
<i>Agamura persica</i>		ZMMU-R-11769-1	Iran	27.07	60.25		<i>ABLRP227-07</i>		
<i>Agamura persica</i>		RuHF-NR-326a	Iran	27.31	60.4		<i>ABLRP284-07</i>		
<i>Agamura persica</i>		RAN-814	Iran	33.333	51.717		<i>ABLRP470-07</i>		
<i>Agamura persica</i>		ZMMU RAN-732	Iran	31.13	56.84		<i>NPLRP390-08</i>		
<i>Agamura persica</i>		ZMMU RAN-625	Iran	32.54	51.73		<i>NPLRP412-08</i>		
<i>Bunopus crassicauda</i>		R/IRA/1193	Iran	32.7	55.3666667	EU589154			
<i>Bunopus crassicauda</i>		ERP3738	Iran	34.05	51.6		KX893096		
<i>Bunopus crassicauda</i>		ERP3737	Iran	34.05	51.6		KX893094		
<i>Bunopus crassicauda</i>		ERP3736	Iran	34.05	51.6		KX893093		
<i>Bunopus crassicauda</i>		ERP2088	Iran	29.45	55.516667		KX893102		
<i>Bunopus crassicauda</i>		ERP2062	Iran	30.233333	54.233333		KX893084		
<i>Bunopus crassicauda</i>		ERP2058	Iran	30.233333	54.233333		KX893083		
<i>Bunopus crassicauda</i>		ERP2057	Iran	30.916667	53.45		KX893079		
<i>Bunopus crassicauda</i>		ERP2053	Iran	30.916667	53.45		KX893081		
<i>Bunopus crassicauda</i>		ERP2052	Iran	30.916667	53.45		KX893080		
<i>Bunopus crassicauda</i>		ERP2028	Iran	31.15	52.533333		KX893074		
<i>Bunopus crassicauda</i>		ERP2000	Iran	31.15	52.533333		KX893073		
<i>Bunopus crassicauda</i>		ERP1934	Iran	32.033333	54.2		KX893104		
<i>Bunopus crassicauda</i>		ERP1885	Iran	36.783333	57.583333		KX893087		
<i>Bunopus crassicauda</i>		ERP1586	Iran	34.716667	52.6		KX893091		
<i>Bunopus crassicauda</i>		ERP1584	Iran	34.716667	52.6		KX893089		
<i>Bunopus crassicauda</i>		ERP344	Iran	36.783333	57.583333		KX893116		
<i>Bunopus crassicauda</i>	MVZ:Herp:234331	MVZ234331	Iran	35.0784	51.787328	PP377696	PP375984	PP353936	PP353857
<i>Bunopus crassicauda</i>	MVZ:Herp:245955	MVZ245955	Iran	34.7665	52.174667	PP377697	PP375985	PP353937	PP353858
<i>Bunopus crassicauda</i>		ZMMU-R-11893-1	Iran				<i>ABLRP223-07</i>		
<i>Bunopus crassicauda</i>		ZMMU-R-11893-2	Iran				<i>ABLRP224-07</i>		
<i>Bunopus crassicauda</i>		RAN-245	Iran	34.717	58.8		<i>ABLRP472-07</i>		
<i>Bunopus orientalis</i>	DJ7839	DJ7839	Pakistan	31.26079	72.03972	PP377707	PP375995	PP353944	PP353853
<i>Bunopus orientalis</i>	DJ7840	DJ7840	Pakistan	31.26079	72.03972	PP377708	PP375996	PP353945	PP353851
<i>Bunopus orientalis</i>	DJ7841	DJ7841	Pakistan	31.26079	72.03972	PP377709	PP375997		PP353854
<i>Bunopus orientalis</i>		A.M.Bauer08(A)	India	26.830185	70.506283	DQ852715			DQ852730
<i>Bunopus orientalis</i>	DJ9513	DJ9513	Pakistan	32.17	70.92	PP377710	PP375998	PP353946	PP353852
<i>Bunopus orientalis</i>		ZMMU-R-11282-3	Pakistan				<i>ABLRP217-07</i>		
<i>Bunopus sp. 1</i>		ZMMU-R-11737-1	Iran	34.31	58.41		<i>ABLRP220-07</i>		
<i>Bunopus sp. 1</i>		R/IRA/1044	Iran	34.866667	58.866667	EU589158			
<i>Bunopus sp. 1</i>	NMP6V 76754/2	T34	Iran	34.969722	58.89556	PP377712	PP376000	PP353947	PP353855
<i>Bunopus sp. 1</i>		ERP1920	Iran	32.5	58.9		KX879649		

Species	Voucher code	Tissue sample	Country	Latitude	Longitude	12S	COI	RAG2	cmos
<i>Bunopus</i> sp. 1		ERP1918	Iran	32.5	58.9		KX879648		
<i>Bunopus</i> sp. 1		ERP1872	Iran	34.166667	60.3		KX879663		
<i>Bunopus</i> sp. 1		ERP1869	Iran	34.166667	60.3		KX879662		
<i>Bunopus</i> sp. 1		ERP1056	Iran	35.366667	60.7		KX889145		
<i>Bunopus</i> sp. 1		ERP1055	Iran	35.366667	60.7		KX889144		
<i>Bunopus</i> sp. 1		ERP780	Iran	33.816667	58.316667		KX879657		
<i>Bunopus</i> sp. 1		ERP779	Iran	33.816667	58.316667		KX879659		
<i>Bunopus</i> sp. 1		ERP686	Iran	34.3	56.9		KX879655		
<i>Bunopus</i> sp. 1		ERP684	Iran	34.3	56.9		KX879654		
<i>Bunopus</i> sp. 2		ERP2095	Iran	30.433333	57.7		KX889148		
<i>Bunopus</i> sp. 2		ERP2093	Iran	30.433333	57.7		KX889149		
<i>Bunopus</i> sp. 2		ERP2092	Iran	30.433333	57.7		KX889150		
<i>Bunopus</i> sp. 3	BEV.10889	BEV.T3750	Jordan	31.761	36.756	PP377713	PP376001	PP353948	PP353900
<i>Bunopus</i> sp. 3		J27	Jordan	31.583	37.25	KT302094		KT302144	KT302127
<i>Bunopus</i> sp. 3	NMP6V 76757/1	JOR_080	Jordan	31.8295	36.80722	PP377714	PP376002	PP353949	PP353901
<i>Bunopus</i> sp. 3		R/IRA/1160	Iran	29.633333	50.433333	EU589156			
<i>Bunopus</i> sp. 3		REPT/SUR/347	Syria			EU589157			
<i>Bunopus</i> sp. 3		SUR 084	Syria	35.311307	40.130929	EU589155			
<i>Bunopus</i> sp. 3	NMP6V 76759/1	T29	Iran	29.633333	50.43333	PP377715		PP353950	PP353880
<i>Bunopus</i> sp. 3	NMP6V 76759/2	T30	Iran	29.633333	50.43333	PP377716	PP376003		
<i>Bunopus</i> sp. 3	NMP6V 76759/3	T31	Iran	29.633333	50.43333	KT302095		KT302145	KT302128
<i>Bunopus</i> sp. 3	ZFMK92881	ZFMK92881	Jordan	31.584206	37.211114	PP377717	PP376004	PP353951	PP353902
<i>Bunopus</i> sp. 3	ZFMK92882	ZFMK92882	Jordan	31.584206	37.211114	PP377718	PP376005	PP353952	PP353903
<i>Bunopus</i> sp. 3		RUZM55	Iran	34.5	45.583333		KX889160		
<i>Bunopus</i> sp. 3		RUZM51	Iran	30.8	49.555557		KX893123		
<i>Bunopus</i> sp. 3		RUZM50	Iran	30.8	49.555557		KX889138		
<i>Bunopus</i> sp. 3		RUZM44	Iran				KX879668		
<i>Bunopus</i> sp. 3		RUZM41	Iran				KX893121		
<i>Bunopus</i> sp. 3		RUZM40	Iran				KX893122		
<i>Bunopus</i> sp. 3		ERP1767	Iran	27.25	52.85		KX889163		
<i>Bunopus</i> sp. 3		ERP1765	Iran	27.25	52.85		KX889161		
<i>Bunopus</i> sp. 3		ERP1189	Iran	28.916667	51		KX879669		
<i>Bunopus</i> sp. 3		ERP1190	Iran	28.916667	51		KX879670		
<i>Bunopus</i> sp. 3		ERP1175	Iran	31.283333	49.233333		KX893120		
<i>Bunopus</i> sp. 3		ERP1173	Iran	31.283333	49.233333		KX893119		
<i>Bunopus</i> sp. 3		ZMMU RAN-967a	Iran	34.483	45.65		<i>NPLRP068-08</i>		
<i>Bunopus</i> sp. 3		ZMMU RAN-967b	Iran	34.483	45.65		<i>NPLRP069-08</i>		
<i>Bunopus</i> sp. 3		ZMMU RAN-1012	Iran	32.567	47.55		<i>NPLRP070-08</i>		
<i>Bunopus</i> sp. 3		ZMMU RAN-1013	Iran	32.567	47.55		<i>NPLRP071-08</i>		
<i>Bunopus</i> sp. 3		ZMMU RAN-1103a	Iran	31.733	48.133		<i>NPLRP073-08</i>		
<i>Bunopus</i> sp. 3		ZMMU RAN-1103b	Iran	31.733	48.133		<i>NPLRP074-08</i>		
<i>Bunopus</i> sp. 4		9016	Kuwait	29.373274	47.592202	EU589160			
<i>Bunopus</i> sp. 4	NMP 74269/1	OM2010_26	Oman	23.021328	57.33448	PP377765			
<i>Bunopus</i> sp. 4		AO38	Oman	22.76444	57.60306	PP377719	PP376006	PP353953	PP353860
<i>Bunopus</i> sp. 4	BEV.10048	BEV.T1470	Kuwait	29.3213	47.868	PP377720			

Species	Voucher code	Tissue sample	Country	Latitude	Longitude	12S	COI	RAG2	cmos
<i>Bunopus</i> sp. 4	BEV.10049	BEV.T1471	Kuwait	29.3213	47.868	PP377721			
<i>Bunopus</i> sp. 4	BEV.10050	BEV.T1472	Kuwait	29.3213	47.868	PP377722			
<i>Bunopus</i> sp. 4	BEV.10051	BEV.T1473	Kuwait	29.4432	47.742	PP377723			
<i>Bunopus</i> sp. 4	BEV.10068	BEV.T1490	Kuwait	29.9632	47.6233	PP377724		PP353954	PP353885
<i>Bunopus</i> sp. 4	BEV.10132	BEV.T2447	Kuwait	29.9437	47.7515	PP377725		PP353955	PP353868
<i>Bunopus</i> sp. 4	BEV.10197	BEV.T2983	Israel	29.6546	34.9862		PP376007	PP353926	PP353921
<i>Bunopus</i> sp. 4	BEV.13519	BEV.T9239	Kuwait	29.5561	47.7095	PP377727	PP376008		
<i>Bunopus</i> sp. 4	BEV.13520	BEV.T9240	Kuwait	29.3675	46.953	PP377728			
<i>Bunopus</i> sp. 4	BEV.14669	BEV.T11382	Kuwait	28.65761	48.37579	PP377729			
<i>Bunopus</i> sp. 4	BEV.15241	BEV.T12592	Kuwait	28.59522	48.39158	PP377731	PP376010	PP353957	PP353869
<i>Bunopus</i> sp. 4		CN10672	Oman	17.84933	54.00504	PP377747			
<i>Bunopus</i> sp. 4		CN10787	Oman	22.49475	58.68279	PP377748			
<i>Bunopus</i> sp. 4	IBE CN11181	CN11181	Saudi Arabia			PP377749		PP353968	PP353870
<i>Bunopus</i> sp. 4	IBE CN3263	CN3263	Oman	22.95566	56.14033	PP377736	PP376015	PP353962	
<i>Bunopus</i> sp. 4	IBE CN3560	CN3560	Oman	20.8069	58.32866	PP377737	PP376016	PP353963	PP353862
<i>Bunopus</i> sp. 4	IBE CN3647	CN3647	Oman	22.24226	58.26999	PP377738	PP376017	PP353964	PP353863
<i>Bunopus</i> sp. 4		CN3687	Oman	22.24226	58.26999	PP377739	PP376018	PP353965	PP353865
<i>Bunopus</i> sp. 4		CN4049	Oman	22.30873	59.22104	PP377740			
<i>Bunopus</i> sp. 4	IBE CN4082	CN4082	Oman	22.30873	59.22104	PP377741	PP376019	PP353928	PP353864
<i>Bunopus</i> sp. 4	IBE CN4245	CN4245	Oman	18.11348	53.22923	PP377742	PP376020	PP353966	PP353906
<i>Bunopus</i> sp. 4		CN703	Oman	22.3744	56.40202	PP377733	PP376012	PP353959	PP353904
<i>Bunopus</i> sp. 4	IBE CN7082	CN7082	Oman	18.45987	53.0983	PP377743			
<i>Bunopus</i> sp. 4		CN7755	Oman	19.17521	54.49364	PP377744	PP376021	PP353967	PP353907
<i>Bunopus</i> sp. 4		CN7798	Oman	19.5195	56.11712	PP377745	PP376022	PP353929	PP353859
<i>Bunopus</i> sp. 4	IBE CN8018	CN8018	Oman	18.7833	54.99401	PP377746	PP376023	PP353930	PP353908
<i>Bunopus</i> sp. 4		CN819	UAE	24.99638	55.66103	PP377734	PP376013	PP353960	PP353905
<i>Bunopus</i> sp. 4		CN828	Oman	20.80809	58.32884	PP377735	PP376014	PP353961	PP353861
<i>Bunopus</i> sp. 4	NMP6V 76768	CN15012	Saudi Arabia	20.82676	45.81416	PP377750			
<i>Bunopus</i> sp. 4		CN15016	Saudi Arabia	20.82676	45.81416	PP377751	PP376024		PP353871
<i>Bunopus</i> sp. 4	NMP6V 76766	CN15154	Saudi Arabia	22.310637	41.754493		PP376025		PP353867
<i>Bunopus</i> sp. 4	NMP6V 76767/1	CN15735	Saudi Arabia	25.45933	46.56276	PP377752		PP353969	PP353886
<i>Bunopus</i> sp. 4	NMP 6V 76765	CN15748	Saudi Arabia	24.542718	46.30234	PP377753	PP376026	PP353970	PP353872
<i>Bunopus</i> sp. 4		CN15760	Saudi Arabia	25.147162	47.559819	PP377754		PP353971	PP353873
<i>Bunopus</i> sp. 4		CN15761	Saudi Arabia	25.147162	47.559819	PP377755	PP376027	PP353972	PP353887
<i>Bunopus</i> sp. 4	NMP6V 76764/2	CN15774	Saudi Arabia	25.147162	47.559819	PP377756	PP376028	PP353931	PP353888
<i>Bunopus</i> sp. 4	NMP6V 76764/1	CN15775	Saudi Arabia	25.147162	47.559819	PP377757	PP376029	PP353973	PP353884
<i>Bunopus</i> sp. 4	NMP6V 76767/2	CN15778	Saudi Arabia	25.45933	46.56276	PP377758	PP376030	PP353974	PP353889
<i>Bunopus</i> sp. 4	NMP6V 76760	JEM_40	Yemen	15.4	45.269167	PP377759			
<i>Bunopus</i> sp. 4	NMP6V 76755	JOR_030	Jordan	29.42565	34.97565	PP377760	PP376031	PP353975	MG990766
<i>Bunopus</i> sp. 4	NMP6V 76756	JOR_031	Jordan	29.466	35.44563	PP377761	PP376032	PP353976	PP353909
<i>Bunopus</i> sp. 4		JORD05	Jordan	29.3159531	36.0023778	PP377762	PP376033	PP353977	PP353910
<i>Bunopus</i> sp. 4		JORD06	Jordan	29.3159531	36.0023778	PP377763	PP376034		PP353911
<i>Bunopus</i> sp. 4	SMNHTAU-R.15249	R.15249	Israel	29.797	35.012	PP377766	PP376036	PP353932	PP353912
<i>Bunopus</i> sp. 4	SMNHTAU-R.18329	R.18329	Israel	29.94	35.068	PP377767	PP376037	PP353979	PP353913
<i>Bunopus</i> sp. 4	SMNHTAU-R.18330	R.18330	Israel	29.94	35.068		PP376038	PP353980	PP353922

Species	Voucher code	Tissue sample	Country	Latitude	Longitude	12S	COI	RAG2	cmos
<i>Bunopus</i> sp. 4	SMNH-TAU-R.18332	R.18332	Israel	29.94	35.068	PP377768	PP376039	PP353981	PP353914
<i>Bunopus</i> sp. 4	IBE S10015	S10015	Saudi Arabia	25.26806	46.62366	PP377772	PP376041	PP353984	PP353890
<i>Bunopus</i> sp. 4	IBE S10027	S10027	Saudi Arabia	26.10437	44.58867	PP377773	PP376042	PP353985	PP353893
<i>Bunopus</i> sp. 4	IBE S10090	S10090	Saudi Arabia	26.10437	44.58867	PP377774	PP376043	PP353986	PP353879
<i>Bunopus</i> sp. 4	IBE S10098	S10098	Saudi Arabia	26.45661	37.9359	PP377775	PP376044	PP353987	PP353915
<i>Bunopus</i> sp. 4	IBE S10137	S10137	Saudi Arabia	25.32252	46.53951	PP377776			
<i>Bunopus</i> sp. 4	IBE S10225	S10225	Saudi Arabia	26.08708	44.6517	PP377777	PP376045	PP353988	PP353874
<i>Bunopus</i> sp. 4	IBE S10269	S10269	Saudi Arabia	25.32252	46.53951	PP377778			
<i>Bunopus</i> sp. 4	IBE S10329	S10329	Saudi Arabia	26.8696	40.06326	PP377779	PP376046	PP353989	PP353891
<i>Bunopus</i> sp. 4	IBE S10369	S10369	Saudi Arabia	25.26806	46.62366	PP377780			
<i>Bunopus</i> sp. 4	IBE S10403	S10403	Saudi Arabia	21.25904	40.79568	PP377781	PP376047	PP353990	PP353875
<i>Bunopus</i> sp. 4		S3767	Oman	19.743058	55.1478	PP377769	PP376040	PP353933	PP353866
<i>Bunopus</i> sp. 4	IBE S7823	S7823	Oman	20.42776	56.74081	PP377770		PP353982	PP353919
<i>Bunopus</i> sp. 4	IBE S8076	S8076	Oman	19.16855	57.65657	PP377771		PP353983	PP353920
<i>Bunopus</i> sp. 4		SA01	Saudi Arabia	24.6308139	39.3202333	PP377782	PP376048		PP353892
<i>Bunopus</i> sp. 4		SA02	Saudi Arabia	24.6308139	39.3202333	PP377783	PP376049		PP353899
<i>Bunopus</i> sp. 4		SPM002890	UAE	25.29167	55.58	PP377784	PP376050	PP353991	PP353894
<i>Bunopus</i> sp. 4		BEV.T12591	Kuwait	28.59728	48.27574	PP377730	PP376009	PP353927	
<i>Bunopus</i> sp. 4		BEV.T12593	Kuwait	29.4736	47.7781	PP377732	PP376011	PP353958	PP353877
<i>Bunopus</i> sp. 4		BEV.T2452	Kuwait	29.9437	47.7515	PP377726		PP353956	PP353878
<i>Bunopus</i> sp. 4	NMP6V 76758	T28	UAE	24.130216	55.80232		PP376051		
<i>Bunopus</i> sp. 4	NMP6V 76761	UAE1DK	UAE	24.78071	54.71581	PP377785			
<i>Bunopus</i> sp. 4		UAE2DK	UAE	24.78071	54.71581	PP377786			
<i>Bunopus</i> sp. 4	ZFMK87215	ZFMK87215	Saudi Arabia	22.4	41.74	PP377787	PP376052		
<i>Bunopus</i> sp. 4	ZFMK87217	ZFMK87217	Saudi Arabia	22.4	41.74	PP377788	PP376053	PP353992	PP353876
<i>Bunopus</i> sp. 4	ZFMK92883	ZFMK92883	Jordan	29.903897	35.406139	PP377789	PP376054	PP353993	PP353916
<i>Bunopus</i> sp. 4	ZFMK92884	ZFMK92884	Jordan	29.903897	35.406139	PP377790	PP376055	PP353994	PP353917
<i>Bunopus</i> sp. 4	ZFMK92885	ZFMK92885	Jordan	29.903897	35.406139	PP377791	PP376056	PP353995	PP353918
<i>Bunopus</i> sp. 4		CN3796	Oman	21.3333333	58.5333333		KX889134		
<i>Bunopus</i> sp. 4		CAS250929	Oman	22.4781	58.7767		KX889136		
<i>Bunopus</i> sp. 4		CAS250876	UAE	25.616667	56.05		KX889155		
<i>Bunopus</i> sp. 4		CAS228738	UAE	25.2701667	55.6966667		KX889154		
<i>Bunopus</i> sp. 4	MVZ:Herp:236485	MVZ236485	Yemen	15.443833	45.311	PP377764	PP376035	PP353978	PP353881
<i>Bunopus</i> sp. 4		AMC005_1	Qatar	25.724	50.995		LIZ008-15		
<i>Bunopus</i> sp. 5		ZMMU-R-11738-1	Iran	30.734	61.23		ABLRP221-07		
<i>Bunopus</i> sp. 5	MVZ:Herp:250430	MVZ250430	Pakistan	29.800667	66.902333	PP377792	PP376057	PP353996	PP353856
<i>Bunopus</i> sp. 5		ERP 1097	Iran	31.1166667	61.7333333		KX889153		
<i>Bunopus tuberculatus</i> sensu stricto		RuHF-NR-332	Iran	27.08	60.15		ABLRP222-07		
<i>Bunopus tuberculatus</i> sensu stricto		ZMMU RAN-1186	Iran	28.317	57.9		NPLRP072-08		
<i>Bunopus tuberculatus</i> sensu stricto		ZMMU RAN-1166	Iran	26.883	57.1		NPLRP075-08		
<i>Bunopus tuberculatus</i> sensu stricto		9014	Iran	25.768707	60.865907	EU589159			
<i>Bunopus tuberculatus</i> sensu stricto		MVZ234334	Iran	25.45	61.25		KX879651		
<i>Bunopus tuberculatus</i> sensu stricto		MVZ234355	Iran	25.45	61.25		KX879650		
<i>Bunopus tuberculatus</i> sensu stricto		MVZ234352	Iran	26.933333	56.4		KX889156		
<i>Bunopus tuberculatus</i> sensu stricto		ERP3956	Iran	27.2	60.45		KY077673		

Species	Voucher code	Tissue sample	Country	Latitude	Longitude	12S	COI	RAG2	cmos
<i>Bunopus tuberculatus</i> sensu stricto		ERP3955	Iran	27.2	60.45		KY077672		
<i>Bunopus tuberculatus</i> sensu stricto		ERP2104	Iran	27.2	60.45		KY077671		
<i>Bunopus tuberculatus</i> sensu stricto		ERP2102	Iran	27.2	60.45		KX077670		
<i>Bunopus tuberculatus</i> sensu stricto		ERP1806	Iran	27.75	55.1		KX889157		
<i>Bunopus tuberculatus</i> sensu stricto	MVZ:Herp:234336	MVZ234336	Iran	25.270333	60.755333	PP377794	PP376059	PP353997	
<i>Bunopus tuberculatus</i> sensu stricto	MVZ:Herp:234337	MVZ234337	Iran	25.270333	60.755333	PP377795	PP376060	PP353998	PP353895
<i>Bunopus tuberculatus</i> sensu stricto	MVZ:Herp:234347	MVZ234347	Iran	26.963333	60.145833	PP377796	PP376061	PP353999	PP353897
<i>Bunopus tuberculatus</i> sensu stricto	MVZ:Herp:234348	MVZ234348	Iran	26.898	60.168	PP377797	PP376062	PP353935	PP353898
<i>Bunopus tuberculatus</i> sensu stricto	MVZ:Herp:234350	MVZ234350	Iran	26.944833	56.240833	PP377798	PP376063	PP354000	PP353882
<i>Bunopus tuberculatus</i> sensu stricto	MVZ:Herp:234351	MVZ234351	Iran	26.944833	56.240833	PP377799	PP376064	PP354001	PP353896
<i>Bunopus tuberculatus</i> sensu stricto	MVZ:Herp:234356	MVZ234356	Iran	25.270333	60.755333	PP377800	PP376065	PP354002	PP353883
<i>Bunopus tuberculatus</i> sensu stricto		ZMMU RAN-1167	Iran	26.883	57.1		NPLRP076-08		
<i>Bunopus tuberculatus</i> sensu stricto		ZMMU RAN-1168	Iran	26.883	57.1		NPLRP077-08		
<i>Crossobamon evermanni</i>		DJ5751	Tajikistan	37.10207	68.22523		PP375987	PP353939	PP353847
<i>Crossobamon evermanni</i>	DJ5755	DJ5755	Tajikistan	37.10207	68.22523	PP377699	PP375988		PP353841
<i>Crossobamon evermanni</i>		DJ5765	Tajikistan	37.10207	68.22523	PP377700	PP375989	PP353940	PP353843
<i>Crossobamon evermanni</i>		ERP1062	Iran	34.5333333	60.4333333		KX893113		
<i>Crossobamon evermanni</i>		ERP1063	Iran	34.5333333	60.4333333		KX893114		
<i>Crossobamon evermanni</i>		DJ8898	Uzbekistan	37.81	67.2	PP377701	PP375990	PP353923	PP353848
<i>Crossobamon evermanni</i>		DJ8899	Uzbekistan	37.81	67.2	PP377702	PP375991	PP353924	PP353849
<i>Crossobamon evermanni</i>		DJ8908	Uzbekistan	37.38	67.28	PP377703		PP353925	PP353842
<i>Crossobamon evermanni</i>		DJ8909	Uzbekistan	37.38	67.28	PP377704	PP375992	PP353941	PP353844
<i>Crossobamon evermanni</i>		DJ8935	Uzbekistan	37.56	67.26	PP377705	PP375993	PP353942	PP353845
<i>Crossobamon evermanni</i>		DJ8936	Uzbekistan	37.56	67.26	PP377706	PP375994	PP353943	PP353850
<i>Crossobamon evermanni</i>	CAS232100	CAS232100	Pakistan	29.4695	65.9808333	PP377701	PP375990	PP353923	PP353848
<i>Crossobamon evermanni</i>		ZMMU-R-12086-1	Uzbekistan	41.21	64.22		ABLRP219-07		
<i>Crossobamon evermanni</i>		ZMMU R-12916	Kazakhstan	44	69		NPLRP401-08		
<i>Crossobamon evermanni</i>		RuHF-NR-259a	Iran	34.22	58.26		ABLRP287-07		
<i>Trachydactylus spatulurus</i>		CN15960	Yemen	13.882402	45.869709	PP377793	PP376058	PP353934	PP353839

Table S3. Results of the biogeographic reconstructions using BioGeoBEARS showing statistics for the competing models.

Model	k	AICc	Delta AICc	AICc weights
DEC	2	21.28	0.569	0.427
DIVALIKE	2	20.71	0	0.568
BAYAREA	2	30.31	9.603	0.005