

Comparative Phylogeography of Four Lizard Taxa Within an Oceanic Island

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Abstract

Comparative phylogeography aims to detect common patterns of differentiation among taxa attributed to the same geological or environmental barriers, thus, to find shared drivers of genomic splits and landscape features that explain patterns of occurrence and genetic diversity. Following this approach, this work focuses on four endemic lizard taxa, namely *Acanthodactylus schreiberi schreiberi*, *Ophisops elegans schlueteri*, *Phoenicolacerta troodica*, and *Laudakia cypriaca*, that co-occur in Cyprus, an isolated island of the Mediterranean. In an attempt to discern possible effects of the geological and ecological history of the region on diversity patterns along the lineages under study, samples were collected from all parts of Cyprus and phylogenetic reconstructions, species delimitation analyses, and biogeographic comparisons were conducted at both genetic and genomic levels (Sanger and ddRAD sequencing data, respectively) for all four taxa. The derived phylogenomic relationships provide evidence of a strong genetic structure within the island that agrees with the geographical origins of each population. A rare case of an island-to-mainland dispersal event is confirmed for one of the focal taxa, making it one of the few documented cases of this type. Estimated diversification times during the Miocene reflect timing of first arrival on the island, while further diversification seems to have been strongly affected by the Pleistocene oscillations.

Keywords: ddRADseq, Cyprus, *Acanthodactylus schreiberi*, *Ophisops elegans schlueteri*, *Phoenicolacerta troodica*, *Laudakia cypriaca*

1. Introduction

Comparative phylogeography seeks to identify shared patterns among species within the same region, which can be linked to common physical or environmental barriers. This approach helps uncover the factors driving of genetic or genomic divergence and highlights landscape features that explain species distribution and diversity patterns (Edwards et al., 2022; Gutiérrez-Garica and Vázquez-Domínguez, 2011). Recent advances in genome-wide data production technologies and respective bioinformatic tools have enhanced the exploration of phylogeny and biogeographic processes at both species and population levels, providing in-depth insights on their evolutionary history (Macías-Hernández et al., 2013; Sherpa et al., 2023; Yang et al., 2021). These new insights are of great importance for insular systems, especially oceanic islands, which are considered model systems for ecology and evolutionary biology (Warren et al., 2015). Oceanic islands are geographically isolated for long periods of time, thus evolving independently from the mainland, resulting in the occurrence of many local endemic and cryptic species (Dimitriou et al., 2022; Pérez-Delgado et al., 2022; Plötner et al., 2012). For this reason, the analysis of genome-wide data from a comparative phylogeography perspective within islands can identify the genetic differentiation of populations between closely related species at a local scale (Edwards et al., 2022; Gutiérrez-Garica and Vázquez-Domínguez, 2011).

Cyprus is an oceanic Mediterranean island (Moores et al., 1984) lying within a biodiversity hotspot (Marchese, 2015; Myers et al., 2000). When the island first surfaced from the sea during the Miocene (~ 15-10 MYA; Constantinou and Panayides, 2013) it consisted of two palaeoislands, which roughly correspond to the two main mountain ranges of the island, namely Troodos Mt. at the central-west, and Pentadaktylos Mt. at the north. These palaeoislands were eventually connected in mid-early Pleistocene, after the formation of the Mesaoria plane in-between them (Constantinou and Panayides, 2013; Kinnaird et al., 2011). Cyprus has been isolated at least since the end of the Messinian Salinity Crisis (MSC) ~ 5.3 MYA (Constantinou and Panayides, 2013; Krijgsman et al., 1999) without strong evidence of a connection with the mainland during or after this period (Aksu et al., 2005; Bache et al., 2012; Hsü et al., 1977; Jolivet et al., 2006; Steininger and Rögl, 1984). Furthermore, the presence of many endemic species indicates a long lasting isolation of the island from the neighbouring mainland regions (Dimitriou et al., 2022; Karameta et al., 2022a; Plötner et al., 2012; Poulakakis et al., 2013). For example, five out of 11 lizard taxa occurring in Cyprus are endemic (three species and two subspecies) (Baier et al., 2013; Karameta et al., 2022a). Overseas dispersal has been suggested as a means of colonisation for many Cypriot taxa since no connection to the mainland has been confirmed, at least during the Pliocene and Pleistocene (Baier et al., 2017; Gvoždík et al., 2010; Karameta et al., 2022a; Poulakakis et al., 2013; Psonis et al., 2016; Simonato et al., 2007).

Recent work on terrestrial isopods (Dimitriou et al., 2022, 2023) has revealed extensive diversification of morphologically homogeneous taxa, leading to the identification of several cryptic species and raising suspicions about similar cases in other groups. This possibility is further supported by accumulated evidence regarding the oceanic character of the island of Cyprus, as explained above, and the documentation of increased genetic divergence in several taxa such as isopods, fungi, **beetles/coleoptera?** (Cardoso et al., 2015; Loizides et al., 2019; Nabozhenko et al., 2022; Sfenthourakis et al., 2017).

Aiming to explore common drivers of lineage splits across multiple taxa within Cyprus, the phylogenetic relationships of Cypriot taxa, as well as their relationships with taxa from adjacent areas

were explored. Genetic and genomic data from four lizard taxa distributed in Cyprus were generated in an attempt to gain new insights into the evolutionary processes that have shaped the present patterns of genetic diversity on the island in a comparative phylogeographic approach. The taxa included in the study are all the three members of the family Lacertidae and the sole representative of Agamidae on the island, all considered endemics due to either morphological and/or genetic differentiation from mainland populations. These taxa are found throughout the island, in various habitats and are easily identified in the field. Each taxon has a well-known ecology, i.e. reproductive period and life cycle characteristics, as well as habitat and microhabitat distribution and activity patterns (Baier et al., 2013). In the past, they have been included in phylogenetic studies (Karameta et al., 2022a; Kyriazi et al., 2008; Poulakakis et al., 2013; Psonis et al., 2016; Tamar et al., 2015, 2014) based only on a few markers (mitochondrial and nuclear gene fragments) and represented by a small number of samples that did not cover their whole island distribution. Thus, even though there are some data on the relationships of focal species with their sister taxa in neighbouring predominantly Levantine countries available, an in-depth analysis of their intra-island evolutionary relationships is still lacking, which makes them the perfect candidate taxa to include in a comparative phylogeographic study.

Among the focal taxa, *Acanthodactylus schreiberi* Boulenger, 1878, was first described from Cyprus and is part of the *boskianus* species group (Arnold, 1983; Salvador, 1982; Sindaco and Jeremčenko, 2008; Tamar et al., 2014). The species includes two subspecies: *A. schreiberi schreiberi* Boulenger, 1878, endemic to Cyprus, and *A. schreiberi ataturi* Yalçinkaya & Göçmen, 2012 restricted to a small coastal area in the Hatay Province, in south-eastern Turkey (Franzen, 1998). Due to their morphological similarities, the Turkish population was identified as a distinct subspecies only recently by Yalçinkaya and Göçmen (2012) on the basis of differences in both morphology and blood serum proteins. Two alternative scenarios regarding the evolutionary history of the two subspecies have been proposed. According to the first, Cyprus was colonised by the ancestor of the species through a land bridge connection at the beginning of the MSC (Tamar et al., 2014) and a secondary island-to-mainland colonisation event of south-eastern Turkey took place very recently (Franzen, 1998; Tamar et al., 2014), giving rise to *A. s. ataturi*. This scenario was supported by the genetic similarities shared between the two subspecies, as well as the absence of the Turkey subspecies from nearby suitable habitats in Turkey. The second scenario, proposed by Sindaco et al. (2000), supports that the Turkish population is a relict of a once wider distribution, as similar distributions have been recorded for other species (e.g., *Phoenicolacerta laevis* and *Ablepharus budaki*). Poulakakis et al. (2013) and Psonis et al. (2016) corroborate this scenario, further highlighting the sister relationships of the two subspecies, but proposed different colonisation events during the Miocene (Poulakakis et al., 2013) and the Pleistocene (Psonis et al., 2016) that involved overseas dispersal from south-eastern Turkey to Cyprus. Both scenarios support that there is no ground for assigning a subspecific rank to the Turkish population due to its low genetic divergence from the Cypriot populations.

The second taxon included in this study is *Ophisops elegans* Ménétriés, 1832. The Cypriot endemic subspecies *Ophisops elegans schlueteri* Böttger, 1880 is considered one of the most abundant and widespread lizards on the island (Baier et al., 2013). Even though the validity of subspecies throughout the species' range and their relationships are still debated, the Cypriot populations clearly form a distinct clade (Kyriazi et al., 2008; Montgelard et al., 2020; Poulakakis et al., 2013). Its divergence time remains uncertain, with diversification times ranging from the first part of the late Miocene (~ 7.6 MYA; Kyriazi et al., 2008; Poulakakis et al., 2013) to the MSC (~ 5 MYA; Montgelard et al., 2020).

The last member of Lacertidae included in this study is *Phoenicolacerta troodica* (Werner, 1936). When first described, *P. troodica* was considered a subspecies of *Lacerta* (= *Phoenicolacerta*) *laevis* Gray,

1838, with a wide distribution in the Levant. It was later given a subspecies rank by Werner (1936), as *Lacerta laevis troodica*, a status also supported by Tosunoğlu et al. (1999) based on blood serum proteins. It was later assigned to the new genus *Phoenicolacerta* and elevated to species level based on mitochondrial markers and morphological characteristics (Arnold et al. 2007). A genus-wide study by Tamar et al. (2015) showed that *P. troodica* diverged from its sister taxon, *P. laevis*, during the MSC, at ~ 5.4 MYA, and presumably dispersed to Cyprus through stepping-stone islands.

The only representative of Agamidae on the island is *Laudakia cypriaca* (Daan, 1967). The taxonomy of the species, as well as of the whole genus, has undergone many changes and modifications. Due to the wide morphological variability observed throughout its distribution, the species *Laudakia stellio* (Linnaeus, 1758) had been divided into seven subspecies, including the Cypriot endemic *Laudakia stellio cypriaca* (Baig et al., 2012; Crochet et al., 2006), whose morphological differences set it apart from the rest. A recent study, including a thorough phylogenetic analysis of all subspecies and populations within the range of *L. stellio*, elevated *L. s. cypriaca* to species level (Karameta et al., 2022a), showing that *L. cypriaca* diversified in the early Pleistocene (~ 2.4 MYA) and presumably colonised the island through overseas dispersal (Karameta et al., 2022a).

Due to the island's unique geological history and the presence of many endemics, Cyprus is an ideal system for studying biodiversity, biogeography, and evolution. Although several molecular ecology studies have investigated Cypriot diversity (Dimitriou et al., 2018; Frynta et al., 2010; Kornilios et al., 2012; Kotsakiozi et al., 2018; Macholán et al., 2007; Poulakakis et al., 2013; Skourtanioti et al., 2016), only a few have used high-throughput sequence data (Dimitriou et al., 2023, 2022; Kotsakiozi et al., 2018; Moysi et al., 2023), but only has focused on a comparative phylogeographic approach within Cyprus (Poulakakis et al., 2013). This study focuses on the four aforementioned endemic lizards of Cyprus, integrating both genetic and genomic data, aiming to explore the evolutionary relationships among populations of each taxon, to identify patterns of population structure within the island, to explore biogeographic patterns and to delimit species boundaries, thereby contributing to a broader understanding of the evolutionary dynamics that have shaped the island's biota. More specifically, the study aims to explore whether modern populations of these quite vagile animals retain any signal of their possible past co-occurrence on two distinct palaeoislands. Another aim is to identify if their distribution changed on the island after the two palaeoislands became united or even after humans colonised the island (~ 10,000 years ago) who subsequently modified the island's habitats and possibly scrambled populations. Furthermore, we aimed to identify the timing of each taxon's arrival on Cyprus and possible effects of major ecological events (e.g. Pleistocene oscillations) on the population genetic structure

2. Materials and Methods

2.1. Taxa sampling and DNA extraction

Tail tips were sampled from up to nine individuals of each taxon from each sampling site (Supplementary Material A). Tail tissue was preferred because the tail of the focal taxa regenerates, thus the sampled animals were released with minimum annoyance after tissue collection. Overall, 326 samples from 35 populations distributed across Cyprus were collected (Fig. 1). The sampled material was preserved in >96% ethanol and stored at -20°C until further processing. Tissue fragments and/or DNA extractions of samples from neighbouring countries (Turkey, Israel, Jordan, Syria, and Egypt) were provided by colleagues and museum collections (Natural History Museum of Crete and the Department of Zoology, The Steinhardt, Museum of Natural History; Supplementary Material A).

Total genomic DNA was extracted from tissue using the DNeasy Blood and Tissue Kit (Qiagen, Hidden, Germany) following the manufacturer's guidelines. Samples that failed to yield sufficient DNA quality and quantity were also treated with the ammonium acetate DNA extraction protocol (Bruford et al., 1998). DNA quality and quantity were assessed with agarose gel electrophoresis (TAE 1.5%, GelRed stained) and fluorescence measurements using Qubit 4 fluorometer (Invitrogen™, Thermo Fisher Scientific, Waltham, USA) following the manufacturer's guidelines.

2.2. Genetic Data

2.2.1. Amplification, genetic data sequencing and estimation of genetic distances

A subsample of the collected material, which includes up to four samples from each locality of each taxon, were included in the amplification and sequencing steps of three mitochondrial gene fragments, cytochrome b (*Cyt b*), 16S ribosomal subunit (16S), and nicotinamide adenine dehydrogenase subunit 4 (ND4). Primers (Arévalo et al., 1994; Palumbi, 1996) and PCR conditions adapted from Dimitriou and Sfenthourakis (2022), are given in Supplementary Material B (Tables SB1 and SB2). Double-stranded sequencing was conducted on an ABI3730XL automated sequencer at MacroGen Europe (Amsterdam, Netherlands). The homology of the retrieved sequences was evaluated through the Basic Local Alignment Search Tool (BLAST; <https://blast.ncbi.nlm.nih.gov/Blast.cgi>) using default settings. Sequences were further inspected and edited using CodonCode Aligner v.5.1.5.6. (CodonCode Corporation, USA). Furthermore, in the cases of the two coding genes (*Cyt b* and ND4), sequences were translated into amino acids to evaluate the presence of internal stop codons. All newly produced sequences have been deposited in GenBank (National Center for Biotechnology Information, NIH, Bethesda, Maryland, USA; Supplementary Material A). Additional sequences were retrieved from GenBank to enrich the dataset (Agarwal and Ramakrishnan, 2017; Garcia-Porta et al., 2019; Gonçalves et al., 2012; Heidari et al., 2014; Karameta et al., 2022a; Kyriazi et al., 2013, 2008; Leaché et al., 2014b; Mendes et al., 2016; Pang et al., 2003; Psonis et al., 2016; Solovyeva et al., 2013; Tamar et al., 2015).

Multiple sequence alignment was performed for each gene fragment separately using MAFFT v.7.520 (Kato et al., 2002) with the default settings. Sequence edges with no overlapping nucleotides were trimmed prior to subsequent analyses. Pair-wise genetic distances (p-distance) between and within populations were estimated with MEGA X v 10.1.8 (Kumar et al., 2018).

2.2.2. Phylogenetic analysis

Phylogenetic trees were inferred using both Maximum Likelihood (ML) and Bayesian Inference (BI) approaches, with all mtDNA genes treated as a single locus (concatenated mtDNA). The best partitioning scheme and the corresponding substitution model excluding the +G+I models (Yang, 2006; Tables SB15 - SB18) were estimated with PartitionFinder2 v2.1.1 (Lanfear et al., 2017) based on the Bayesian information criterion (BIC; (Schwarz, 1978)) using the greedy algorithm and linked branch lengths.

The ML inference was carried out with RAxML v.8.2 (Stamatakis, 2014) implemented in raxmlGUI v.2.0 (Edler et al., 2021) under the GTRGAMMA model with 100 runs. Statistical confidence was assessed with 1,000 standard bootstraps (Felsenstein, 1985). MrBayes v.3.2.6 (Ronquist et al., 2012) was used to perform BI in two runs with four independent sampling chains for each run. Each chain ran for 10^7 generations and samples were collected every 100 generations. Convergence and stationarity were evaluated using the MCMC diagnostics generated by MrBayes. The first 25% of samples were discarded as burn-in, after the inspection of the MCMC traces in Tracer v.1.7.2 (Rambaut et al., 2018).

A 50% majority-rule consensus tree was generated from the posterior distribution of trees and the posterior probabilities were calculated as the percentage of samples recovering and branch.

2.2.3. Divergence times estimation

Gene trees for each taxon and divergence time estimations were conducted using the concatenated mitochondrial sequences with BEAST2 v.2.6.7 (Bouckaert et al., 2019). The input file for BEAST2 was edited in BEUTi v.2.6.7 implemented in BEAST2. Model parameters were unlinked across partitions except for the tree model, which was set to linked. The uncorrelated lognormal model was used to describe the relaxed clock, while the birth-death model was used for the tree prior. Secondary calibration points used for each species were retrieved from previously published data (Table SB19; Garcia-Porta et al., 2019; Karameta et al., 2022a; Leaché et al., 2014b). BEAST2 was run five independent times with random starting seeds, with chain lengths of 500 million generations each, and sampling taking place every 5,000 generations. As per the default settings, the first 25% of samples were discarded as burn-in. Results were examined in Tracer to ensure convergence between runs. The final trees with divergence time estimations were produced in TreeAnnotator v.2.6.7 (BEAST2 package) by combining the trees from all runs.

2.3. Genomic Data

2.3.1. ddRADseq library construction, Sequencing and Initial Data Handling

The double-digested restriction site-associated DNA sequencing (ddRADseq) libraries were constructed following the protocol described by Peterson et al. (2012), using 800ng of genomic DNA as starting material and two restriction enzymes (SbfI and MspI) for DNA digestion, including the entirety of the collected samples (up to eight) from each locality. A combination of Illumina sequencing adapters and custom barcodes were used to tag each specimen. Size-selection of fragment in the range of 415-515 bp was performed with Pippin Prep (Sage Science, Beverly, Massachusetts, USA). DNA quantities were evaluated using Qubit 4 fluorometer. The final libraries were sequenced on a HiSeqX platform (Illumina, San Diego, CA, USA) at Macrogen NGS facilities (Seoul, South Korea).

Demultiplexing of raw Illumina reads was implemented with ipyrad v 0.9.84 (Eaton and Overcast, 2020). All settings were set to their default values except 'clust_threshold' option which was set to 0.9. The 'assembly_method' was set to 'denovo'. Samples with low coverage compared to the rest of the samples were removed from further analyses. All samples of all taxa were sequenced using paired-end sequencing chemistry, except for *A. schreiberi* that also included previously sequenced single-read data..

To minimize loci with a large amount of missing data while keeping phylogenetic informative loci in the ddRADseq datasets, an additional filtering step was performed after the initial ipyrad filtering, following the R script of Psonis et al. (2021). Specifically, 'min_var' and 'min_info' were both set to -1, while 'min_taxa' was run multiple times and was finally set to 4, 10, 16 and 4 for *Acanthodactylus*, *Ophisops*, *Phoenicolacerta*, and *Laudakia*, respectively, retaining loci with at least 4, 10, 16 and 4 unique sequences, respectively. Furthermore, 'snp.select' was set to 'snp.select.all' in order to retain one SNP per locus from the filtered datasets, and specifically the SNP with the least missing data and ambiguous characters.

2.3.2. Phylogenomic Analyses

Maximum Likelihood analyses were conducted in RAxML-NG v.1.0.2 (Kozlov et al., 2019) using the concatenated supermatrix of the ddRADseq data under the GTR+G model, as recommended for ddRADseq datasets (Leaché et al., 2015). The results were evaluated with 300 bootstrap replicates. Bayesian Inference analyses were conducted in ExaBayes v.1.5 (Aberer et al., 2014) and were run two independent times with four chains each, with one million generations per chain and sampling every 1,000 generations. The first 25% of samples were discarded as burn-in. Convergence of the independent runs was assessed with Tracer (Rambaut et al., 2018) by examining the effective sample sizes, as well as monitoring the standard deviation of split frequencies (sdsfConvergence; set at 5%) in ExaBayes.

2.3.3. Divergence times estimation

Divergence time estimations were conducted with the SNP datasets using BEAST2. All parameters and runs were the set as in the mtDNA, except the model parameters which were all unlinked across partitions. Secondary calibration points used for each species were retrieved from the mitochondrial analyses above (Table SC1). Results were examined in Tracer to ensure convergence between the runs.

2.3.4. Species Delimitation and Species Trees

Species delimitation with a guide tree (A10) was performed using BPP v. 4.3.8 (Rannala and Yang, 2003; Yang and Rannala, 2010) under the multispecies coalescent model (Flouri et al., 2018). Due to computational constraints, the filtered datasets were further refined to retain four samples from each phylogenetic cluster (see Supplementary Material A) with the least number of missing data. The python script ‘pyrad_filter.py’ (<https://github.com/pimbongaerts/radseq>) was implemented to keep the common loci between the retained samples. The maximum number of retained loci per dataset was 50. Nevertheless, if this threshold was exceeded after refinement, loci were then randomly selected for downstream analyses. Specimens were assigned to potential species based on the observed phylogenomic patterns of strongly supported clades which reflect the geographic origin of samples. The inferred ML tree was used as a guide tree. Analyses were conducted using the ‘rjMCMC algorithm’=1. The inverse-gamma prior θ and τ_0 were assigned a diffuse prior with shape $\alpha=3$ and scale β adjusted to the genetic diversity of each taxon as calculated for SNAPP (see below; Table SC2). The sequences for each species were set as unphased diploid for each species, while the species model prior was set to 1. The analyses were run for a total of 1,000,000 iterations, with a burn-in phase of 100,000 iterations and sampling taking place every 50 iterations.

Species delimitation was also carried out using the Bayes Factor Delimitation (BFD*) method (Leaché et al., 2014) on the SNP datasets (i.e. retaining only one SNP per locus from the filtered datasets). All outgroups were excluded from BFD*. Various species delimitation scenarios were tested reflecting the geographic and phylogenomic patterns observed, using the path sampling analysis implemented in the model-selection package v1.5.3. (Leaché et al., 2014a) of BEAST2. Each delimitation scenario was ranked by the marginal likelihood reported from path sampling and Bayes Factor (BF) was used to assess the support of each scenario. Path sampling was run with chain length of 100,000, alpha parameter was set to 0.3 (Xie et al., 2011), the burn-in percentage was set to 50% and it included 24 steps.

Following the results of the BFD* method, a species tree was estimated for the scenario with the best BF using SNAPP v.1.5.2 (Bryant et al., 2012) implemented in BEAST2. SNAPP is sensitive to missing data and becomes computationally demanding as the number of analysed samples increases. Therefore, datasets for SNAPP included only three individuals per phylogenomic cluster (based on the ML and BI results in the current study), similar to the retained samples in BPP (see Supplementary A), and

outgroups were excluded. Additionally, further filtering of the SNP datasets was performed using VCFtools v.0.1.16 (Danecek et al., 2011) allowing for 5% of missing data in *Acanthodactylus*, 15% in *Ophisops*, 10% in *Phoenicolacerta*, and 2% in *Laudakia* based on the trade-off of loci and missing data retained. One random SNP per RAD fragment was selected to avoid possible effects of linkage disequilibrium (LD) using a freely available Perl script (https://github.com/santiagosnchez/sing_snp_vcf). Each dataset was converted to PHYLIP format using the Python script 'vcf2phylip.py' (<https://github.com/edgardomortiz/vcf2phylip>). The R package 'phrynomics v.2.0' (Leaché et al., 2015) was used to filter out invariant and non-binary loci, as well as to translate each dataset to biallelic SNPs. SNAPP uses a Yule prior for the speciation rate, which is determined by the parameter λ . Using the Python 'pyule' script (<https://github.com/joaks1/pyule>) the mean of λ was calculated by providing the height of the tree (calculated from the ML tree, using the R package 'ape v.5.8'; Paradis and Schliep (2019)) and the number of potential species. The input file for SNAPP was created using BEAUti and λ was set using a gamma prior with the parameter 'a' set to 2 and the mean as calculated above. The prior of the expected divergence (θ) was a gamma distribution (Rateprior) with ' α ' =1 and a mean estimated as the percentage of polymorphic sites within a genetic cluster. The mutation rates 'u' and 'v' were set to one and were not sampled. The parameters of the priors for each species are detailed in Supplementary Material C (Table SC3). Species trees were run for 20 million generations, sampling every 1,000 generations. Convergence of the independent runs and ESS values were assessed with Tracer .

Using the filtered SNP datasets with three individuals per phylogenomic cluster as in SNAPP, species trees were also estimated using the coalescent method SVDQuartets (Chifman and Kubatko, 2014) implemented in PAUP v.4.0a168 (Swofford, 2002). VCFtools was used to filter out samples, and the R package 'dartR v.2.9.7' (Mijangos et al., 2022) was used to create the input file for SVDQuartets. All possible quarters were evaluated both with and without prior assignments to well-supported clades identified. The results were assessed with 10,000 standard bootstrap replicates.

2.3.5. Testing for Shared Divergence Events

To test shared divergence events among the taxa on the two palaeoislands of Cyprus, a full-likelihood Bayesian approach was implemented using ecoevolity v.1.0.0 (Oaks, 2019). The ecoevolity tool uses pairs of populations as species trees with two tips and a Dirichlet process prior to estimate possible numbers and times of divergence events (Oaks, 2019). The filtered datasets with three samples per genetic cluster were used, including full alignments for each locus, as suggested by Oaks et al. (2020). Samples for all species were assigned to two populations (north-eastern and central-west clades) based on the results of the species trees and phylogenomic analysis (Table SC4), so that in total there were four comparisons between two populations among the four taxa. The 'event_model_prior' was set so that 50% of the estimated probability of the number of categories was at the maximum number of categories and the 'mutation_rate' was set to 1. As suggested by Oaks et al. (2020), ecoevolity was run multiple times, changing the values of the 'event_time_prior', which was set as a gamma distribution with shape=2 and mean set as 0.01, 0.1 and 0.5, to assess whether the results are sensitive to the prior assumptions. Various population sizes were tested as well. In particular, 'population_size' was set to 10 (shape=2, mean 0.5) for all taxa, and different values for each taxon were calculated based on the theta values used in SNAPP and BPP for each taxon (shape=2), as proposed by the developers. The parameters for each run can be found at the Supplementary Material C (Table SC5). Each analysis was run twice for 150,000 generations, sampling every 100 generations. The first 100 samples were discarded as burn-in. Results were examined in Tracer to ensure convergence between runs.

3. Results

3.1. mtDNA Dataset: Genetic Distances, Phylogenies and Divergence Times Estimations

The concatenated mitochondrial sequences obtained for *Acanthodactylus* included a total of 1,711 bp and 57 samples, for *Ophisops* 1,728 bp and 55 samples, for *Phoenicolacerta* 1,664 bp and 51 samples, and for *Laudakia* 1,659 bp for 50 samples. The total length, variable and parsimony informative sites can be found in Table SB1.

For each taxon genetic distances (p-distance) were similarly low among the island localities for all three mitochondrial gene fragments. In particular, the intra-specific distances among Cypriot populations ranged from 0.05% to 1.4% for 16S, 0.4% to 8% for Cyt *b* and 0.3% to 5% for ND4. Comparing Cypriot populations of focal taxa with populations outside Cyprus, the distances ranged from 2% to 17% for 16S, 5% to 23% for Cyt *b* and 8% to 24% for ND4. Within population distances for the focal taxa ranged from 0 – 0.56% for 16S, 0-5.41% for Cyt *b* and 0-2.77% for ND4. (for more details see Tables SB3-14), while some populations seem to exhibit higher within than inter-population diversity (i.e. Troodos for *A. schreiberi* Cyt *b* and ND4 and for of *L. cypriaca* 16S and Cyt *b*).

The mtDNA gene trees reconstructed via both ML and BI resulted in largely similar topologies within each taxon. The BI trees are presented for each taxon separately in Fig. SB1-4, showing both posterior probabilities and ML bootstrap support. The Cypriot taxa form monophyletic clades, except for *Acanthodactylus*. Within each taxon further substructure is evident, reflecting the geographic origin of samples and are predominantly grouped based on their sampling localities, which is more prominent for *O. elegans*, although these groupings are not statistically supported. For, *A. schreiberi*, the Turkish subspecies clusters within the Cypriot taxa, and specifically with samples from Rizokarpaso. The relationships within the Cypriot populations of *P. troodica* show that the two northern populations cluster together, while some of the **branches** identified predominantly correspond to geography, with low statistical support. Lastly, *L. cypriaca* forms a monophyletic clade with both low posterior probability and bootstrap support..

Divergence times estimations (Table SB20) showed two major diversification events among focal taxa. Specifically, the diversification of *A. schreiberi* from its sister species, *A. boskianus*, took place during the Miocene, at ~ 11.60 MYA (Fig. SB5), while within-island populations seem to have diversified at ~ 1.88 MYA. *Ophisops elegans schlueteri* (Fig. SB6) shows a similar pattern, diverging from populations in neighbouring countries at ~ 11.49 MYA. Within Cyprus, diversification of this taxon took place at ~ 3.56 MYA.

The other two taxa appear to have diversified from their sister taxa at more recent times, about the end of the Messinian and the early Pliocene. In particular, the diversification of *P. troodica* from its sister species is estimated at ~ 5.78 MYA (Fig. SB7) and within Cyprus at ~ 1.53 MYA. Similarly, *L. cypriaca* (Fig. SB8) is estimated to have diverged from its sister species during the Pliocene (~ 4.46 MYA) and within the island divergence took place at ~ 0.53 MYA.

3.2. Genomic Dataset

The ddRADseq libraries resulted in an average of 2.4 million reads per sample for *Acanthodactylus*. With the additional filtering steps, the supermatrices produced consisted of 1.2 million sites of concatenated ddRAD loci sequences, and 8,752 unlinked SNPs. The respective values for the other three taxa were 3.7 million reads, 2.55 million sites and 8,800 unlinked SNPs for *Ophisops*, 3.9 million reads, 2.72 million sites and 9,314 unlinked SNPs for *Phoenicolacerta* and, lastly, 3.5 million reads, 2.69 million sites and 9,096 unlinked SNPs for *Laudakia*.

3.2.1. Phylogenomic Reconstructions and Divergence Times Estimations

The ML and BI analyses produced similar phylogenies (see Figs 2-5) for each taxon. As in the case of mtDNA gene trees, the Cypriot populations of each taxon form monophyletic groups except for *Acanthodactylus*. These phylogenies provided higher within-taxon resolution, with strongly supported subclades consisting of samples with distinct geographical distributions.

In the phylogenomic tree of *A. schreiberi* (Fig. 2), nine highly supported subclades are observed with clear geographic differentiation. Cladogenesis appears to have a west-east direction, while a single sample of a northern locality (Kormakitis) seems to cluster with the west-central cluster of Troodos. It is worth noticing that the *A. s. ataturi* subclade is nested within *A. s. schreiberi*, as was the case in the mtDNA tree. The basal subclade of the tree consists of samples from Pafos, located in the western part of the island, similar to the mtDNA tree.

Regarding the phylogeny of *O. e. schlueteri* (Fig. 3), two major clades are observed; a well-supported central-western clade that includes three subclades (Pafos, Limassol and Troodos), and a north-eastern clade that includes five subclades (Nicosia, Kamyli, Charkia, Ammochostos and Rizokarpaso). The monophyly of the north-eastern clade is only supported based on posterior probabilities but not based on bootstraps, but its well-supported subclades predominantly correspond to geography (Nicosia, Ammochostos, Kyrenia, and Rizokarpaso), except for two samples from Nicosia and Kyrenia.

For *P. troodica* (Fig. 4), the basal clade of the tree consists of two subclades, each of them corresponding to a northern population (Kamyli and Charkia). Two more clades follow, one central-western (Pafos and Troodos) and one south-central (Limassol, Larnaka and Nicosia), with subclades including individuals from distinct populations. The only exception is a sample from Nicosia which falls within the central-western clade, and specifically with samples from Troodos Mt.

In the phylogenomic tree of *L. cypriaca* (Fig. 5), the population from Troodos Mt. lies at the base of the tree, forming one of the three major clades. The second clade includes two well supported subclades from the western part of the island, grouped into two well-supported subclades with samples from Limassol and Pafos, respectively. Both of these subclades are further structured, especially the Pafos one, predominantly reflecting the geographic localities of the samples. The third clade includes populations from the north-eastern part of the island. It is worth noticing that two samples from Akamas peninsula, at the northwestern part of the island, are grouped within the north-central clade.

Divergence times using the ddRADseq datasets (Table SC6) are similar to those produced using the mtDNA datasets, even though most clades were not statistically supported. In particular, *A. schreiberi* diversification within the island began at ~ 1.84 MYA. *O. e. schlueteri* two main clades began diversifying at ~ 2.4 MYA. Within the subclades, diversification started shortly afterwards at ~ 2.1 MYA for the central-western and at ~ 2.2 MYA for the north-eastern subclade, respectively. Regarding the two remaining species, intra-island diversification is estimated at more recent times than the previous two. *Phoenicolacerta troodica* diversified at ~ 0.56 MYA, while *L. cypriaca* at ~ 0.093 MYA, both younger estimates than the mtDNA-based ones.

3.2.2. Species Delimitation and Species Trees

Bayes Factor Delimitation (BFD*) supported a scenario in which each locality represents a distinct genetic cluster for all taxa (Table SC7). Species delimitation using BPP resulted in low posterior probabilities regarding the delimitation of conspecific populations (Table SC8). For *Acanthodactylus*, the analysis identified 10 clusters with 55% support, with each one predominantly representing a sampling locality. There were only two exceptions where samples from two localities were defined as

a single cluster. Samples from Rizokarpaso and Turkey form a single genetic cluster with high posterior probability. The second grouping included samples from Troodos Mt. and one from Kormakitis (Table SC8) which is located in the north, in accordance with the rest of the phylogenomic analyses. Regarding *O. elegans*, the best species delimitation scheme supported eight genetic clusters with 74% support, with each locality representing a single cluster except for the neighbouring localities of Pafos and Troodos which were grouped as a single genetic cluster (Table SC8). For *Phoenicolacerta*, species delimitation supported six genetic clusters with 76% posterior support. All five sampling localities from Pafos were grouped together in one genetic cluster, while the samples from Troodos Mt., Limassol, Larnaka, and Nicosia formed a single genetic cluster (Table SC8). Samples from Chalefka and Kamyli formed two distinct clusters. Lastly, species delimitation for *Laudakia* supported eight genetic clusters, with low posterior support (39%). The best delimitation scheme supported the grouping of only two out of the four sampling localities from Pafos, the grouping of samples from the north-eastern localities of Rizokarpaso and Ammochostos, and the clustering of the neighbouring north-central ones from Kamyli and Nicosia (Table SC8). Comparison between the two methods and the possible number of genetic clusters present within the island can be found on Fig. 2-5.

Species trees from both SNAPP and SVDQuartets for all taxa (Fig. SC1-4) revealed a close relationship of delimited clusters from central-western localities. A close relationship was also evident among the north-eastern populations of the island, with minor exceptions. The SVDQuartets species trees provided higher resolution of relationships among clusters than those produced with SNAPP.

For *A. schreiberi*, both species trees supported the close relationship between the Turkish samples and those from Rizokarpaso. The grouping of the central-western populations from Limassol, and Troodos Mt. are evident in both species' trees but only the one produced from SNAPP offered high support for this clade (Fig. SC1), while the population of Pafos holds a basal position on the trees.

In the *O. elegans* species trees, both methods identified two major clusters, central-western and north-eastern, with high support. The relationships within the central-western clade were well supported in both species' trees, with the populations from Troodos Mt. and Pafos clustering together. In contrast, the relationships among the eastern clades were only partially resolved in SVDQuartets, with samples from Limassol clustering with north-eastern localities rather than the central-western ones (Fig. SC2).

Regarding *P. troodica*, the central-western clade was supported in SVDQuartets analysis, which grouped all sampling localities from Pafos with the population from Troodos Mt. The relationships among the remaining clusters were not resolved in the SNAPP analysis but were clarified in SVDQuartets, where the northern clusters of Kamyli and Charkia had a sister relationship and belong to a single cluster with samples from Larkana, Nicosia and Limassol (Fig. SC3).

Lastly, the species trees of *L. cypriaca* showed a well-supported central-western clade in both methods (SNAPP and SVDQuartets), with SVDQuartets providing a higher resolution within the clade. More specifically, western (Pafos) clusters appeared more closely related to each other than to the central (Troodos) and southern-central (Limassol) clusters. Consistent with the rest of the phylogenomic analyses, the Akamas cluster (at the northwestern part of Cyprus) had a sister relationship to the Ammochostos cluster in both methods (Fig. SC4), based on both analyses, but only SVDQuartets showed high statistical support.

3.2.3. Shared Divergence Events

Ecovoly was run multiple times with varying values for the 'event_time_prior' and the 'population_size' parameter. The results were consistent across all combinations, indicating they are not sensitive to prior assumptions. All runs of ecovoly support three divergence events with high

posterior probability between the two palaeoislands of Cyprus (Fig. 6). Two taxa, *A. schreiberi* and *P. troodica* share similar divergent times. *Ophisops elegans* is inferred to have diversified at older times than the rest of the taxa, while *L. cypriaca* has the youngest divergence times among the taxa.

4. Discussion

This study utilized an extensive nuclear dataset comprising thousands of loci across the genomes of four lizard taxa from Cyprus, viewed through a comparative phylogeographic lens. The findings confirmed that similar factors, primarily the island's palaeogeography, drive the genetic variation observed in these focal taxa. The monophyly of focal taxa and hidden diversity within the island is revealed. The phylogenetic and phylogenomic analyses provided a clearer picture of the evolutionary history of the studied taxa, as well as the within-taxon population structure of *A. schreiberi*, *O. e. shlueteri*, *P. troodica* and *L. cypriaca*. In most cases, the diversification of these taxa from their continental counterparts occurred at the end of the Miocene and during the Pliocene, indicating that the MSC could have facilitated the arrival and divergence of their ancestral populations on the island. The onset of their within-island diversification can be traced somewhat later, when Cyprus had been completely isolated from the mainland. Further divergence within the island seems to have been triggered by the Pleistocene glacial-interglacial cycles for all taxa.

4.1. Comparisons of datasets and methods

According to the phylogenomic trees produced in this study, the monophyletic origin of all four taxa is confirmed, in line with previous studies that included only a limited number of individuals from the island (Karameta et al., 2022; Kyriazi et al., 2008; Montgelard et al., 2020; Poulakakis et al., 2013; Psonis et al., 2016; Tamar et al., 2014, 2015). In addition, clear genetic clusters are revealed within the island, most of which match the geographic origin of each sample. The higher resolution of ddRADseq-based phylogenomic analyses compared to mtDNA-based phylogenetic trees is rather expected since the former efficiently sample loci over the entire genome, providing more in-depth results (Baird et al., 2008; Davey et al., 2013).

It is worth noticing that even though ML and BI analyses of ddRADseq data for each taxon produced almost identical topologies, BI analysis using ExaBayes yielded higher estimates of posterior probabilities for all clades in all four taxa (greater than 90%), while ML trees showed relatively low bootstrap support for certain clades. This is not uncommon for large datasets, in which posterior probabilities can be overestimated (Yang and Rannala, 2005), thus caution should be taken when interpreting support of BI phylogenetic analyses.

4.2. Genetic Distances and Phylogenetic Relationships

The phylogenetic trees portray a general pattern of diversification within the island. Presented patterns reflect the island's palaeogeography, despite the fact that most within-island divergence took place recently, in the Pleistocene. This is probably due to the fact that the two palaeoislands that formed Cyprus for several million years, became connected only recently, in the upper Pleistocene (Constantinou and Panayides, 2013; Kinnaird et al., 2011), so that the beginning of glacial periods predates their unification. Furthermore, the preservation of this palaeogeographical signal has been enhanced by the fact that, despite the low genetic variation of taxa within the island and the absence of geological barriers among them today, phylogenomic data reveal quite a strong geographic structure, with each locality hosting discrete genetic markers.

Genetic distances on mtDNA among the Cypriot taxa (ranging from 0.05% to 1.4 % within all taxa for 16S, 0.4% to 8% for Cyt *b* and 0.3% to 5% for ND4) and their close relatives from neighbouring

countries are in accordance with those observed in accordance with inter-specific distances of other lacertids. For example, p-distances for *Podarcis* 16S gene fragment range between 2.2–7.3% and for Cyt *b* p-distances range from 10.4–17.6% (Psonis et al., 2017; Spilani et al., 2019). Cyt *b* p-distances for *Acanthodactylus* range from 4.3–26.9% (Tamar et al., 2014), for *Anatololacerta* range from 6.1–7.8% (Bellati et al., 2015). For *Mesalina*, 16S p-distances range between 4.3–6.8%, and for Cyt *b* 10–13.1% (Simó-Riudalbas et al., 2019). Genetic distances are also in accordance with inter-specific values reported for other agamid genera, such as *Phrynocephalus* in which p-distance was 4.5% for 16S and 6.3% for ND4 (Pang et al., 2003), *Agama* in which p-distance was 13.1% for ND4 (Gonçalves et al., 2012), and *Pseudotrapelus* in which p-distances ranged from 2.2%–7.1% for 16S and 11.2%–19.9% for ND4 (Tamar et al., 2016). The generally low genetic divergence within the island could suggest a recent diversification event at least as indicated by the mtDNA data. This could be a result of mtDNA not having enough time to accumulate mutations due to genetic drift.

With regards to *A. schreiberi*, a sample from the northern population of Kormakitis clusters with samples from Mt. Troodos. This could indicate a human aided transport event within the island. It is interesting to note that the Turkish samples are nested within those from Cyprus and exhibit low genetic differences from Cypriot samples, especially those from Rizokarpaso, and have an apical position on the tree. This strongly supports the hypothesis proposed by Tamar et al. (2014) that an island-to-mainland dispersal event, i.e., from Cyprus to Turkey, has shaped its modern distribution. This is one of the very few documented cases of this type of dispersal (Hedges et al., 1992; Glor et al., 2005; Hass & Hedges, 1991; Seidel, 1988). Perhaps the most known such example is that of the *Anolis* lizards in Central America, many of which have colonised mainland areas uninhabited by these taxa before from the Caribbean islands (i.e. Nicholson et al., 2005; Patton et al., 2021; Poe et al., 2017). Such events are important in reconsidering the roles of islands in a biogeographic concept.

In contrast, *O. e. schlueteri* is divided into two major clades within the island, a central-western one and a north-eastern one, reflecting the palaeogeography of Cyprus. Two samples from Nicosia and Kyrenia do not cluster with the rest of the samples from the same geographic locality. This could be a misidentification of their sample codes, due to similar numbering or it could indicate another human aided transport between the neighbouring Nicosia and Myrtou/Kampyli. The high p-distances between *O. e. schlueteri* and populations of *O. elegans* from neighbouring countries are consistent with species-level genetic distances among other lacertids (Psonis et al., 2017; Sagonas et al., 2014; Spilani et al., 2019; present study).

Phoenicolacerta troodica and *L. cypriaca* exhibit similar phylogenetic patterns, with distinct northern, western, and central groups, differing only in their basal clades. In the former, the populations that diverge first are those of the northern part (Pentadankylos Mt.), whereas in the latter, it is the west-central population (Troodos Mt.) that splits first at the base of the tree. Furthermore, a sample from Nicosia seems to be clustering with samples from Troodos in *P. troodica*, while two samples of *L. cypriaca* from the Akamas peninsula at the northwestern part of the island cluster together with north-eastern populations, with strong support. These could indicate recent human-aided transportation, given also the well-known close interactions of humans with both these taxa and especially with the large and popular starred agama, even today. Human-aided transportation has been reported for other lacertid taxa as well as for other *Laudakia* species (i.e. Antinucci et al., 2023; Flower, 1933; Klapotocz, 1910; Koch, 1932; Silva-Rocha et al., 2012; Spaneli and Lymberakis, 2014; Toli et al., 2024).

4.3. Species Delimitation, Species Trees and Taxonomic Implementations

Species delimitation was used to identify genetic clusters that might reveal some geographic structure within the island rather than to identify possible species, taking into account also the shallow levels of

diversification within taxa (Pyron et al., 2016). Species delimitation analyses with BFD* supported the scenario where each putative population is a distinct, genetically isolated cluster. Similarly, BPP produced comparable, but slightly more conservative results.

SVDquartets grouped samples according to the geographic distribution of sampling localities and the genetic clusters identified had strong statistical support, reflecting diversification at the population level within the island in all four focal taxa. SNAPP produced species trees similar to those of SVDquartets, but most clades exhibited low posterior probabilities. In both analyses, the species trees of all four taxa, except *A. schreiberi*, identified two major clades within the island, consistent with the patterns observed in the other phylogenomic trees. The differences between the two species trees refer to position changes of a few sites within each major subclade and could be attributed to the shallow level of diversification at this geographical level. In details, the species tree of *A. schreiberi* is similar to the phylogenetic tree based on the sampled from Pafos which split off first, and samples from Ruzikarpaso and Turkey which cluster together. Regarding the species tree of *O. elegans*, is similar to the phylogenomic tree with the exception of samples from Limassol which cluster with the north-eastern subclade. The species tree of *P. troodica* is similar to the ML tree with regards to the western-central subclade, but the two northern localities cluster with the other south-central localities in contrast to the ML. Lastly, for *L. cypriaca*, the species tree differs from the phylogenomic tree based on the position of samples from Troodos, which cluster within the west-central cluster.

The identification of these genetically isolated clusters could be also a result of ecological factors, in view of the habitat variation within the island. Cyprus is a mosaic of over 50 different habitat types (Nicolau et al., 2014). The extreme fragmentation of these habitats due to the long human presence on the island could also impact gene flow among populations. Moreover, the island's semi-arid Mediterranean climate (Giannakopoulos et al., 2010; Peel et al., 2007), especially the extreme heat during extensive periods of the year, could restrict the movement of these animals due to depletion of crucial resources in large areas (Karameta et al., 2022b). Further population genetic analyses will assess gene flow among populations, and landscape genomics could explore how various ecological factors affect the distribution of the taxa on the island. It is important to note that species delimitation methods can sometimes fall short in identifying species or population boundaries and may over-split genetically isolated populations (Huang, 2018; Pyron et al., 2016; Sukumaran and Knowles, 2017). These methods can be biased when dealing with large datasets containing numerous loci and/or a substantial amount of missing data, as is the case with the ddRADseq datasets (Leaché et al., 2019, 2018).

Additionally, based on species delimitation results, genetic distances estimated in this study, and the generated phylogenetic trees, it is proposed to reject the subspecies *A. s. ataturi*. This aligns with previous suggestions (Psonis et al., 2016; Tamar et al., 2014) that a subspecific rank is not justified for the Turkish populations of this species. Furthermore, *O. e. schlueteri*'s genetic distances and species delimitation results confirm the genetic distinctiveness of the Cypriot subspecies and suggest a thorough revision of the whole species, possibly even elevating the taxon to the species level.

4.4. Cladochronology within Cyprus

Based on the cladochronological analyses, *A. schreiberi* split from *A. boskianus* during the Miocene, at ~11 MYA, based on mtDNA estimates. This timing is slightly older than those reported by Tamar et al. 2014 (~ 6 MYA) but falls within the range suggested by Poulakakis et al. (2013) and Psonis et al. (2016), at ~ 9.17 MYA (95% HPD: 5.61-13.4) and ~ 8.56 MYA (95% HPD: 11.13-6.14), respectively. The first split within the taxon occurred during the late Pleistocene, ~ 1.84 MYA, based on both mtDNA and ddRADSeq estimates, thus any further diversification within the island should have taken place after this period. Based on the results of this study, samples from the northernmost population of

Rizokarpaso and Turkey split at ~ 1.07 MYA. This finding contrasts previous studies that estimated the split of the two ‘subspecies’ at ~ 0.85 MYA (Poulakakis et al., 2013) and ~ 0.46 MYA (Psonis et al. 2016), although this estimate has lower posterior probability. The timing of this divergence corroborates the scenario of a recent island-to-mainland colonisation event proposed by Franzen (1998) and Tamar et al. (2014).

Ophisops elegans diverged from its continental counterpart during the Miocene at ~ 11.45 MYA, based on mtDNA estimates, a date close to the one estimated for *A. schreiberi*. This timing is older than what has been proposed by previous studies (~ 5.3 MYA; Montgelard et al., 2020), but falls within the range estimated by Poulakakis et al. (2013), at ~ 7.6 MYA (95% HPD: 4.5-11.7 MYA). Diversification within *O. e. schlueteri* also took place during the Pleistocene, ~2-3 MYA based on estimates of both datasets, at a slightly older period than *A. schreiberi* and quite older than those of the other two taxa.

The diversification of *P. troodica* is estimated to have occurred during the MSC, in agreement with previous studies (~ 5.4 MYA; Tamar et al., 2015). Intra-island diversification within *P. troodica* took place at ~ 1.5 MYA based on mtDNA estimations, and ~ 0.57 MYA based on the ddRADSeq estimations, which are younger than previous estimates of ~ 2.8 MYA (Tamar et al., 2015).

Laudakia cypriaca seems to have diversified shortly after the MSC, at ~ 4.6 MYA. This time of diversification of *L. cypriaca* is inconsistent with the results of Karameta et al. (2022a), who suggested a much later diversification, at ~ 2.37 MYA. The difference of estimations could be due to the different molecular markers used, as Karameta et al. (2022a) also included nuclear genes that evolve much slower than mitochondrial ones. Furthermore, the results of the present study corroborates the results of Karameta et al. (2022a) on rapid diversification events among the three *Laudakia* species, which could explain why the split of *L. cypriaca* is not statistically supported. Diversification within the island took place at later times compared to the previous three taxa, namely during the late Pleistocene, at 0.53 MYA based on mtDNA estimates, but this event is much more recent in ddRADSeq estimates.

Furthermore, three diversification events within the island were identified among the four taxa, as evident by ecoevolution results. *L. cypriaca* seems to have the younger diversification time than the rest of the taxa while *O. elegans* the oldest, which is consistent with the results of cladochronological analysis. On the other hand, *A. schreiberi* and *P. troodica*, seem to share similar divergence times (Fig. 6), consistent with estimates of mtDNA datasets but not so much with those of ddRADSeq. These three diversification events could have been triggered or enhanced by the Pleistocene oscillations. *Ophisops elegans*’ diversification within the island seems to have already been taking place by the time the Pleistocene Ice Ages begun (~ 2.6 MYA), but the climatic and habitat changes during this period could have promoted diversification within this taxon. For the remaining three taxa and especially for *A. schreiberi* and *P. troodica*, the glacial-interglacial cycles in the Pleistocene are the only reasonable explanation of their similarities in diversification patterns, as the two taxa differ in ecology (*A. schreiberi* is restricted to sandy habitats while *P. troodica* can be found on many habitats, but mainly rocky forested habitats; Baier et al., 2013).

4.5. Biogeographical implications and Comparative Phylogeography

As described in the introduction, Cyprus originally consisted of two palaeoislands that were recently merged to form the modern island (Constantinou and Panayides, 2013; Kinnaird et al., 2011). There is no evidence supporting the island’s connection with the mainland at any period, even during the MSC and the Pleistocene Ice Ages, when major sea level fluctuations were observed in the region (Aksu et al., 2005; Bache et al., 2012; Constantinou and Panayides, 2013; Hsü et al., 1977; Jolivet et al., 2006; Krijgsman et al., 1999; Steininger and Rögl, 1984). Nevertheless, our results cannot shed light on the question of a possible MSC mainland connection, since three out of four taxa diverged after the end of

MSC while one much earlier. Hence, even if the post-MSC divergence might be indirect evidence for a land connection during this critical period for the Mediterranean, the much older divergence of one taxon points to the exact opposite direction.

The recovery of the ‘palaeoisland signal’ does not corroborate one or the other hypothesis either, given that these remained separate for millions of years also after the end of the MSC. This finding is important in itself, though, and shows parallelisms with the patterns found in terrestrial isopods (Dimitriou et al., 2022, 2023), where the signal is much stronger of course due to the lower mobility of these animals. Moreover, further diversification within the island, which occurred in the Pleistocene, were likely further triggered by the climatic oscillations of glaciations, as mentioned in section 4.4.

The phylogenomic analyses could offer insights into on the colonization history of the taxa, as basal splits might be considered as evidence for the areas of first arrival of ancestors on the palaeoislands. Of course, the basal splits could reflect last detectable diversification events, irrelevant to the origins of each taxon. Whichever scenario might be true, diversification followed a clear path. In the case of *A. schreiberi*, first diversification appears to have started from the west, followed by divergence towards the northeast, leading to the recent recolonization of the mainland, at south-eastern Turkey.

Ophisops elegans populations diversified on palaeoislands, in isolation from each other. It is worth noticing that both *O. elegans* and *A. schreiberi* belong to the Eremiadini tribe of Lacertidae and are adapted to mesic and xeric climates (Arnold et al., 2007), suggesting that ecological factors too could have played a role in their diversification.

Similarly, *P. troodica* appears to have diversified first on the northern palaeoisland and then on Troodos Mt., which led to independent diversification on western and eastern parts of the island. In contrast, *L. cypriaca* seems to have first diversified on the ‘Troodos Mt. palaeoisland’, expanding to the rest of the area from there. Since it is not clear which of the two taxa (*L. vulgaris* or *L. stellio*) is the sister species of the Cypriot taxon due to the rapid diversification events (Karameta et al., 2022a), the ancestor of *L. cypriaca* that colonized Cyprus remains unidentified.

5. Conclusions

In conclusion, similar patterns drive the divergence of populations among the four lizard species of Cyprus studied herein. Their phylogenetic patterns generally reflect the palaeogeography of the island, and a strong geographic structure of populations, with nearly all clades corresponding to local populations, has been identified. The most striking finding is that the signal of a long divergence on the two palaeoislands that recently merged to form modern Cyprus can still be retrieved in the genetic structure of populations even of mobile taxa like lizards. The Pleistocene oscillations seem to have facilitated intra-island diversification in all focal taxa more prominently than the MSC. Finally, it is strongly suggested that the Cypriot populations of *O. elegans* form a clearly distinct taxon, whereas there is no valid ground for any *A. schreiberi* subspecies, for which an island-to-mainland dispersal scenario is the most plausible explanation for the modern distribution of this taxon.

Data availability

The mtDNA sequences are available in GenBank under the accession numbers PQ657297 - PQ657410 and PQ657437 - PQ657447 for 16S, xxxxxxx-xxxxxxx for Cyt *b*, and xxxxxx-xxxxxxx for ND4. The ddRADSeq are available in demultiplexed form on the NCBI Sequence Read Archive (SRA) with accession numbers SAMN44492602 - SAMN44492877 under BioProject PRJNA1179422.

CRedit authorship contribution statement

Theodora Antoniou: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing, Visualization. Andreas C. Dimitriou: Methodology, Formal analysis, Writing – review & editing. Emmanouela Karameta: Formal analysis, Writing – review & editing. Aglaia Antoniou: Methodology, Formal analysis, Writing – review & editing. Nikos Poulakakis: Methodology, Resources, Writing – review & editing. Spyros Sfenthourakis: Conceptualization, Resources, Data curation, Funding acquisition, Project administration, Writing – review & editing.

Acknowledgements

The authors would like to express their gratitude to Petros Lymperakis from the Natural History Museum of Crete and Karim Tamar from Department of Zoology, The Steinhardt, Museum of Natural History for providing museum specimens, as well as Giorgos Konstantinou for assistance during field sampling in Cyprus. The present work was conducted in the framework of the Project EXCELLENCE/0918/0161, co-financed by the European Regional Development Fund and the Republic of Cyprus through the Research and Innovation Foundation of Cyprus. The authors would also like to thank the anonymous reviewers.

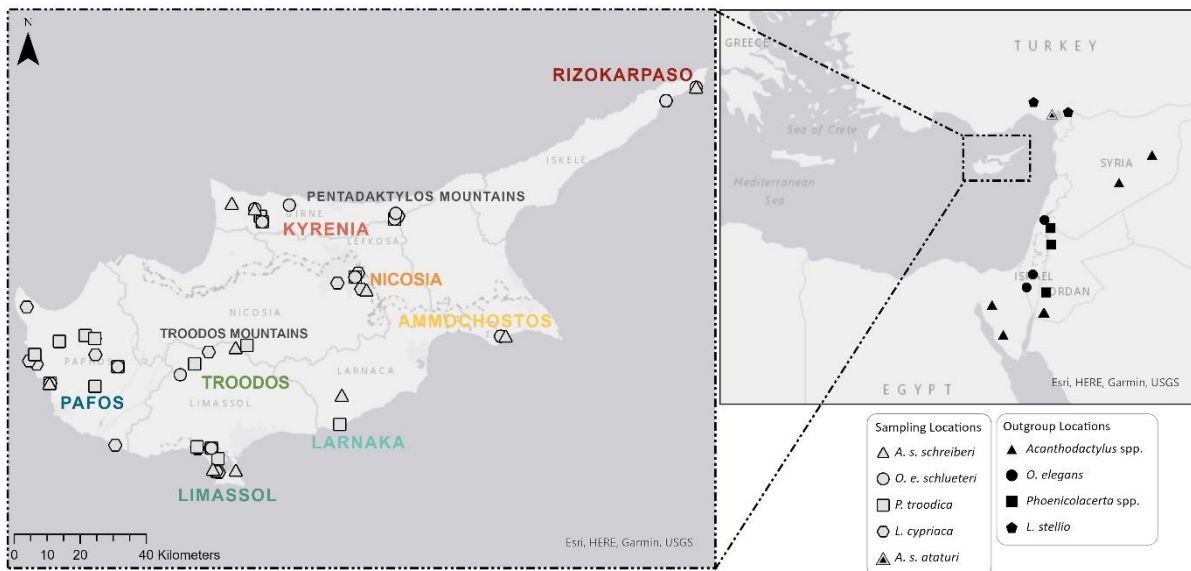


Fig. 1: Sampling locations for the four lizard taxa; A. Within Cyprus and Turkey; B. Samples included as outgroups. Genetic clusters identified on the phylogenomic trees correspond to Cyprus districts, which are presented in colored text on the figure for simplified view.

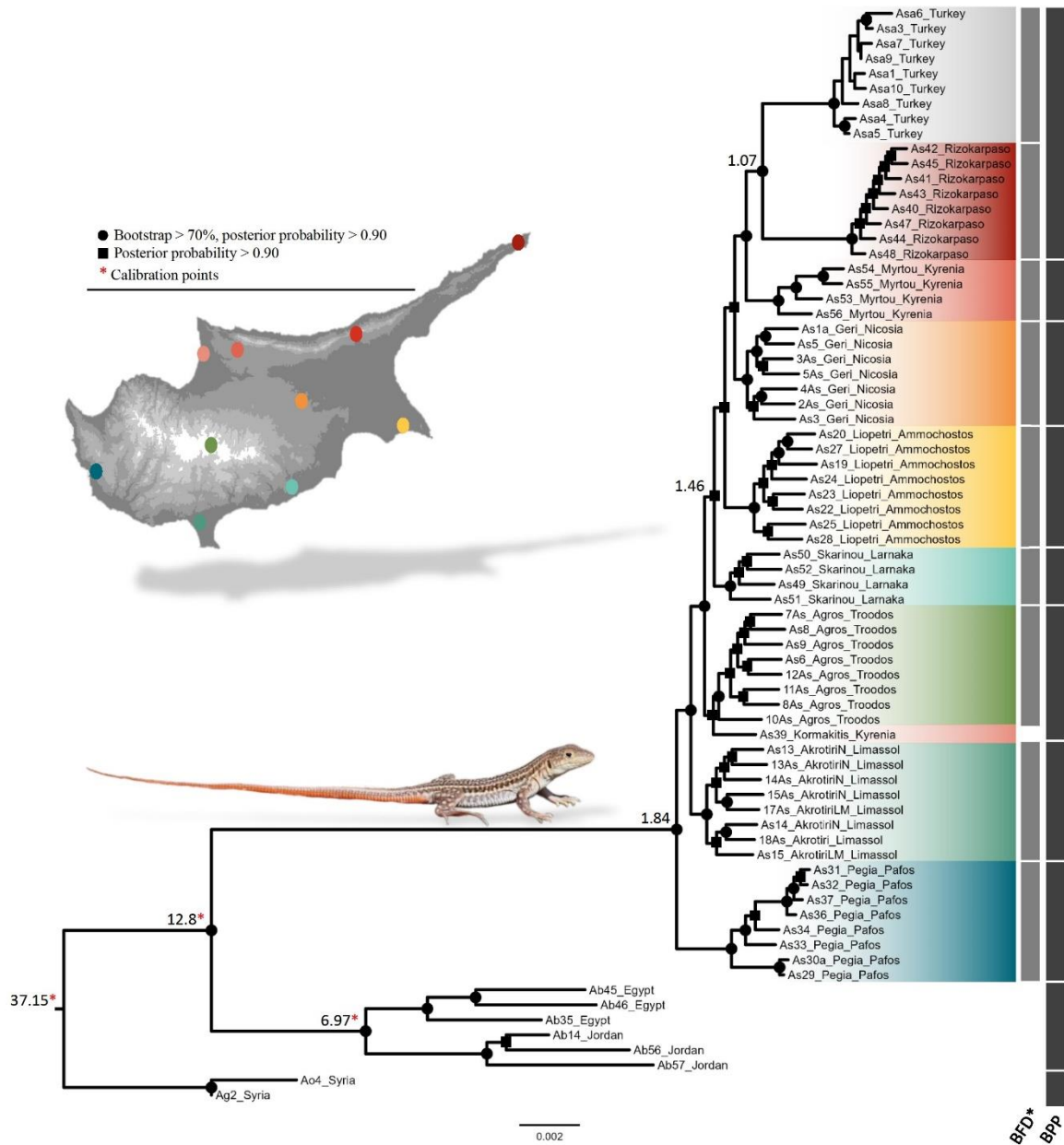


Fig. 2: *Acanthodactylus schreiberi* Maximum Likelihood tree based on the concatenated ddRADseq dataset. A circle on nodes indicates RAXML-NG bootstrap support > 70% and ExaBayes posterior probabilities > 90%. A square on nodes indicates ExaBayes posterior probabilities > 90%. Divergence times (in MY) with high posterior probabilities estimated with BEAST can be found on nodes. Asterisks next to divergence times indicate calibration points. Species delimitation based on BFD* and BPP are indicated by the rectangle boxes on the right (light gray and dark gray, respectively). Cluster colors correspond to sampling localities as presented in the map.

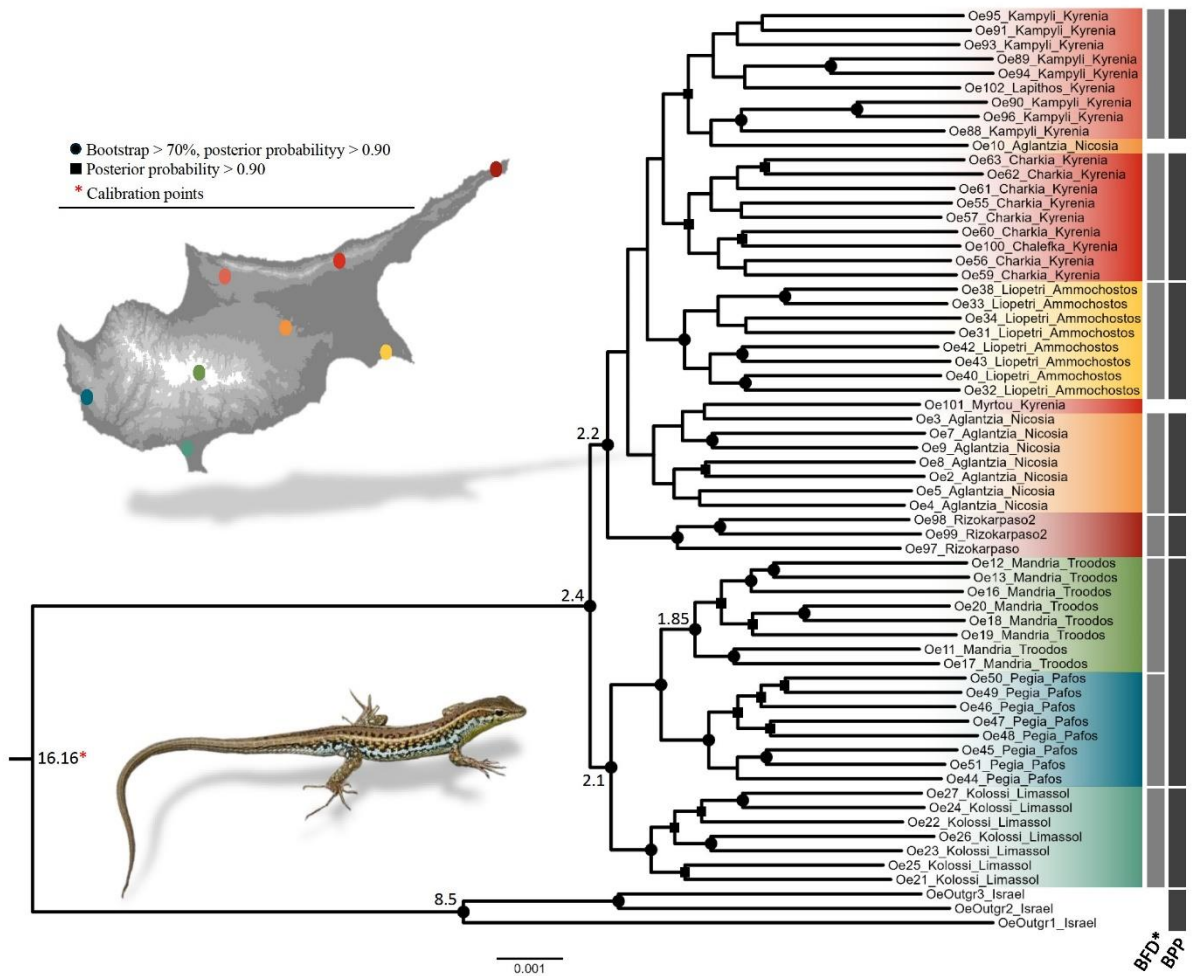


Fig. 3: *Ophisops elegans* Maximum Likelihood tree based on the concatenated ddRADseq dataset. A circle on nodes indicates RAxML-NG bootstrap support > 70% and ExaBayes posterior probabilities >90%. A square on nodes indicates ExaBayes posterior probabilities >90%. Divergence times (in MY) with high posterior probabilities estimated with BEAST can be found on nodes. Asterisks next to divergence times indicate calibration points. Species delimitation based on BFD* and BPP are indicated by the rectangle boxes on the right (light gray and dark gray, respectively). Cluster colors correspond to sampling localities as presented in the map.

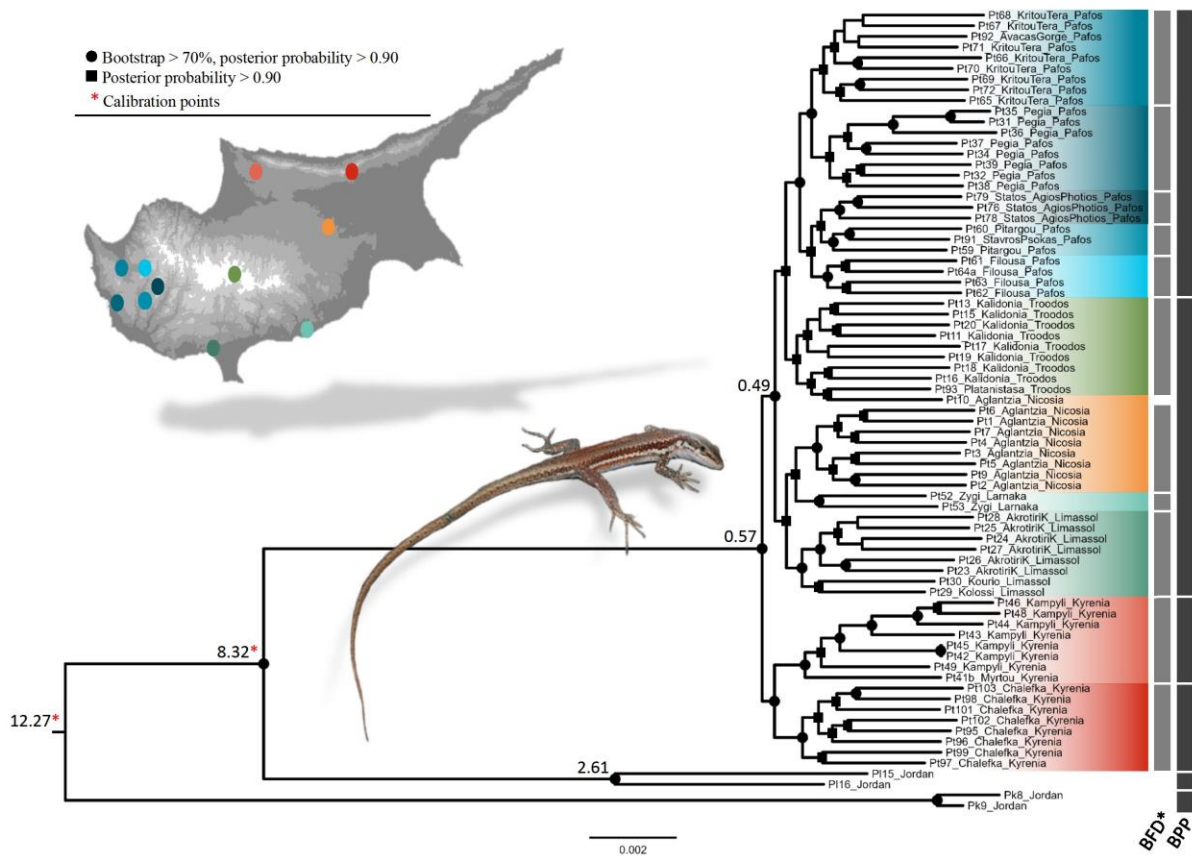


Fig. 4: *Pphoenicolacerta troodica* Maximum Likelihood tree based on the concatenated ddRADseq dataset. A circle on nodes indicates RAXML-NG bootstrap support > 70% and ExaBayes posterior probabilities >90%. A square on nodes indicates ExaBayes posterior probabilities >90%. Divergence times (in MY) with high posterior probabilities estimated with BEAST can be found on nodes. Asterisks next to divergence times indicate calibration points. Species delimitation based on BFD* and BPP are indicated by the rectangle boxes on the right (light gray and dark gray, respectively). Cluster colors correspond to sampling localities as presented in the map.

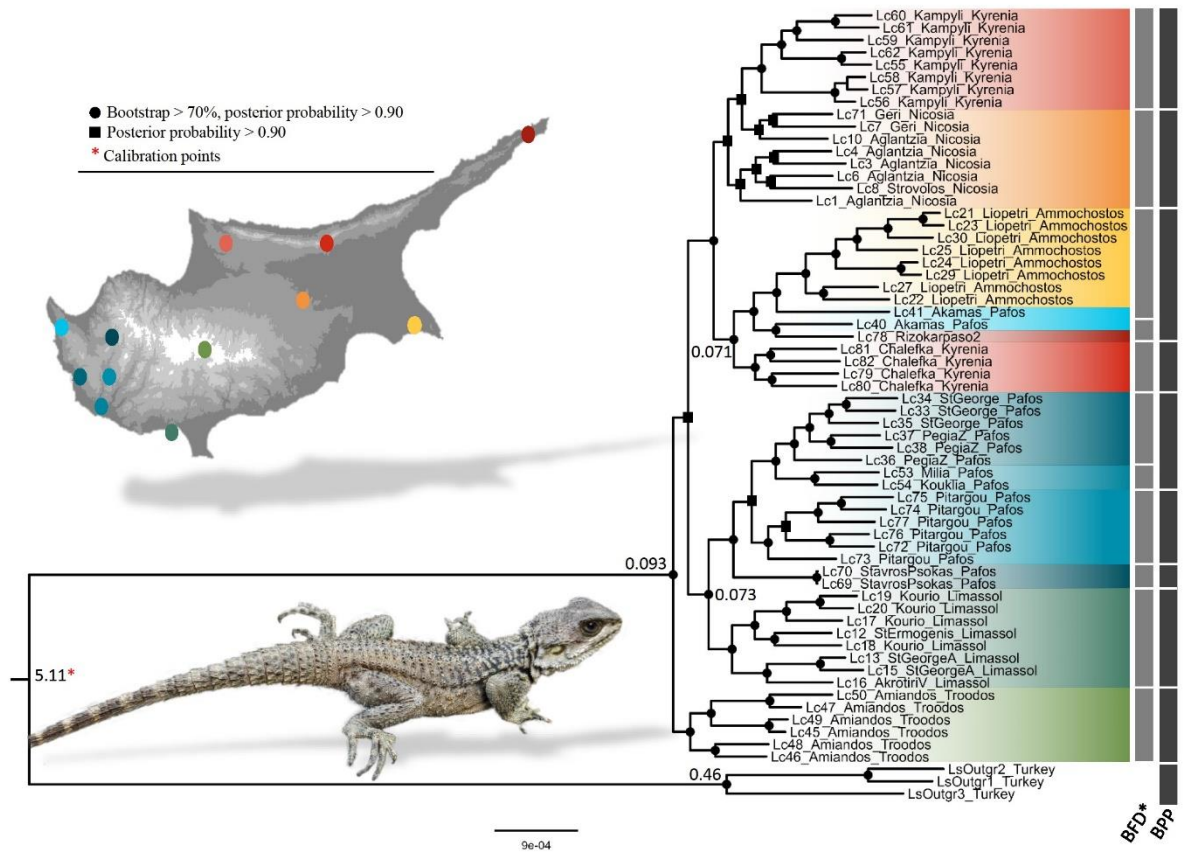


Fig. 5: *Laudakia cypriaca* Maximum Likelihood tree based on the concatenated ddRADseq dataset. A circle on nodes indicates RAxML-NG bootstrap support > 70% and ExaBayes posterior probabilities >90%. A square on nodes indicates ExaBayes posterior probabilities >90%. Divergence times (in MY) with high posterior probabilities estimated with BEAST can be found on nodes. Asterisks next to divergence times indicate calibration points. Species delimitation based on BFD* and BPP are indicated by the rectangle boxes on the right (light gray and dark gray, respectively). Cluster colors correspond to sampling localities as presented in the map.

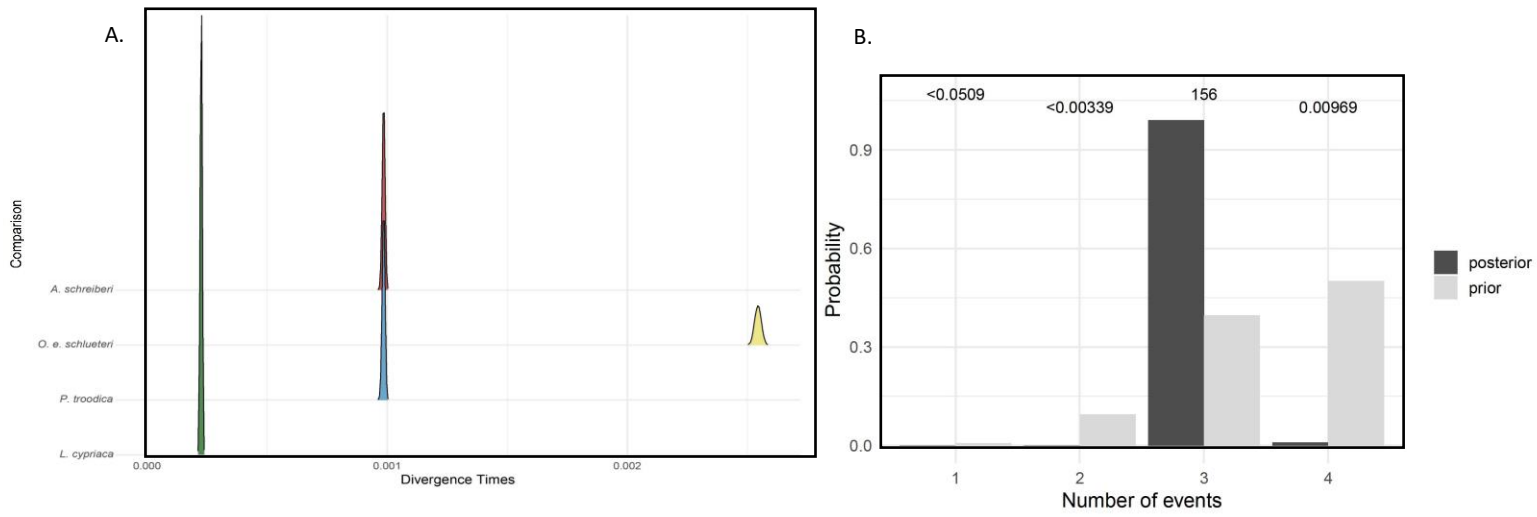


Fig. 6: A. Marginal distributions of divergence times (in expected substitutions per site) between the west-central and north-eastern clades among the four taxa. B. Posterior and prior probabilities on the number of divergence events.

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