

Hidden in the Arabian Mountains: Multilocus phylogeny reveals cryptic diversity in the endemic *Omanosaura* lizards

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Abstract

An increase in studies in the Hajar Mountains from the southeastern Arabian Peninsula has revealed a high richness of endemic evolutionary lineages with many cryptic taxa. *Omanosaura* is the only lacertid lizard genus endemic to the Hajar Mountains, with two species *O. cyanura* and *O. jayakari* distributed throughout this mountain range. The phylogenetic relationships and genetic diversity between and within these species have been poorly studied. In this study, we collected mitochondrial (*12S*, *cytb*, and *nd4*) and nuclear (*cmos* and *mc1r*) sequences for 25 specimens of *Omanosaura*, including 15 individuals of *O. jayakari* and 10 of *O. cyanura*. We performed phylogenetic analyses based on network reconstruction, maximum likelihood and Bayesian inference to estimate the relationships and intraspecific genetic diversity of these species. We estimated the time of divergence between the two species in the Miocene, around 8.5 million years ago. *Omanosaura jayakari* shows little genetic diversity, while *O. cyanura* presents two differentiated lineages. These are reciprocally monophyletic at mitochondrial and nuclear genes and present a high genetic distance between them. These two lineages are associated with the geographic features of the Hajar Mountains, with one lineage distributed in the northernmost part of the Hajar Mountains and the other in the rest of the western Hajars, the Jebel Akhdar, and the eastern Hajars. This geographic relationship has been recovered previously in other reptile taxa and is generally associated with high levels of local genetic diversity. Our results suggest the existence of cryptic diversity within *O. cyanura* and support a general biogeographic pattern of high diversity and endemism in the northern Hajar Mountains that certainly deserves additional research in the future.

KEYWORDS

biodiversity, biogeography, Eremiadini, Hajar Mountains, Lacertidae, species tree

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1 | INTRODUCTION

Knowledge concerning biodiversity patterns around the globe is imbalanced. The existence of whole regions for which information is either absent or very scarce can be associated with difficult or impossible access to these areas, whether connected with remote

or isolated geographic features (Ficetola, Bonardi, Sindaco, & Padoa-Schioppa, 2013), or with sociopolitical instability (Brito et al., 2014). The lack of data normally culminates in a general underestimation of the local biodiversity levels. Case examples of regions with recently discovered hidden genetic variability are the arid mountains in North Africa and the Arabian Peninsula (e.g., Carranza, Simó-Riudalbas, Jaysinghe, Wilms, & Els, 2016; Garcia-Porta, Simó-Riudalbas, Robinson, & Carranza, 2017; Metallinou et al., 2015; Rato, Harris, Carranza, Machado, & Perera, 2016; Rosado, Rato, Salvi, & Harris, 2017).

The Atlas Mountains in the Maghreb, for instance, belong to the Mediterranean basin hot spot but, contrary to the European margin, still hide a considerable amount of genetic diversity. Over the last years, an increase in expeditions to the Maghreb, together with the application of new tools in molecular analyses, led to the discovery of cryptic diversity in this area (Barata, Carranza, & Harris, 2012; Metallinou et al., 2015; Rato et al., 2016; Rosado et al., 2017; Salvi, Perera, Sampaio, Carranza & Harris, 2018; Tamar, Geniez, Brito, & Crochet, 2017). A similar scenario can be found in the Hajar Mountains of southeastern Arabia. This impressive mountain range, with the highest peaks reaching 3,000 m a.s.l., extends from the Musandam Peninsula in the north and runs almost parallel to the Gulf of Oman through the eastern United

Arab Emirates (UAE) and northern Oman for 650 km (Edgell, 2006; Figure 1). Despite being close to the sea, the general low precipitation and high evaporation levels make it an arid mountain desert (Edgell, 2006; Mandaville, 1977). However, the deep gorges running between the peaks (wadis) have water and vegetation, at least intermittently, and are the places where the majority of fauna and flora can be found. The geological setting, together with a local microclimate and the presence of wadis, makes the Hajar Mountains an important refuge for endemic and relict species (Mandaville, 1977), including, among others, endemic species of plants (MacLaren, 2016) and of reptiles, such as two species of the lizard genus *Omanosaura* Lutz, Bischoff, & Mayer, 1986; several species of the geckos of the genus *Asaccus* Dixon & Anderson, 1973 (Carranza et al., 2016; Simó-Riudalbas, Tarroso, Papenfuss, Al-Sariri, & Carranza, 2017), *Hemidactylus* Oken, 1817 (Carranza & Arnold, 2012), *Pristurus* Rüppell, 1835 (Arnold, 2009; Badiane et al., 2014; Garcia-Porta et al., 2017), *Ptyodactylus* Godfuss, 1820 (Metallinou et al., 2015; Simó-Riudalbas, Metallinou, et al., 2017), and *Trachydactylus* Haas and Battersby, 1959 (de Pous et al., 2016), an agamid of the genus *Pseudotrapelus* Fitzinger, 1843 (Tamar, Scholz, et al., 2016), and a viper of the genus *Echis* Merrem, 1820 (Babocsay, 2004; Robinson, Carranza, & Arnold, 2009). With an increase in scientific attention given to the

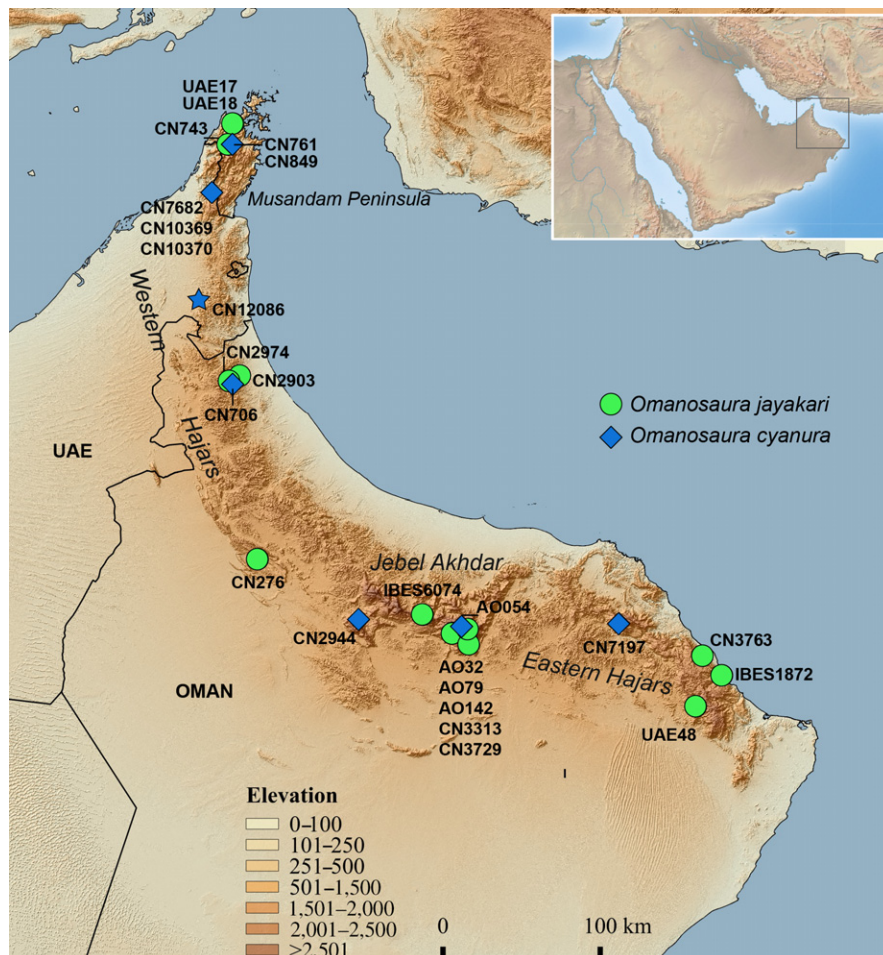


FIGURE 1 Sampling localities in the Hajar Mountains of the individuals of *Omanosaura cyanura* and *O. jayakari* included in this study. The blue star represents the type locality of *O. cyanura*

Hajar Mountains, the number of microendemic species or lineages in this area has increased remarkably over the last few years, particularly among reptiles (Carranza et al., 2016; Garcia-Porta et al., 2017; Simó-Riudalbas, Metallinou, et al., 2017), an indication of very high levels of cryptic diversity in a still understudied biodiversity hot spot.

Omanosaura is the only endemic genus of the family Lacertidae in the Arabian Peninsula and the only endemic reptile genus of the Hajar Mountains. The genus has two species, *O. cyanura* (Arnold, 1972) and *O. jayakari* (Boulenger, 1887), with similar distribution ranges, including many areas of sympatry (Carranza et al., 2018; Gardner, 2013; Sindaco & Jeremčenko, 2008; Sindaco, Venchi, & Grieco, 2011). These species are morphologically very distinct, although both have very long tails of up to 2.75 times their mean body sizes (snout-vent length, SVL). *Omanosaura cyanura* is a small-bodied lizard, with SVL of about 60 mm, and presents a flattened head and body, with dorsal coloration that can be brown or blue, with a long electric blue tail, the feature to which it owes its name. Little is known about this lizard, which is normally spotted in wadis with vegetation and water, from sea level up to 2,400 m a.s.l (Carranza et al., 2018; Gardner, 2013). On the other hand, *O. jayakari* is the largest lacertid lizard in the Hajar Mountains, with SVL up to 200 mm. This robust species is an active hunter and can predate on other lizards, including juveniles of *O. cyanura* (Gardner, 2013). First described as *Lacerta cyanura* and *L. jayakari*, these species were placed in a separate subgenus, *Omanosaura*, by Lutz et al. (1986), based on the genetic distance between *O. jayakari* and the rest of the former members of the genus *Lacerta*. The inclusion of *O. cyanura* in the same subgenus was based on morphological grounds (Arnold, 1972, 1973), and only later, the relatively low immunological distance to *O. jayakari* corroborated their close relationship (Mayer & Benyr, 1994). *Omanosaura* was elevated to the generic level by Mayer and Bischoff (1996). Despite the interest from an evolutionary point of view, sequences in GenBank are only available for one specimen of *O. cyanura* (three mitochondrial genes—Harris, Arnold, and Thomas (1998)) and two specimens of *O. jayakari*, with one specimen sequenced for three mitochondrial genes (Harris et al., 1998) and a different specimen sequenced for two slow-evolving nuclear genes (Mayer & Pavlicev, 2007). Most of these studies had the main purpose of establishing the phylogenetic relationships among genera of Lacertidae or within the tribe Eremiadini, to which *Omanosaura* belongs (Arnold, Arribas, & Carranza, 2007). The results show that *O. jayakari* and *O. cyanura* form a well-supported clade (Harris et al., 1998) of unresolved phylogenetic position within the Eremiadini. However, the genetic diversity and phylogeography of the two *Omanosaura* species remain essentially unknown.

In this study, we analyze for the first time multiple samples of *O. cyanura* and *O. jayakari* from across their distribution ranges in the Hajar Mountains. We performed phylogenetic analyses based on a multilocus approach, including both mitochondrial and nuclear genes, and estimated the divergence time between and within species. The main aim of this study was to infer the phylogeographic relationships and intraspecific genetic diversity within *Omanosaura*

and to increase our knowledge concerning biogeographic patterns and diversity in this understudied region.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling

We included in the phylogenetic analyses 15 samples of *O. jayakari* and 10 of *O. cyanura*, covering the species distribution ranges in the Hajar Mountains (Figure 1). All *Omanosaura* samples and vouchers belong to the collection of the Institute of Evolutionary Biology (IBE-CSIC). Two samples of the closely related Eremiadini species *Acanthodactylus blanfordii* Boulenger, 1918, *Acanthodactylus schmidti* Haas, 1957, and *Mesalina guttulata* Lichtenstein, 1823, were included in the analyses as outgroups (Greenbaum, Villanueva, Kusamba, Aristote, & Branch, 2011; Mayer & Pavlicev, 2007). Sample codes, geographic coordinates, and GenBank accession numbers are reported in Table 1.

2.2 | DNA extraction, amplification, and sequence analyses

Total genomic DNA was obtained from ethanol-preserved tissue samples following the standard high-salt protocol (Sambrook, Fritsch, & Maniatis, 1989). We amplified three mitochondrial gene fragments—*ribosomal 12S rRNA* (*12S*), *cytochrome b* (*cytb*), and *NADH dehydrogenase 4* with flanking tRNAs Serine, Histidine, and Leucine (*nd4*)—and two nuclear genes—*oocyte maturation factor mos* (*cmos*) and *melanocortin 1 receptor* (*mc1r*). These markers have been successfully used in many intra- and interspecific studies on lacertid lizards (Mendes, Harris, Carranza, & Salvi, 2016; Salvi, Harris, Bombi, Carretero, & Bologna, 2010; Salvi, Schembri, Sciberras, & Harris, 2014; Tamar, Carranza et al., 2016). Amplification was performed through polymerase chain reaction (PCR). Primers, PCR conditions, and references are listed in the Supporting Information (Table S1; see also Mendes et al. (2016) and Salvi et al. (2017)). Purification of PCR products and sequencing were carried out by Macrogen (www.macrogen.com) with the same primers used for amplification.

Nucleotide sequences were manually checked and edited in GENEIOUS 4.8.5 (Kearse et al., 2012). Heterozygous positions in the nuclear genes *cmos* and *mc1r* were coded according to the IUPAC ambiguity codes. All protein-coding gene fragments (*cytb*, *nd4*, *cmos*, and *mc1r*) were translated into amino acids sequences, and no stop codons were observed, suggesting that all the sequences were functional. Multiple DNA sequences were aligned using the MUSCLE algorithm (Edgar, 2004) implemented in GENEIOUS. For each nuclear gene, the possible occurrence of recombination events was assessed using the Pairwise Homoplasmy Index (ϕ) test (Bruen, Philippe, & Bryant, 2006) implemented in SPLITSTREE 4.14.4 (Huson & Bryant, 2006). We used MEGA 6.0 (Tamura, Stecher, Peterson, Filipksi, & Kumar, 2013) to calculate pairwise genetic distances (p -distance) of mitochondrial haplotypes and the number of variable and parsimony informative sites in all genes.

TABLE 1 Code and geographic coordinates of the samples of *Omanosaura jayakari* and *O. cyanura* lineages and of outgroup species included in this study. GenBank accession numbers of *12S*, *cytb*, *nd4*, *cmos*, and *mc1r* are MG672294–318, MG672340–364, MG672389–410, MG672319–339, and MG672365–388, respectively

Species (lineage)	Code	Geographic coordinates (Latitude, Longitude)	Geographic coordinates				
			<i>12S</i>	<i>cytb</i>	<i>nd4</i>	<i>cmos</i>	<i>mc1r</i>
<i>O. jayakari</i>	UAE17	26.18N, 56.26E	MG672297	MG672343	MG672392	MG672322	MG672368
<i>O. jayakari</i>	UAE18	26.18N, 56.26E	MG672298	MG672344		MG672323	MG672369
<i>O. jayakari</i>	CN743	26.05N, 56.23E	MG672302	MG672348	MG672396	MG672327	MG672373
<i>O. jayakari</i>	CN2974	24.61N, 56.24E	MG672304	MG672350	MG672398	MG672329	MG672375
<i>O. jayakari</i>	CN2903	24.64N, 56.30E	MG672305	MG672351	MG672399		MG672376
<i>O. jayakari</i>	CN276	23.52N, 56.41E	MG672303	MG672349	MG672397	MG672328	MG672374
<i>O. jayakari</i>	IBES6074	23.18N, 57.42E	MG672308	MG672354	MG672402	MG672331	MG672379
<i>O. jayakari</i>	AO32	23.07N, 57.60E	MG672294	MG672340	MG672389	MG672319	MG672365
<i>O. jayakari</i>	AO79	23.09N, 57.69E	MG672295	MG672341	MG672390	MG672320	MG672366
<i>O. jayakari</i>	AO142	23.09N, 57.69E	MG672296	MG672342	MG672391	MG672321	MG672367
<i>O. jayakari</i>	CN3313	23.07N, 57.63E	MG672306	MG672352	MG672400		MG672377
<i>O. jayakari</i>	CN3729	23.00N, 57.70E	MG672307	MG672353	MG672401	MG672330	MG672378
<i>O. jayakari</i>	CN3763	22.93N, 59.13E	MG672301	MG672347	MG672395	MG672326	MG672372
<i>O. jayakari</i>	IBES1872	22.81N, 59.25E	MG672300	MG672346	MG672394	MG672325	MG672371
<i>O. jayakari</i>	UAE48	22.62N, 59.09E	MG672299	MG672345	MG672393	MG672324	MG672370
<i>O. cyanura</i> (North)	CN761 ^b	26.05N, 56.23E	MG672311	MG672357	MG672404	MG672334	MG672382
<i>O. cyanura</i> (North)	CN849 ^b	26.05N, 56.23E	MG672310	MG672356	MG672403	MG672333	MG672381
<i>O. cyanura</i> (North)	CN7682	25.76N, 56.13E	MG672315	MG672361	MG672408		MG672386
<i>O. cyanura</i> (North)	CN10369	25.76N, 56.13E	MG672314	MG672360	MG672407	MG672337	MG672385
<i>O. cyanura</i> (North)	CN10370	25.76N, 56.13E	MG672313	MG672359	MG672406	MG672336	MG672384
<i>O. cyanura</i> (North)	CN12086	25.10N, 56.07E	MG672318	MG672364	MG672410	MG672339	
<i>O. cyanura</i> (South)	CN706	24.61N, 56.24E	MG672316	MG672362	MG672409	MG672338	MG672387
<i>O. cyanura</i> (South)	CN2944 ^b	23.15N, 57.03E	MG672309	MG672355		MG672332	MG672380
<i>O. cyanura</i> (South)	AO054	23.11N, 57.66E	MG672317	MG672363			MG672388
<i>O. cyanura</i> (South)	CN7197 ^b	23.13N, 58.62E	MG672312	MG672358	MG672405	MG672335	MG672383
<i>Mesalina guttulata</i>	M17		KX296984 ^a	KX297187 ^a		KX297735 ^a	KX297361 ^a
<i>M. guttulata</i>	M18		KX296985 ^a	KX297188 ^a		KX297736 ^a	KX297362 ^a
<i>Acanthodactylus blanfordii</i>	A59		KX296907 ^a	KX297018 ^a		KX297577 ^a	KX297306 ^a
<i>A. blanfordii</i>	A290		KX296906 ^a	KX297017 ^a		KX297575 ^a	KX297305 ^a
<i>A. schmidti</i>	A51		KX296911 ^a	KX297020 ^a		KX297583 ^a	KX297308 ^a
<i>A. schmidti</i>	A228		KX296910 ^a	KX297019 ^a		KX297576 ^a	KX297307 ^a
<i>Gallotia caesaris gomerae</i>	DB19355		MF684894 ^a	MF684934 ^a	MF684983 ^a	AY152005 ^a	MF684960 ^a
<i>G. c. gomerae</i>	DB19375		MF684895 ^a	MF684935 ^a	MF684984 ^a	AF435101 ^a	MF684961 ^a
<i>G. c. caesaris</i>	DB19413		MF684896 ^a	MF684936 ^a	MF684985 ^a	AY152006 ^a	MF684962 ^a
<i>G. c. caesaris</i>	DB19470		MF684897 ^a	MF684937 ^a	MF684986 ^a		MF684963 ^a
<i>Atlantolacerta andreanskyi</i>	5015		JX462057 ^a		JX462200 ^a	JX485204 ^a	JX461803 ^a
<i>A. andreanskyi</i>	5058		JX462054 ^a		JX462196 ^a	JX485206 ^a	JX461816 ^a

^aSequences downloaded from GenBank.

^bSpecimens with vouchers.

2.3 | Phylogenetic analyses and divergence time estimation

To reconstruct the phylogenetic relationships of *Omanosaura* species, we performed haplotype network reconstructions based on

individual loci; maximum likelihood (ML) and Bayesian inference (BI) analyses based on the concatenated mitochondrial (mtDNA), and mitochondrial and nuclear (mt-nucDNA) datasets; and species tree based on the multispecies coalescent approach (Heled & Drummond, 2010). The best-fitting models of sequence evolution for the gene

partition and phased nuclear sequences were inferred with jMODELTEST 2.1.7 (Posada, 2008) under the corrected Akaike information criterion.

Haplotype networks were performed for the concatenated mtDNA genes and for the phased nucDNA genes *cmos* and *mc1r* using only full-length sequences. The haplotype reconstruction for *cmos* and *mc1r* was performed in PHASE 2.1 (Stephens & Scheet, 2005; Stephens, Smith, & Donnelly, 2001). The input files were converted in SEQPHASE (Flot, 2010; available at <http://seqphase.mpg.de/seqphase/>). PHASE was run three times with 100 iterations, phase probability of 70%, and remaining settings by default. Haplotype networks were inferred with median-joining algorithm in the software NETWORK 5.0.0.0. (available at <http://www.fluxus-engineering.com/sharenet.htm>), with default parameters.

Maximum likelihood analyses were performed with RAxML 7.4.2 (Stamatakis, 2006), using the graphical front-end RaxML GUI 1.3 (Silvestro & Michalak, 2012). ML searches were conducted with 10 random addition replicates using the GTR+G model of evolution with parameters estimated independently for each gene partition. To assess the node support, we performed 1,000 nonparametric bootstrap replicates.

Currently, no fossils of *Omanosaura* are known, preventing the use of internal calibration points to directly estimate the divergence time within the genus. Therefore, we used two strategies to estimate cladogenetic events within *Omanosaura* based on previous estimates on lacertid lizards by Carranza and Arnold (2012): (i) We applied the rate of evolution of 12S and *cytb* estimated by Carranza and Arnold (2012) based on seven biogeographic calibration points; and (ii) we calibrated our tree by applying directly the node prior for the split between *Gallotia caesaris caesaris* and *G. c. gomerae* used in Carranza and Arnold (2012) (Table 1). This allowed consistency of time estimates using priors on rates versus nodes (i.e., secondary versus primary calibrations) and including or excluding the biogeographic calibration centered on the Messinian salinity crisis event, which has been recently criticized (Hewitt, 2011; Mendes, Harris, Carranza, & Salvi, 2017). The BI and the divergence time estimation were performed in BEAST 1.8.0. (Drummond & Rambaut, 2007). We implemented the relaxed uncorrelated lognormal clock model for all genes because it overcomes the hard assumptions of the strict clock. We built the input file with evolutionary models, tree priors, and Markov Chain Monte Carlo

(MCMC) options using the BEAUTi utility included in the BEAST package. Models and prior specifications applied were as follows (otherwise by default): Nucleotide substitution and clock models were unlinked; models of nucleotide substitution as specified in Table 2; relaxed uncorrelated lognormal clock for all genes; Yule process of speciation; random starting tree; base substitution Uniform (0, 100); alpha Uniform (0, 10); ucl.d.mean of 12S Normal (initial: 0.00553, mean: 0.00553, stdev: 0.00128); ucl.d.mean of *cytb* Normal (initial: 0.0164, mean: 0.0164, stdev: 0.00317); clock rate of *nd4*, *cmos* and *mc1r* Uniform (0, 0.25); and operator kappa (2.0). The xml file was manually modified to set "Ambiguities = true" for the nuclear partitions to allow a full account of nuclear polymorphisms during phylogeny estimation. BEAST was run three times, with 100 million generations, sampling every 10,000 generations. The use of the Yule process of speciation prior requires only one sequence per species, whereas our concatenated alignments contained multiple samples per species. Therefore, to investigate the sensitivity of our estimates to the choice of tree prior, we performed an additional run applying the same settings as above but using only one representative sequence for each species.

In addition, we inferred a phylogeny using the species tree approach implemented in the *BEAST extension of the BEAST software because we found evidence for three evolutionary independent lineages (which were defined as "species" in *BEAST) within *Omanosaura* taxa analyzed (*O. jayakari*, *O. cyanura* North lineage, and *O. cyanura* South lineage, see Results). We used the mtDNA sequences and the phased alignments of the nuclear genes and their relative models of nucleotide evolution (Table 2). The settings applied in *BEAST for the species tree reconstruction were similar to the concatenated BEAST analyses, except the tree model of the mitochondrial genes 12S, *cytb*, and *nd4* was linked, as these genes are genetically linked. To calibrate the species tree, we applied the 12S and *cytb* substitution rates estimated by Carranza and Arnold (2012), as in the concatenated BEAST analysis. *BEAST was run three times with 200 million generations, sampling every 20,000 generations. All BEAST runs were performed on the CIPRES Science Gateway 3.3 (Miller, Pfeiffer, & Schwartz, 2010, at <http://www.phylo.org/>). Results were analyzed in TRACER 1.6 (Rambaut & Drummond, 2007), applying a 10% burn-in, to check for convergence and to ensure that all ESS parameters were higher than 200, as recommended in the software manual. LOGCOMBINER and

TABLE 2 Length of the alignment and of the amplicons, in base pairs, models of nucleotide substitution, number of intra- and interspecific variable positions (Var. pos), parsimony informative sites (Pars. Inf) for each gene fragment used in this study

Gene	Length		Model		Var. pos. <i>Omanosaura jayakari</i>	Var. pos. <i>O. cyanura</i>	Var. pos. <i>Omanosaura</i>	Pars. Inf
	Alignment	Amplicon	Unphased	Phased				
12S	387	435	GTR+I		1	27	47	41
<i>cytb</i>	425	460	GTR+I		8	76	103	93
<i>nd4</i>	851	900	GTR+G		12	120	185	144
<i>cmos</i>	353	390	HKY	TN93	1	1	3	2
<i>mc1r</i>	629	690	HKY+I	HKY+I	3	7	12	8

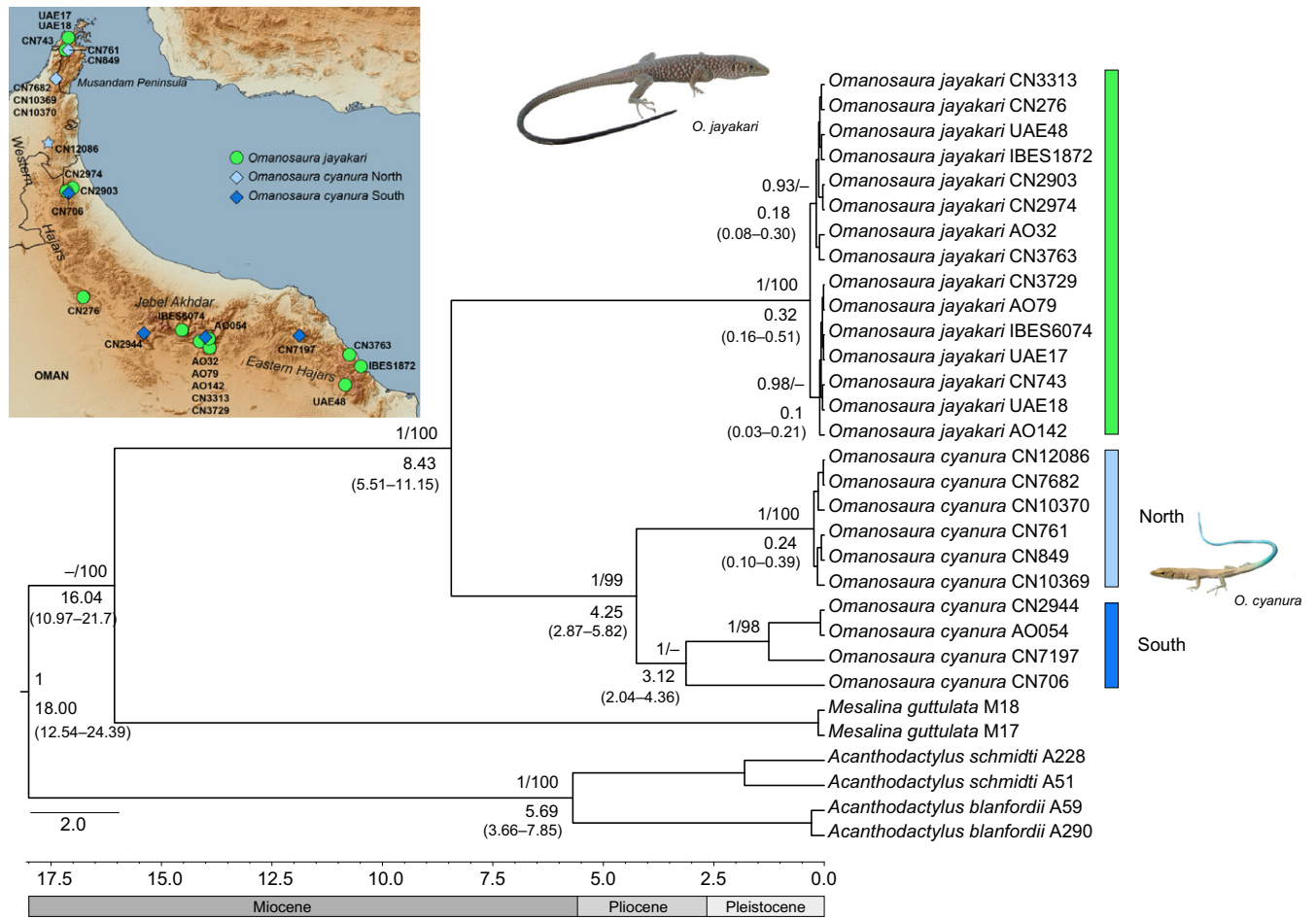


FIGURE 2 Bayesian tree topology of *Omanosaura* inferred using mtDNA (12S, *cytb*, and *nd4*) and nucDNA (*cmos* and *mc1r*) sequences. Bayesian posterior probability (left) and maximum likelihood bootstrap support (right) values are represented above nodes. Age estimates are represented below the relevant nodes and include the mean and, between brackets, the HPD 95% confidence interval (in million years). Photographs of *O. jayakari* by Salvador Carranza and of *O. cyanura* by Roberto Sindaco

TREEANNOTATOR (both included in the BEAST package) were used to calculate the maximum clade credibility (MCC) tree summarizing the posterior distribution of tree topologies and branch lengths. All trees were visualized in FIGTREE 1.4 (available at <http://tree.bio.ed.ac.uk/software/figtree/>).

3 | RESULTS

A total of 117 new sequences of *Omanosaura* were generated and deposited in GenBank; the accession numbers are reported in Table 1. The concatenated mt-nucDNA alignment of *Omanosaura* was

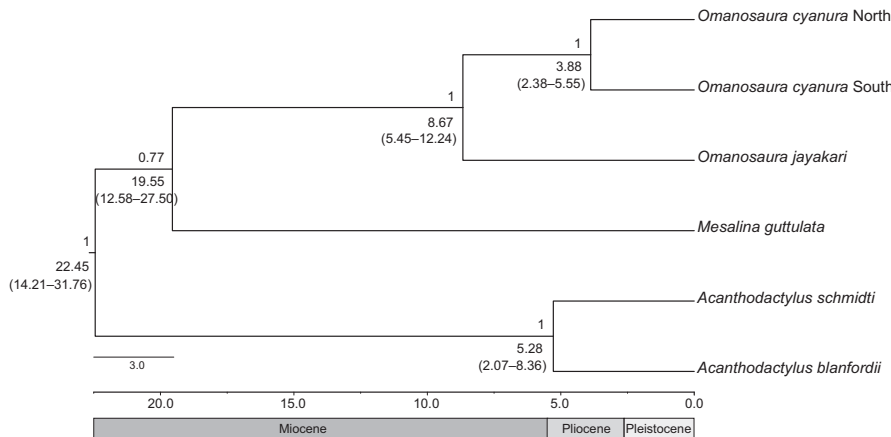


FIGURE 3 Species tree of *Omanosaura* lizards inferred from mitochondrial (12S, *cytb*, and *nd4*) and nuclear (*cmos* and *mc1r*) sequences using the multispecies coalescent approach. Bayesian posterior probabilities are represented above nodes, and the age estimates are represented below nodes and include the mean and, between brackets, the HPD 95% confidence interval (in million years)

2,648 bp long. The phi test did not find statistically significant evidence for recombination in the nuclear gene fragments ($p > .05$). The length of each gene fragment is reported in Table 2, along with the number of variable positions between and within *Omanosaura* species.

3.1 | Phylogenetic relationships within *Omanosaura*

The phylogenetic relationships inferred by the ML, BI, and species tree analyses are similar and present overall high levels of bootstrap support (BS) and Bayesian posterior probabilities (BPP) (Figures 2, 3, S1 and S2). The age estimates based on the substitution rates were similar between the concatenated BI tree (Figure 2) and the species tree (Figure 3) and are in agreement with the estimates obtained using the split between *G. c. caesaris* and *G. c. gomerae* as calibration (Figure S3); thus, we will refer only to the estimates of the concatenated BI tree (Figure 2). The Two *Omanosaura* species, *O. jayakari* and *O. cyanura*, are reciprocally monophyletic (BPP = 1, BS = 100; Figures 2 and 3), and the results from the time-calibrated tree (Figures 2, 3 and S3) indicate that they diverged around 8.4 million years ago (Ma) (95% HPD: 5.51–11.15). *Omanosaura jayakari* presents low levels of genetic diversity, with two very recent clades, recovered only in the BI analyses. On the other hand, *O. cyanura*

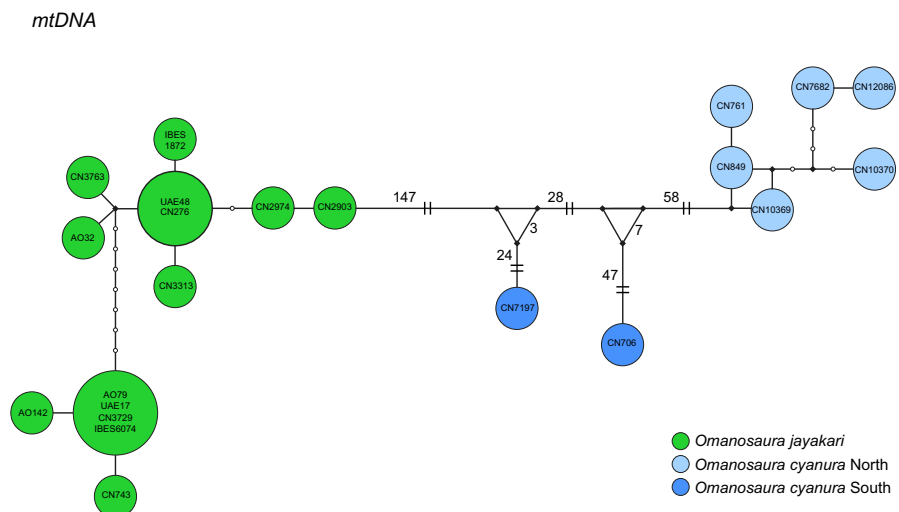
presents two highly divergent lineages (p -distance: 12S: 5%, *cytb*: 12%, *nd4*: 9%; Table 3) that are strictly associated with the geographic distribution of the samples (Figures 1 and 2). One lineage is distributed in the northern Hajar Mountains, *O. cyanura* North; and the second lineage is distributed in the remaining range of the Hajar Mountains, *O. cyanura* South. The divergence time between the two *O. cyanura* lineages is estimated at 4.25 Ma (95% HPD: 2.87–5.82). The northern lineage of *O. cyanura* presents low levels of genetic diversity, with diversification starting recently at 0.24 Ma (95% HPD: 0.10–0.41), while the southern lineage presents higher levels of diversity, with deeper intralinear divergence starting around 3.12 Ma (95% HPD: 2.04–4.36).

The same phylogenetic structure was recovered by the network analyses (Figures 4 and 5). The mtDNA network recovered the same clades described in the BI analyses (Figures 2, 4 and S2): the *O. jayakari* clade (showing low intra-clade differentiation) and the two lineages of *O. cyanura* (Figure 4). The same clades are also recovered by the two nuclear networks, with a sharp pattern of no allele sharing between species and between *O. cyanura* lineages. In particular, the nuclear gene *cmos* presents four unique haplotypes, each separated from neighboring haplotypes by one mutational step. The two lineages of *O. cyanura* have one private haplotype each,

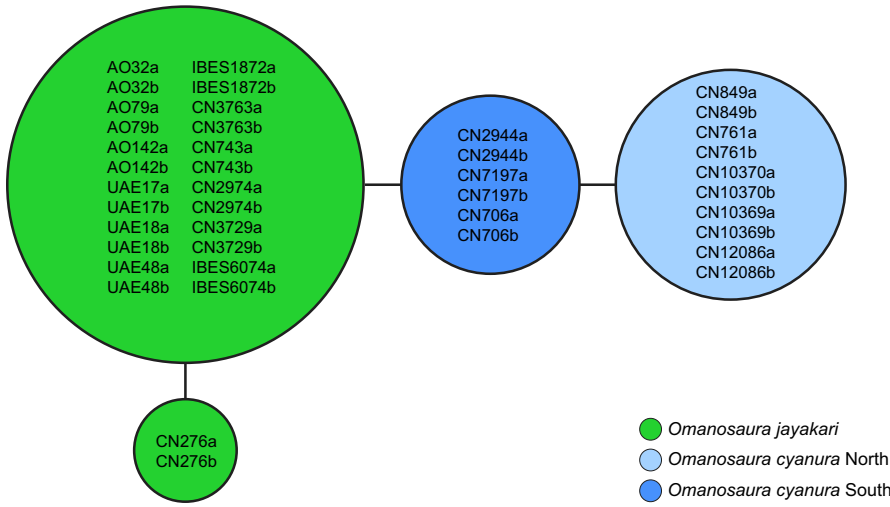
TABLE 3 Genetic pairwise p -distance values (d), range (minimum and maximum values), and standard error (SE) between and within *Omanosaura jayakari* and *O. cyanura* lineages for the mitochondrial genes 12S, *cytb*, and *nd4*

Between groups	12S		<i>cytb</i>		<i>nd4</i>	
	days (min–max)	SE	days (min–max)	SE	days (min–max)	SE
<i>O. jayakari</i> – <i>O. cyanura</i> North	0.085 (0.081–0.090)	0.014	0.166 (0.158–0.170)	0.017	0.155 (0.148–0.177)	0.014
<i>O. jayakari</i> – <i>O. cyanura</i> South	0.085 (0.081–0.092)	0.012	0.153 (0.148–0.160)	0.017	0.148 (0.143–0.161)	0.011
<i>O. cyanura</i> North– <i>O. cyanura</i> South	0.052 (0.047–0.060)	0.009	0.124 (0.0–0.141)	0.015	0.094 (0.0–0.112)	0.009
Within groups	12S		<i>cytb</i>		<i>nd4</i>	
	days (min–max)	SE	days (min–max)	SE	days (min–max)	SE
<i>O. jayakari</i>	0.0014 (0.0–0.003)	0.0014	0.0028 (0.0–0.0070)	0.0009	0.0059 (0.0–0.011)	0.0018
<i>O. cyanura</i> North	0.0 (0.0–0.0)	0.0	0.0050 (0.0–0.0090)	0.0023	0.004 (0.0–0.007)	0.0015
<i>O. cyanura</i> South	0.0201 (0.0–0.0340)	0.005	0.0635 (0.002–0.096)	0.0078	0.0989 (0.0989–0.099)	0.0101

FIGURE 4 Median-joining haplotype networks for *Omanosaura* species inferred from concatenated mtDNA (12S, *cytb* and *nd4*). Circles represent different haplotypes, and the size is proportional to sample frequency. Small diamonds represent median vectors. Mutations are represented by white circles or by two black bars with a number next to the line indicating mutational steps



cmos



mc1r

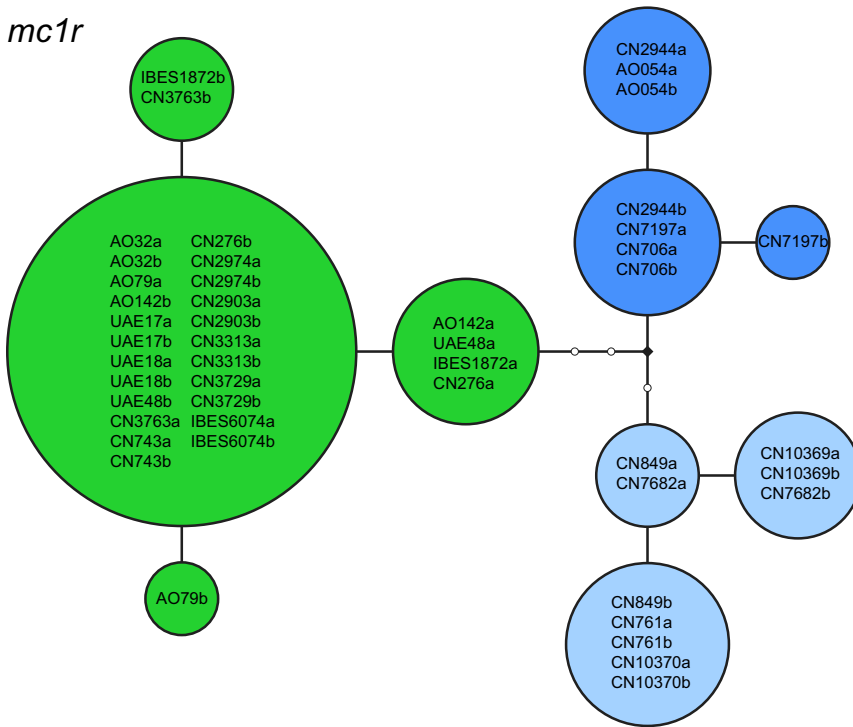


FIGURE 5 Median-joining haplotype networks for *Omanosaura* species inferred from nucDNA *cmos* and *mc1r*. Circles represent different haplotypes, and the size is proportional to sample frequency. Alleles are represented by the letters “a” and “b” after the sample code. Small diamonds represent median vectors, and mutations are represented by white circles

and the remaining two haplotypes are found in *O. jayakari* (Figure 5). The *mc1r* is more variable and presents 10 unique haplotypes, with a shallow level of diversity within *O. jayakari*, with four neighboring haplotypes separated by one mutation. The two lineages of *O. cyanura*, North and South, are recovered with three mutational steps between them and three haplotypes each (Figure 5).

4 | DISCUSSION

Our molecular assessment provides a clear phylogenetic and biogeographic pattern for the two *Omanosaura* species and allows the

identification of a sharp intraspecific partition of the observed genetic diversity within *O. cyanura*. Overall, inter- and intraspecific phylogenetic patterns are congruent between mtDNA and nucDNA, highlighting the importance of including fast-evolving nuclear genes to obtain a robust multilocus phylogeography below the genus level, in this case within *Omanosaura*.

The divergence time between the two *Omanosaura* species estimated in this study, approximately 8 Ma, is much more recent than the estimated 35 Ma from a recent squamate timetree by Zheng and Wiens (2016). Such difference is not limited to this study and seems to present a general discordance between divergence time estimates obtained in the squamate timetree and in studies focused

on terminal groups of squamates such as lacertids (Kapli et al., 2015; Mendes et al., 2016; Tamar, Carranza et al., 2016), amphisbaenians (Albert, Zardoya, & Garcia-Paris, 2007; Sampaio, Harris, Perera, & Salvi, 2014), geckos (Carranza & Arnold, 2012; Gamble et al., 2011; Šmíd et al., 2013), skinks (Carranza, Arnold, Geniez, Roca, & Mateo, 2008; Pereira & Schrago, 2017), and snakes (Chen, Lemmon, Lemmon, Pyron, & Burbrink, 2017; Daza, Smith, Páez, & Parkinson, 2009). This discordance might be attributed to the differences in the calibration methods—fossils of higher taxa in Zheng and Wiens (2016) versus calibration based on rates or recent nodes in other studies. It might also be caused by the methodological approximations in phylogenetic and divergence time estimates required by analyses with thousands of taxa as the supermatrix approach applied by Zheng and Wiens (2016) (see Mendes et al. (2016) for a comparison between phylogenetic estimates based on the supermatrix and the multispecies coalescent approaches in lacertids). The tendency to overestimate of divergence times by Zheng and Wiens (2016) is exemplified by the observation that, according to their study, the divergence within the endemic Canary Islands' *Gallotia* is older than the appearance of the Canary Islands.

Despite sharing the distribution range and being found in sympatry, the two morphologically distinct species of *Omanosaura* present contrasting levels of intraspecific genetic differentiation (Figures 2, 4 and 5, Table 3) both in the mtDNA (Figures 2, 4 and S2, Table 3) and in the nucDNA genes *cmos* and *mc1r* (Figures 2 and 5). The much larger and robust *O. jayakari* presents fairly homogeneous low levels of genetic variation across its distribution range, with two very recent clades recovered by the mtDNA data, which diverged by the end of the Middle Pleistocene, around 0.3 Ma. Such low levels of genetic diversity could tentatively be related to the body size and the ecology of *O. jayakari* (e.g., Gaston & Blackburn, 1996; Meiri, 2008). The relatively large size of these lizards, together with a generalist feeding and habitat traits (Gardner, 2013), may confer them with a higher dispersal ability, hence making them less susceptible to mild historic climatic variation and thus to structure in distinct phylogeographic groups. In contrast, the small and delicately built *O. cyanura* presents two very well differentiated lineages that diverged in the Pliocene, more than 4.25 Ma. The mtDNA genetic distance between *O. cyanura* lineages is very high (12S: 5%, *cytb*: 12%, *nd4*: 9%; Table 3). Similar levels of genetic distances have been reported within the Eremiadini species *Acanthodactylus schreiberi* (12S and *cytb*; Tamar, Carranza, Sindaco, Moravec, & Meiri, 2014), which is considered a species complex. Unfortunately, there are not sufficient museum vouchers or photographic material to properly assess morphological differentiation between the two *O. cyanura* lineages, especially from the southern lineage. The inclusion of a genetic sample from the type locality in Wadi Shawkah, UAE (see Figure 1; Arnold, 1972), shows that the holotype of *O. cyanura* is likely to belong to the northern lineage. Both paratypes fall within the distribution range of the northern lineage, one (BM1972.710) is from Wadi Qidah (Qadah in GoogleEarth), near Qasab (26.18N 56.22E), and the other (BM1971.1292) is from Wadi Siji, near Masafi (25.31N 56.15E). Although the paratypes could not be genetically assigned to

any of the two lineages, their distribution indicates that, similar to the holotype, they belong to the northern lineage of *O. cyanura*. Therefore, in a future taxonomical assessment of this species, the northern lineage would retain the name *O. cyanura*. However, in order to perform an integrative and comprehensive taxonomic assessment of this species, it will be necessary to collect additional morphological and ecological data across the distribution range of *O. cyanura* in the Hajar Mountains, including other areas within the geographic gap between the two lineages.

The distribution of the two lineages of *O. cyanura* presents a clear geographic association with different regions within the Hajar Mountains, with a lineage mostly restricted to the northernmost part of the Hajar Mountains and a southern lineage occurring in the remaining part of the western Hajars, the Jebel Akhdar, and the eastern Hajars (Figure 2). The northern lineage shows little genetic structure, with a very recent diversification starting around 0.24 Ma, whereas the southern lineage shows higher levels of genetic diversity, with an ancient split (3.12 Ma) between the northernmost sample (CN706) of the southern lineage and the samples located in the Jebel Akhdar and the eastern Hajars (Figure 2). The inclusion of more samples between these sublineages of the southern *O. cyanura* lineage would allow to better locate the geographic break between them.

The main phylogeographic partition between the different lineages observed within *O. cyanura* strictly matches the biogeographic pattern recovered by previous studies on reptiles of the genera *Asaccus* (Carranza et al., 2016; Simó-Riudalbas, Tarroso, et al., 2017), *Trachydactylus* (de Pous et al., 2016), and *Ptyodactylus* (Metallinou et al., 2015; Simó-Riudalbas, Metallinou, et al., 2017). Historically, knowledge of biodiversity patterns was not equally distributed across the Hajar Mountains. The Jebel Akhdar, which includes the highest peaks in the Hajar Mountains, and the eastern Hajars have received more scientific attention over the last decades and have recently been shown to be areas with maximum genetic diversity for the reptile genera *Asaccus* (Simó-Riudalbas, Tarroso, et al., 2017), *Hemidactylus* (Carranza & Arnold, 2012), *Pristurus* Rüppell, 1835 (Badiane et al., 2014), and *Trachydactylus* (de Pous et al., 2016). Comparatively, less research effort has been devoted to the northernmost part of the Hajar Mountains and especially to the Musandam Peninsula until very recently, when the discovery of high genetic diversity and new species of other reptile genera such as *Ptyodactylus* (Metallinou et al., 2015; Simó-Riudalbas, Metallinou, et al., 2017) and *Asaccus* (Carranza et al., 2016) highlighted this area as a hot spot of diversity within the Hajar Mountains. The processes that have shaped the distribution patterns of taxa in the Hajar Mountains remain unclear, although a relation with geological and climatic events could be suggested. The Hajar Mountains have had a complex geological history dating back to 300 Ma, but the uplift into a mountain range started around 30 Ma with the opening of the Gulf of Aden (Bosworth, Huchon, & McClay, 2005; Glennie, 2006; Laughton, 1966), and it probably rose to a high mountain range in the last 4–6 Ma, during an intense plate tectonic phase that affected Oman (Glennie, 2006). The diversification of the *Omanosaura* species might have been influenced by the uplift of the mountain range,

particularly the divergence between the two *O. cyanura* lineages, which seems to coincide with the most recent part of the final uplift of these mountains, around 4 Ma. Climatic events might also have influenced the diversification of *Omanosaura* lineages, as the high elevation areas of the Hajar Mountains, which harbor the highest levels of genetic diversity of *O. cyanura* among many other taxa—the Musandam Peninsula and the Jebel Akhdar massif—could have acted as refuge and center of diversification for these reptile groups during periods of climatic changes.

The distribution of the two *Omanosaura* species as currently assessed by the IUCN Red List of Threatened Species (Soorae, Wilms, & Al Rasbi, 2012) is more restricted than our sampling locations and records for *Omanosaura* shown by Gardner (2013) and Carranza et al. (2018) (*O. cyanura* CN706 and *O. jayakari* UAE17, UAE18, CN743 and CN276; Figure 1), and reflect record gaps, rather than the true absence (Gardner, 2013). This can be associated with (i) the low number of expeditions to the Hajar Mountains until very recently and the inaccessibility of some of the areas, (ii) the lack of scientific attention given to this genus, and also (iii) with the general elusive nature of *O. cyanura*, which makes it particularly difficult to see and capture. Further studies are needed to complete the diversity inventory of this region and to better understand the association of the current biodiversity patterns with past geologic and climatic events. Finally, the results of this study highlight the importance of biodiversity assessments in mountainous regions characterized by high endemism but which are difficult to access.

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SUPPORTING INFORMATION

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