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Cutting the Gordian Knot: Phylogenetic and ecological diversification of the *Mesalina brevirostris* species complex (Squamata, Lacertidae)

Jiří Šmíd[1,2] | Jiří Moravec[1] | Václav Gvoždík[1] | Jan Štundl[1,3] | Daniel Frynta[3] | Petros Lymberakis[4] | Paschalia Kapli[5] | Thomas Wilms[6] | Andreas Schmitz[7] | Mohammed Shobrak[8] | Saeed Hosseinian Yousefkhani[9] | Eskandar Rastegar-Pouyani[10] | Aurora M. Castilla[11] | Johannes Els[12] | Werner Mayer[13,†]

[1]Department of Zoology, National Museum, Prague, Czech Republic

[2]South African National Biodiversity Institute, Claremont, Cape Town, South Africa

[3]Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic

[4]Natural History Museum of Crete – University of Crete, Herakleio, Greece

[5]The Exelixis Lab, Scientific Computing Group, Heidelberg Institute for Theoretical Studies, Heidelberg, Germany

[6]Allwetterzoo Münster, Münster, Germany

[7]Department of Herpetology and Ichthyology, Natural History Museum of Geneva, Geneva, Switzerland

[8]Biology Department, Faculty of Science, Taif University, Taif, Saudi Arabia

[9]Young Researchers and Elite Club, Islamic Azad University, Shirvan, Iran

[10]Department of Biology, Hakim Sabzevari University, Sabzevar, Iran

[11]Qatar Environment and Energy Research Institute, Hamad Bin Khalifa University (Qatar Foundation), Doha, Qatar

[12]Breeding Centre for Endangered Arabian Wildlife, Environment and Protected Areas Authority, Sharjah, United Arab Emirates

[13]Natural History Museum, Vienna, Austria

Correspondence
Jiří Šmíd, Department of Zoology, National Museum, Prague, Czech Republic.
Email: jirismd@gmail.com

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Mesalina are small lacertid lizards occurring in the Saharo-Sindian deserts from North Africa to the east of the Iranian plateau. Earlier phylogenetic studies indicated that there are several species complexes within the genus and that thorough taxonomic revisions are needed. In this study, we aim at resolving the phylogeny and taxonomy of the *M. brevirostris* species complex distributed from the Middle East to the Arabian/Persian Gulf region and Pakistan. We sequenced three mitochondrial and three nuclear gene fragments, and in combination with species delimitation and species-tree estimation, we infer a time-calibrated phylogeny of the complex. The results of the genetic analyses support the presence of four clearly delimited species in the complex that diverged approximately between the middle Pliocene and the Pliocene/Pleistocene boundary. Species distribution models of the four species show that the areas of suitable habitat are geographically well delineated and nearly allopatric, and that most of the species have rather divergent environmental niches. Morphological characters also confirm the differences between the species, although

[†]Author deceased August 2015.

sometimes minute. As a result of all these lines of evidence, we revise the taxonomy of the *Mesalina brevirostris* species complex. We designate a lectotype for *Mesalina brevirostris* Blanford, 1874; resurrect the available name *Eremias bernoullii* Schenkel, 1901 from the synonymy of *M. brevirostris*; elevate *M. brevirostris microlepis* (Angel, 1936) to species status; and describe *Mesalina saudiarabica*, a new species from Saudi Arabia.

1 | INTRODUCTION

Lacertid lizards (Lacertidae) represent the dominant and conspicuous group of reptiles in the Western Palearctic. The family currently consists of 323 species in 42 genera (Uetz & Hošek, 2017). Molecular phylogenetic studies unanimously support the family being divided into two subfamilies, Gallotiinae and Lacertinae, with the latter further divided into two tribes, Lacertini and Eremiadini (Arnold, Arribas, & Carranza, 2007; Fu, 2000; Kapli, Poulakakis, Lymberakis, & Mylonas, 2011). Lacertini are distributed mainly in Eurasia with the core of their distribution around the Mediterranean, while Eremiadini are mostly African and Asian. There are two main clades within Eremiadini that have almost exclusive geographic ranges and that have been accordingly termed the Ethiopian (i.e., south of the Sahara) and Saharo-Eurasian clades (Mayer & Pavlicev, 2007).

Mesalina Gray, 1838 is part of the Saharo-Eurasian clade and with its 14 species it is the third most species-rich genus of Eremiadini after *Acanthodactylus* and *Eremias*. The distribution of the genus spans from western Africa throughout the arid zone of the North Africa, Arabia and as far as eastern India. Systematics of the genus has been addressed using both morphological and genetic data. Arnold (1986a) divided the genus into two groups on the basis of hemipenial morphology: one group formed by *M. martini* (Boulenger, 1897), *M. olivieri* (Audouin, 1829), *M. pasteuri* (Bons, 1960) and *M. simoni* (Boettger, 1881) with relatively short hemipenes with less developed armature; and a second group formed by *M. adramitana* (Boulenger, 1917), *M. ayunensis* Arnold, 1980; *M. balfouri* (Blanford, 1881), *M. brevirostris* Blanford, 1874; *M. guttulata* (Lichtenstein, 1823), *M. rubropunctata* (Lichtenstein, 1823) and *M. watsonana* (Stoliczka, 1872) with relatively long hemipenes with elongated armature and unfolded basal parts. He subsequently divided the second group into four subgroups based on further detailed examinations of male copulatory organs: (i) *M. brevirostris*; (ii) *M. rubropunctata*; (iii) *M. adramitana* and *M. ayunensis*; (iv) *M. guttulata* and *M. watsonana* (Arnold, 1986b).

Several molecular phylogenetic studies have also contributed to our understanding of the relationships within and among *Mesalina* species since Arnold's (1986a, 1986b) morphological works. While the studies of Joger and Mayer (2002), Kapli et al. (2008), Šmíd and Frynta (2012), and Abukashawa and Hassan (2016) were all rather narrowly focused on a certain species or species group and always used only mitochondrial data, the recent work by Kapli et al. (2015) was the first to have almost all species included (12 of 14) and which besides mitochondrial markers used also one nuclear gene. The consensus of these studies is that the easternmost species, *M. watsonana*, is sister to the rest of the genus from which it separated ca. 15.9–23.2 million years ago (Myr) depending on the calibration approach used. The rest of the genus is divided into several groups that approximately correspond to Arnold's division. However, some of the species have been shown to exhibit pronounced genetic differentiation and they may, in fact, represent complexes of cryptic species. For instance, *M. pasteuri* is polyphyletic, *M. guttulata* is formed by at least three deeply diverged clades and is paraphyletic with respect to *M. bahaeldini* Segoli, Cohen, & Werner, 2002 (Kapli et al., 2015). Already Arnold (1980, 1986c) noticed the existence of two undescribed species (labelled as *Mesalina* sp. A and *Mesalina* sp. B) from the mountains (sp. A) and dry flat plains (sp. B) of southern and south-western Arabia, yet he (and nobody else) never described them. Other morphologically indeterminable forms nested within or close to *M. pasteuri* and *M. olivieri* have been recorded from Mauritania and Libya, respectively (Kapli et al., 2015). All these cases clearly indicate that the taxonomy of *Mesalina* is far from sorted and call for necessary taxonomic revisions.

Mesalina brevirostris is an example of a widely distributed and morphologically very plastic species with a rich history of taxonomic and nomenclatural adjustments. According to its very brief original description, the species originates from "insula Tumb dicta sinus Persici, et ad Kalabagh in regione Punjab Indiae" and is characterised by 12 longitudinal series of ventral scales and short head (Blanford, 1874). Two years later, Blanford (1876) completed the description and remarked that he only obtained the species on the island of Tumb, whereas the Kalabagh specimen was sent to him by Dr Stoliczka, who considered it to be *Eremias watsonana*. In his seminal catalogue, Boulenger (1887) also placed the species under the genus *Eremias*. He (Boulenger, 1921) also placed *Eremias bernoullii*, a species described by Schenkel (1901) from Palmyra, Syria, into the synonymy of *E. brevirostris*.

Angel (1936) recognised two forms of *E. brevirostris* in Syria—the widely distributed nominotypical one and a new subspecies, *E. brevirostris microlepis*, which differed in having a higher number of dorsal scales and subdigital lamellae, and which he described on the basis of a single specimen from "Haouarine" (=Hawarin in W Syria). Schmidt (1939) attempted to restrict the type locality of *E. brevirostris* to "Kalabagh, Punjab", however, he did not designate a lectotype. Eventually, Haas and Werner (1969) described the subspecies *E. brevirostris fieldi* from SW Iran showing lower counts of dorsal and gular scales and subdigital lamellae.

The knowledge of the distribution of *M. brevirostris* has since been steadily improving with several important range extensions reported (Anderson, 1999; Arnold, 1986c; Baha El Din, 2006; in den Bosch, 2001; Hoofien, 1957; Ilgaz, Baran, Kumlutaş, & Avci, 2005; Kamali, 2013; Kumlutaş, Taskavak, Baran, Ilgaz, & Avci, 2002; Ross, 1988; Werner, 1971). On the other hand, recognition of the subspecies and their geographic delimitation have often been problematic. Whereas the majority of authors accept the validity of *M. b. fieldi*, the validity of *M. b. microlepis* has been a subject of debate. For instance, Haas (1957) did not find the subspecies *microlepis* sufficiently established, while Werner (1971) argued that it was a valid taxon. The subspecific name *microlepis* was later used by some authors for populations of *M. brevirostris* from western Syria and Jordan (e.g., Bischoff, 1991; Disi, 1991, 1996) and some even applied it for the Arabian, Iraqi and Iranian populations (Disi & Amr, 1998). Contrary to this, Anderson (1999) concluded that the subspecies have no zoogeographic significance.

The existence of two morphologically different forms of *M. brevirostris* was first mentioned from Jordan (Disi, Modrý, Necas, & Rifai, 2001) and Moravec (2004) later confirmed pronounced morphological variation between populations from Syria, Jordan and Iraq. This was further supported by genetic data that also indicated the presence of two deeply divergent lineages of *M. brevirostris* from Syria and the United Arab Emirates (UAE; Mayer, Moravec, & Pavlicev, 2006). Subsequent phylogenetic studies (Kapli et al., 2008, 2015) confirmed these results and, moreover, uncovered yet another lineage of *M. brevirostris* in western Saudi Arabia. Considering the above findings it is obvious that *M. brevirostris* represents a species complex whose distribution, phylogeny, taxonomy and nomenclature require a thorough revision.

In this study, we analyse multiple lines of evidence in order to rectify the taxonomy of the species complex. We use multilocus data from three mitochondrial (mtDNA) and three nuclear (nDNA) gene fragments and reconstruct the phylogenetic relationships in a multispecies coalescent framework. Furthermore, we develop predictive models of potential distributions for all identified lineages and test their ecological similarity. Finally, we examine morphological characters to assess morphological differentiation. Based on our findings, we revise the taxonomy and nomenclature of the species complex. One existing subspecies is elevated to species level, one name is resurrected from the synonymy of *M. brevirostris*, a lectotype of *M. brevirostris* is designated, and a new species is described from western Saudi Arabia.

2 | MATERIAL AND METHODS

2.1 | Sampling, DNA extraction and sequencing

We used a total of 61 samples representing all recognised (including synonymised) subspecies of *Mesalina brevirostris*. New sequences were produced for 42 samples that originated from Bahrain (1 sample), Egypt (1), Iran (4), Iraq (2), Jordan (7), Lebanon (3), Qatar (2), Saudi Arabia (2), Syria (19) and the UAE (1). Sequences of additional 19 samples available in GenBank and originating from Kuwait (5), Saudi Arabia (8), Syria (5) and the UAE (1) were added to the data set. The sampling localities are shown in Figure 1. Representatives of five other *Mesalina* species (*M. adramitana*, *M. balfouri*, *M. bahaeldini*, *M. kuri* Joger & Mayer, 2002; *M. rubropunctata*; one of each) were used as outgroups for some of the phylogenetic analyses (see below). Sample codes, museum voucher codes, localities and GenBank accession numbers are listed in Table S1. Table S2 gives acronyms of collections that provided tissue samples.

Genomic DNA was extracted from ethanol-preserved tissue samples using Geneaid Extraction Kit. We PCR-amplified and sequenced both strands of three mtDNA and three nDNA gene fragments; these were as follows: 12S rRNA (*12S*), 16S rRNA (*16S*), cytochrome b (*cytb*) from the mtDNA and the melano-cortin 1 receptor (MC1R), beta-fibrinogen intron 7 (β-*fibint7*) and oocyte maturation factor MOS (*c-mos*) from the nDNA. The *cytb* was amplified with two pairs of primers depending on the amplification success; one pair for the complete gene and one for 425 bp at the beginning of the gene. The primers, PCR conditions and fragment lengths are detailed in Table S3. Chromatograms were checked by eye, and contigs were assembled and edited in Geneious v.6 (Kearse et al., 2012). Heterozygous positions were identified based on the presence of two peaks of approximately equal height for a single nucleotide site in both strands (assessed by eye and Heterozygote plugin implemented in Geneious) and were coded according to the IUPAC ambiguity codes.

All genes were aligned independently in MAFFT v.7 (Katoh & Standley, 2013). For the alignments of *12S* and *16S,* we used the Q-INS-I strategy that considers the secondary structure of RNA, while the "auto" strategy was used for all the other genes. Alignments of protein-coding genes (*cytb*, MC1R, *c-mos*) were translated into amino acids using appropriate genetic codes, and no stop codons were detected. To remove poorly aligned gap regions of the *12S*, *16S* and β-*fibint7,* we used Gblocks

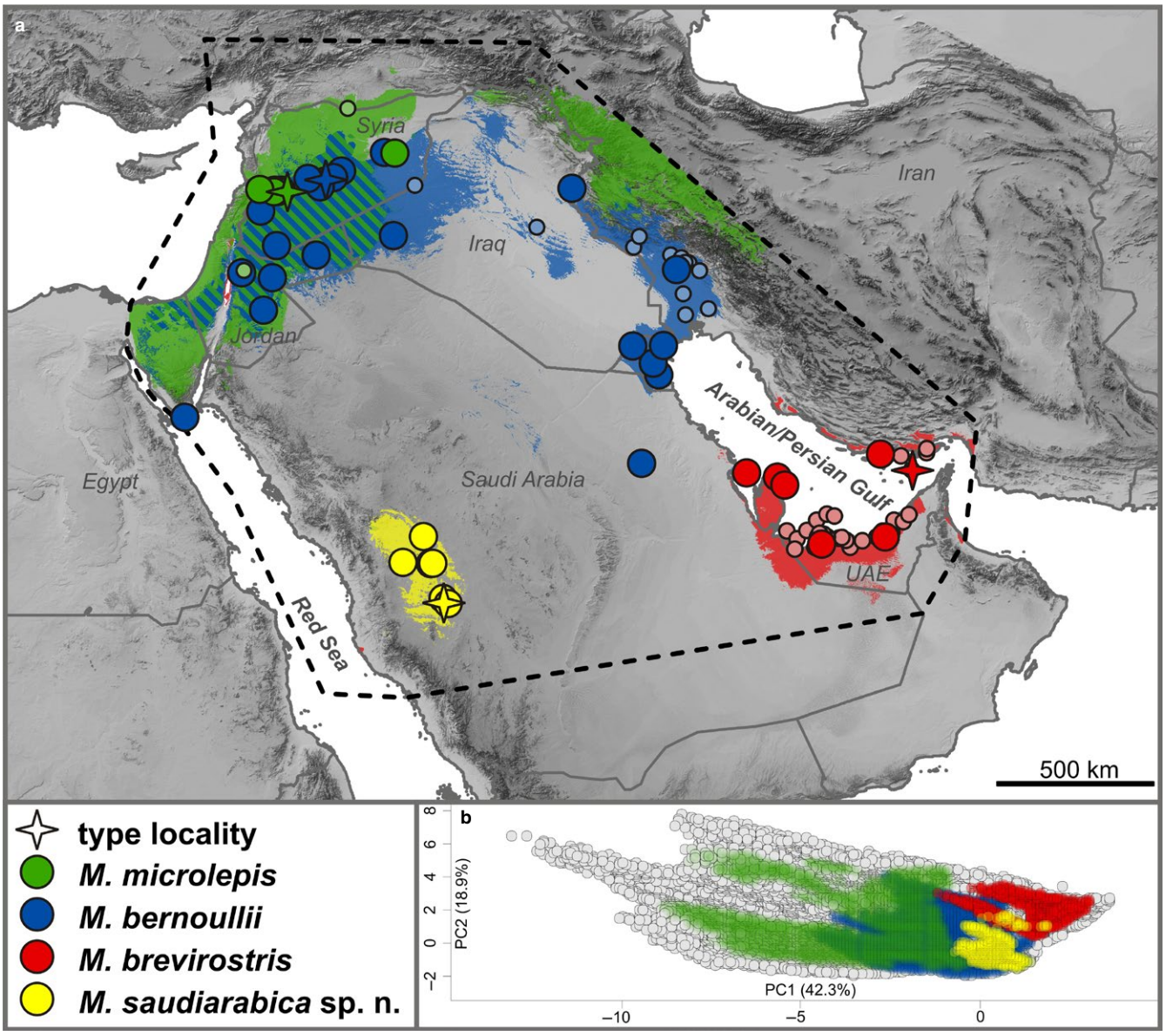

FIGURE 1 (a) Map of the Arabian Peninsula showing localities of material examined in this study. Large circles indicate material used for the phylogenetic analyses; smaller paler circles indicate additional records used for the SDM. Dashed line delimits the background for developing the models. Potential distributions of *Mesalina bernoullii*, *M. brevirostris*, *M. microlepis* and *M. saudiarabica* sp. n. based on the MTSS threshold are shown in corresponding colours. The green and blue striped region shows the overlap of the potential distributions of *M. bernoullii* and *M. microlepis*. (b) Plot of the environmental space of the study background and its respective parts occupied by the four species as identified by the PCA. The first two principal components and their contributions to general variation are shown. The species environmental spaces are based on their modelled distributions. Names of taxa correspond to changes proposed in this study

(Castresana, 2000) under the less stringent options (Talavera & Castresana, 2007). Uncorrected genetic distances (*p* distances; pairwise deletion) were calculated in MEGA6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013).

2.2 | Phylogenetic analyses

We inferred the evolutionary history of the *Mesalina brevirostris* species complex using three different phylogenetic approaches.

2.2.1 | Concatenated mtDNA data

Bayesian Inference (BI) analysis was performed with the three mtDNA genes concatenated. The data were partitioned by gene, and the most appropriate model of nucleotide evolution for each partition was identified using the Bayesian information criterion (BIC) in jModelTest v.2.1 (Darriba, Taboada, Doallo, & Posada, 2012) as follows: *12S* – K80 + I, *16S* – GTR + I, *cytb* – HKY + I. The BI analysis was performed using BEAST v.1.7.5 (Drummond & Rambaut, 2007;

Drummond, Suchard, Xie, & Rambaut, 2012). The outgroups were included in this analysis. Substitution and clock models were unlinked across partitions, and base frequencies of all partitions were set to empirical. HKY model of nucleotide evolution was chosen for the *12S* partition as the closest alternative to K80 available in BEAST. We applied an independent relaxed uncorrelated lognormal clock prior for each partition and the Yule tree prior. Other prior settings were as follows (otherwise by default): GTR base substitution prior uniform (lower: 0, upper: 100), Yule process tree prior with birth rate uniform (0, 1,000). Three individual runs were ran each of 10^8 generations with parameters logged every 10^5 generations. Posterior trace plots, stationarity, convergence and effective sample size (ESS) of all parameters were inspected in Tracer v.1.5 (Rambaut & Drummond, 2007). Tree files were combined in LogCombiner v.1.7.5 with 10% of sampled trees in each run discarded as burn-in, and maximum clade credibility (MCC) tree was identified using TreeAnnotator v.1.7.5 (both programs are part of the BEAST package).

The MCC tree that resulted from this analysis was further used for estimating species boundaries by the general mixed Yule coalescent (GMYC) method (Pons et al., 2006). The GMYC method uses single locus data to identify boundaries between putative species by determining the shift from interspecific (speciation) to intraspecific (coalescence) evolutionary processes on an ultrametric tree. GMYC species delimitation was conducted using the "splits" package in R (Ezard, Fujisawa, & Barraclough, 2009) under the single-threshold method. Outgroups were retained in the analysis as recommended for small data sets of up to five species (Talavera, Dincă, & Vila, 2013).

2.2.2 | Species-tree and divergence time estimation

We further estimated the phylogeny of the complex by means of a coalescent-based species-tree estimation using *BEAST (Heled & Drummond, 2010). The three nDNA genes were phased prior to the analysis with PHASE v.2.1 software (Stephens, Smith, & Donnelly, 2001) with the probability threshold set to .7 and SeqPHASE (Flot, 2010) employed to convert input files. The outgroups were not included in the phase analysis because the presence of distant taxa can affect the phasing results. No a priori outgroup was also needed for the species-tree analysis because BEAST samples the root position from the posterior along with the rest of the tree topology (Drummond & Bouckaert, 2015). The data set was pruned to contain only specimens with as many genes sequenced as possible. The samples used are indicated in Table S1. In total, 19 specimens (38 phased alleles) were included in this analysis. We used the putative species identified by GMYC as the "species" that need to be defined for the species-tree estimation. GMYC identified four putative species and to remain consistent throughout the text of this study, we use their taxonomic names proposed here: *M. microlepis*, *M. bernoullii*, *M. brevirostris sensu stricto* (s. s.) and the new Saudi species which is described below. Substitution, clock and tree models were unlinked across all partitions. Base frequencies were set to empirical and the ploidy type of the mtDNA genes to mitochondrial. Appropriate substitution models identified using the BIC in jModelTest were as follows (closest alternative available in BEAST in brackets): *12S* - K80 + I (HKY + I); *16S* – GTR + I; *cytb* – HKY + I; MC1R – HKY + I; β-*fibint7* – HKY; *c-mos* – JC (HKY). Given that BEAST assumes no recombination within loci (Heled & Drummond, 2010) we tested all nDNA loci for recombination using all available tests implemented in RDP4 (Martin et al., 2010), and no recombination was detected. To test whether the genes studied evolve in a clock-like manner (strict clock) we used a likelihood-ratio test (LRT) implemented in MEGA6 (Tamura et al., 2013). The strict-clock model was rejected at a 5% significance level for all of them, we therefore selected relaxed uncorrelated lognormal clock prior for all partitions. To account for variability in heterozygous positions that were still present in the alignments of all nDNA genes after phasing we removed the operator on kappa (HKY transition-transversion parameter) gave it an initial value of 0.5 and modified manually the.xml file by changing the "useAmbiguities" parameter to TRUE. We run three individual runs for 10^9 generations with parameters logged every 10^6 generations. Other settings were specified, logs inspected and MCC tree produced as described above for the analysis of mtDNA data.

Simultaneously with estimating the species-tree topology we estimated the divergence times. We used priors on the global substitution rates of the *12S* and *cytb* regions that were calculated based on a calibrated phylogeny of the lacertid genus *Gallotia* from the Canary Islands (Carranza & Arnold, 2012; Cox, Carranza, & Brown, 2010). We set a lognormal prior distribution for the ucld.mean parameter with mean value = 0.00553 for the *12S* and 0.0164 for the *cytb* and a uniform prior distribution for the ucld.stdev parameter with mean value = 0.00128 for the *12S* and 0.00317 for the *cytb*. The ucld.mean parameter was estimated with a lognormal prior distribution with initial value = 1.0, mean = 0.1, *SD* = 0.5 for the *16S* and initial value = 0.1, mean = 0.1, *SD* = 1.0 for the nDNA genes.

2.2.3 | Haplotype networks

We used haplotype (allele) networks to explore the genealogical relationships within *Mesalina brevirostris* complex in the three nDNA loci studied. Alignments were phased as described above. Networks were constructed using the statistical parsimony algorithm (Templeton, Crandall, & Sing,

1992) implemented in TCS v.1.21 (Clement, Posada, & Crandall, 2000) with 95% connection limit and were visualised with tcsBU (dos Santos, Cabezas, Tavares, Xavier, & Branco, 2015).

2.3 | Species distribution modelling

We used the maximum entropy approach implemented in Maxent v.3.3 (Phillips, Anderson, & Schapire, 2006) to generate species distribution models (SDM) of the four putative species identified by GMYC and to assess the environmental variables contributing to their distribution. Maxent has been shown to provide robust performance even with a relatively small number of occurrence samples (Elith et al., 2006), and it was, therefore, an appropriate method for our data set. Each species was represented by all samples that were used for the genetic analyses. Additional records that could be unambiguously assigned to species based on morphology and/or geographic origin were assembled from literature (Angel, 1936; Gardner, 2013; Haas & Werner, 1969; Kumlutaş et al., 2002; Šmíd et al., 2014) and from the NMP collection. Given the uncertainty of the position of the contact zone between two of the species in coastal Iran we did not include records from the Bushehr Province (Šmíd et al., 2014). The final number of unique localities was 7 for *M. microlepis*, 39 for *M. bernoullii*, 50 for *M. brevirostris* s. s. and 8 for the Saudi species. The background defined for developing the models was chosen to encompass the presumed range of all the species of the complex (Figure 1; Sindaco & Jeremčenko, 2008) with the exception being the Pakistani and extreme eastern Iranian parts of the range. They were not included for their geographic isolation and because we believe them to be an eastern extension of the range of *M. brevirostris* s. s., although we do not have any direct genetic or morphological evidence for this assumption. Moreover, no georeferenced localities from Pakistan are available in public databases (GBIF, HerpNet) or, to our knowledge, in the literature.

Nineteen present-day bioclimatic variables were downloaded from the WorldClim database v. 1.4 (www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at a resolution of 30 arc seconds (nearly 1 × 1 km). We created a slope layer from the original WorldClim altitude data using ArcGIS v.10.0 and included it among the bioclimatic variables. Although it is not a widely used environmental variable for SDM, it has proven to be informative for predicting the distribution of other *Mesalina* species (Hosseinian Yousefkhani, Rastegar-Pouyani, Rastegar-Pouyani, Masroor, & Šmíd, 2013). Spatial autocorrelation of the 20 variables was measured by Pearson's correlation coefficient (r) in ENMTools (Warren, Glor, & Turelli, 2010). Of the highly correlated variable pairs (with $r \geq .75$) the more biologically meaningful one was retained for the analysis. The final set of environmental variables included: altitude, slope, mean diurnal temperature range (BIO2), temperature seasonality (BIO4), mean temperature of warmest quarter (BIO10), mean temperature of coldest quarter (BIO11), precipitation seasonality (BIO15), precipitation of wettest quarter (BIO16) and precipitation of driest quarter (BIO17). Models were generated with the following settings (otherwise by default): maximum number of iterations = 5,000; replicates = 10; replicated run type = cross-validate. The final models were reclassified into binary presence–absence maps using the maximum training sensitivity plus specificity threshold (MTSS), which maximises the proportions of correctly identified positives and correctly identified negatives and which is considered to most accurately predict presence/absence (Jiménez-Valverde & Lobo, 2007). The area under the receiver operating characteristics curve (AUC) was taken as a measure of overall model accuracy.

We tested for significance of all four models against null models (Raes & ter Steege, 2007). For each species we generated sets of 100 distribution records randomly distributed in the same study area using ENMTools, with the number of random records equal to the actual number of records of each species. The same Maxent settings were used. The model based on real data deems statistically significant if it ranks among 5% of the best performing null models with highest AUC values.

2.4 | Quantifying niche overlap

In order to gauge the degree of niche overlap between the four species, we used ENMTools to calculate Schoener's D metric (Schoener, 1968) that permits direct comparison of niche similarity and ranges from 0 (no overlap) to 1 (identical niches; Warren, Glor, & Turelli, 2008). We run a series of 100 niche identity tests for each species pair to assess whether the predicted distributions exhibit statistically significant ecological differences. For the identity test, records of the two species are pooled and two new sets with the same numbers of observations as the empirical data are drawn at random. Because niche differences may simply be a result of different environmental conditions available for the geographical regions occupied by the two compared species, we also run a series of 100 background tests to determine whether the predicted niches of the two species are more similar than expected by chance given the available niche-space of the region.

As an alternative to the niche overlap tests we also performed a principal component analysis (PCA) of the nine environmental variables across all grid cells of the background to determine whether the species occupy the same environment. The environmental variables were standardised prior to the analysis. We tested for significant differences between species using a multivariate analysis of variance (MANOVA) of the PCA scores.

2.5 | Morphological comparison

To obtain comparative morphological data, 61 voucher specimens from Iraq, Iran, Jordan, Lebanon, Saudi Arabia and Syria were examined. Additional morphological data for five specimens (four of which were syntypes) of *M. brevirostris* s. s. were taken from Boulenger (1921) (Table S4). The following metric characters were taken using a digital caliper and a dissecting microscope: snout-vent length (SVL)—distance from the snout tip to cloaca; head length (HL)—distance from the snout tip to the anterior edge of the ear; head width (HW)—greatest width of the head; head depth (HD)—greatest depth of the head; tail length (TL)—from cloaca to the tail tip, if original. All examined characters were taken to the nearest 0.1 mm. Meristic and qualitative pholidotic characters were counted and evaluated as follows: upper labials—number of upper labials anterior to the subocular, examined bilaterally; gulars—number of gular scales in a straight median series; plates in collar—number of enlarged scales in collar; dorsals—number of dorsal scales across midbody; ventrals—number of complete transverse series of ventral scales counted along the ventral side to (and excluding) the row of scales separating the series of femoral pores; preanals—number of preanal scales in a straight median series between cloaca and the row of scales separating the series of femoral pores; femoral pores—examined bilaterally; subdigital lamellae—counted along the underside of 4th toe, defined by their width, the one touching the claw included, examined bilaterally; structure of the semitransparent window of the lower eyelid—number and size of semitransparent scales. We tested for differences between the four putative species by means of ANOVA and Student's *t* test corrected for multiple comparisons with a Bonferroni correction. High-resolution photographs of all name-bearing type specimens of the species complex were deposited in MorphoBank (project 2355).

3 | RESULTS

3.1 | Phylogenetic analyses and divergence time estimation

All three runs of all BEAST and *BEAST analyses converged with ESS values >200 for all parameters indicating adequate mixing of the MCMC analyses. The result of the BI of the concatenated mtDNA data is shown in Fig. S1. All four species were highly supported (posterior probability [pp] = 1.0 for all) and all four species together were supported as a monophyletic group (pp = 1.0). The Saudi species was recovered as sister to *Mesalina brevirostris* s. s. (pp = 1.0). Otherwise the relationships remained unresolved due to low support. Mean uncorrected *p* distances within and between the four species for the three mtDNA genes are given in Table 1. The GMYC analysis recovered four putative species (Fig. S1), according to the likelihood function and the lineage-through-time plot ($\log L_{null} = 525.6$, $\log L_{GMYC} = 532.3$, LRT = 13.3, $p < .005$). The significant result of the LRT indicates that the null model with a single population was rejected.

TABLE 1 Mean uncorrected *p* distances (pairwise deletion) within (in bold on diagonal) and between (below diagonal) the four *Mesalina* species studied herein based on the mtDNA *12S*, *16S*, and *cytb* gene fragments. Names of taxa correspond to changes proposed in this study

	M. microlepis	*M. bernoullii*	*M. brevirostris*	*M. saudiarabica* sp. n.
12S				
M. microlepis	**.001**			
M. bernoullii	.032	**.006**		
M. brevirostris	.028	.038	**.003**	
M. saudiarabica sp. n.	.028	.027	.020	**.003**
16S				
M. microlepis	**.007**			
M. bernoullii	.034	**.007**		
M. brevirostris	.049	.043	**.007**	
M. saudiarabica sp. n.	.040	.033	.029	**.0**
cytb				
M. microlepis	**.014**			
M. bernoullii	.102	**.022**		
M. brevirostris	.098	.091	**.010**	
M. saudiarabica sp. n.	.108	.075	.095	**.005**

In the species-tree analysis (Figure 2), *M. microlepis* was reconstructed as sister to the three remaining species. The split was dated to 3.7 Myr (95% highest posterior density interval [HPD]: 2.4–5.1). The three other species form a well-supported monophylum (pp = .98) and the speciation in this node was dated to 1.7 Myr (HPD: 0.7–2.8). Within this group, the topology of the trees sampled in the posterior and visualised by DensiTree v.2.2 (Bouckaert, 2010) indicates a sister relationship between *M. bernoullii* and *M. brevirostris* s. s.; however, the node received relatively low support (pp = .72) and the relationships between the three species could not be resolved.

The results of the allele network reconstructions (Figure 2) of the three nDNA genes show that all alleles of all genes are private for the Saudi species and not shared with any other species. *Mesalina microlepis* does not share alleles with any other species in the MC1R and β-*fibint7*, and share only one derived (not ancestral) allele with *M. bernoullii* in the *c-mos*. On the contrary, *M. bernoullii* and *M. brevirostris* s. s. share multiple alleles in all three genes.

3.2 | Species distribution modelling and niche overlap

Maxent-produced models of excellent predictive accuracy (Araújo, Pearson, Thuiller, & Erhard, 2005; i.e., AUC > 0.9 following Swets, 1988) for all four putative species identified by GMYC, with the AUC values averaged over the ten replicate runs being 0.916 ± 0.07 for *M. bernoullii*, 0.993 ± 0.004 for *M. brevirostris* s. s., 0.931 ± 0.07 for *M. microlepis*, and 0.986 ± 0.01 for the Saudi species. All SDMs performed significantly better than null models.

The first three main environmental predictors for *M. bernoullii* were BIO10 (51.4%), BIO17 (23.4%), BIO16 (7.5%); for *M. brevirostris* s. s. BIO2 (27.3%), altitude (24.1%), BIO4 (20.2%); for *M. microlepis* BIO10 (51.1%), BIO17 (18.6%), altitude (13.7%); for the Saudi species BIO2 (31.3%), BIO11 (19.7%), BIO4 (17.3%). The SDM for *M. bernoullii* revealed two disjunct areas of suitability: a large one in southern Syria, Jordan, Israel, northern Sinai and western Iraq and the other comprising extreme western Iran and Kuwait. The predicted range of *M. microlepis* spans from the Sinai Peninsula, Egypt across the Levant to southern Turkey borders and further east to Iran. *Mesalina brevirostris* s. s. was predicted to occur mostly in lowlands of the southern Arabian/Persian Gulf. The Saudi species has a relatively restricted predicted range east of the Hejaz and Asir Mountains of Saudi Arabia. From the four putative species only the SDMs of *M. bernoullii* and *M. microlepis* overlap. The other two species are well geographically delineated (Figure 1).

Niche overlap between most species pairs is extremely low and ranges from $D = 0.003$ to 0.005. The only exception was found between *M. microlepis* and *M. bernoullii* whose niches

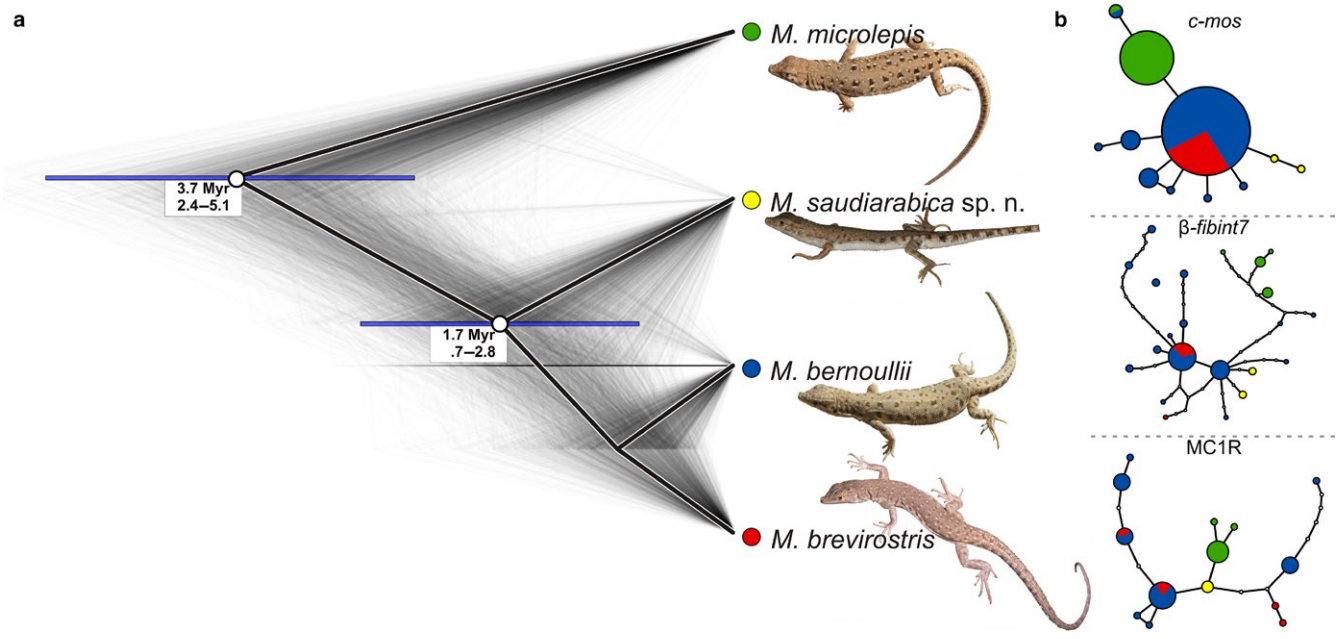

FIGURE 2 (a) Species-tree cloudogram (grey shading) superimposed with the MCC tree (black) inferred using three mtDNA and three nDNA gene fragments. White dots mark nodes with pp support ≥.95. Mean ages are indicated for supported nodes in white rectangles by nodes together with 95% HPD (also indicated as blue bars). Higher colour densities in the cloudogram represent higher levels of certainty that given clade exists. The depicted individuals are as follows: *Mesalina microlepis* from Hermel, Lebanon (voucher NMP 74214/2); *M. saudiarabica* sp. n. from Mahazat as-Sayd, Saudi Arabia (photovoucher NMP6F 29-30, not sampled); *M. bernoullii* from Chosrevi, Iran (unvouchered, sample I02), *M. brevirostris* from the Marawah Island, UAE (unvouchered, not sampled). Specimens are not to scale. (b) Allele networks of the three nDNA gene fragments analysed. Circle sizes are proportional to the number of alleles, lines represent mutational steps. Names of taxa correspond to changes proposed in this study

were very similar ($D = 0.63$; Figure 3). Null hypotheses assuming the species' niches being identical were rejected for all species pairs with low D value ($p < .005$), indicating significant differences between their niches. However, the null hypothesis could not be rejected for the *M. microlepis* and *M. bernoullii* species pair, which means the two species have identical environmental niches. The results of the randomisation test of background similarity show that the observed overlap between most species pairs is neither significantly more similar nor less similar than can be expected given the underlying environmental conditions of their ranges. The role of the environmental differences on the observed low similarity of their niches can therefore not be ruled out. On the contrary, the background comparison between *M. bernoullii* versus the Saudi species shows that *M. bernoullii* is significantly ($p < .05$) less similar to the Saudi background, while the Saudi species is significantly ($p < .05$) more similar to the *M. bernoullii* background (Figure 3). The same was found for the Saudi species whose niche is significantly ($p < .05$) less similar to the *M. microlepis* background. In other words, the environmental conditions prevailing within the range of the Saudi species are not suitable for *M. bernoullii*, but the Saudi species could potentially occur in the conditions of the range of *M. bernoullii*. Also, the Saudi species could not occur in the conditions of *M. microlepis*.

The first PCA component accounted for 42.3% of variability and was influenced mostly by BIO10 and BIO11; the second component accounted for 18.9% of variability and was influenced by BIO2 and BIO4. Concordantly with the high observed niche overlap between *M. microlepis* and *M. bernoullii*, their environmental requirements also largely overlap (Figure 1, Fig. S2). On the contrary, *M. bernoullii* and the

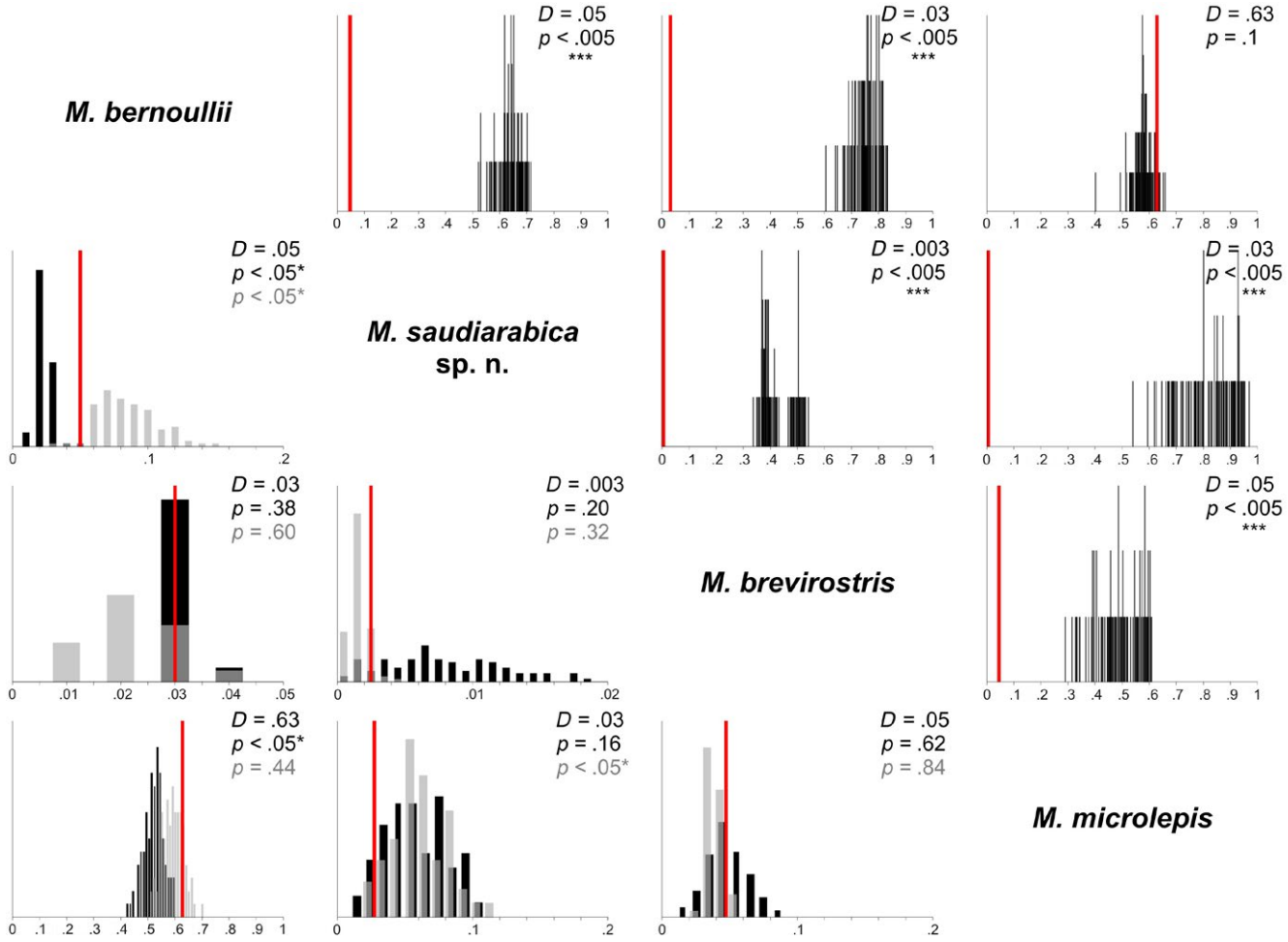

FIGURE 3 Results of 100 replicates of niche identity (above diagonal) and background tests (below diagonal). Observed niche overlap (Schoener's D) is given in the upper right corner of each graph and is also indicated by red bars. The identity tests show that the niches are significantly different from models based on pooled and randomly resampled records for all species pairs except *M. bernoullii—M. microlepis*. Scales of the *x* axis of all identity tests are 0–1. Background tests show two comparisons, one of the occurrences of the species in row against the background for the species in column (black bars and *p* values), the other of occurrences of the species in column compared with the background for the species in row (grey bars and *p* values). Note that the scale of the *x* axes differs in the background graphs. Asterisks by *p* values denote significant results. Names of taxa correspond to changes proposed in this study

Saudi species that were identified as having extremely low niche overlap have similar environmental requirements. Only *M. brevirostris* s. s. occupies unique environmental conditions. This was also supported by the MANOVA test, which suggests that there are significant environmental differences among the species ($F_{3,7832} = 1{,}532.4$; $p < .001$ for PC1 and $F_{3,7832} = 359.7$; $p < .001$ for PC2).

3.3 | Morphological analyses

Original measurements of all individuals examined as well as those obtained from the literature are given in Table S4, and descriptive statistics for all four putative species are in Table S5. The four species show only subtle morphological differentiation. Significant differences were found in the number of enlarged plates in collar (ANOVA: $F_{3,61} = 6.9205$, $p < .001$), number of dorsals (ANOVA: $F_{3,62} = 3.8082$, $p < .05$) and in the number of femoral pores (ANOVA: $F_{3,61} = 22.223$, $p < .001$). Details on the *t* test results of pairwise comparisons are given in the comparisons section below.

3.4 | Taxonomic implications

Given the genetic, morphological and geographical differences between the four putative species and in concordance with the general lineage species concept (de Queiroz, 1998, 2007), we assign species level to all four of them. Although some of the species do not show differentiation in all above attributes, we adopt the framework of integrative taxonomy that is based on the assumption that divergences in any of the attributes can provide evidence for the species' existence (Dayrat, 2005; Padial, Miralles, De la Riva, & Vences, 2010). As a result, we suggest the following nomenclatural and taxonomic actions: (i) we formally designate a lectotype of *Mesalina brevirostris* Blanford, 1874; restrict the type locality of this species to Tumb Island, Iran, and apply the name *M. brevirostris* for the taxon defined as *M. brevirostris* s. s. in this study; (ii) we resurrect the available name *Eremias bernoullii* Schenkel, 1901 from the synonymy of *M. brevirostris* and apply it in a new combination *Mesalina bernoullii* (Schenkel, 1901) to the species occurring in the Mesopotamia and Syrian desert; (iii) we synonymise *Eremias brevirostris fieldi* Haas & Werner, 1969 with the name *Eremias bernoullii* and apply the herein proposed name *Mesalina bernoullii* to populations previously recognised as *Mesalina brevirostris fieldi*; (iv) we elevate to the species status the name *M. brevirostris microlepis* (Angel, 1936) and use the name *Mesalina microlepis* for the species occurring in the Levant; and (v) we formally describe a new species from Saudi Arabia.

Below we provide a shortened version of the content of the *M. brevirostris* species complex as revised herein. The full description of the new species from Saudi Arabia, which is only indicated here by the new species name, including collection codes of all type specimens, description of the holotype, distribution and ecology, etymology, comparisons with other species and variation, is provided in the Supplementary Materials. Likewise, more details regarding the distribution and other relevant notes for the other newly recognised species of the complex are in the Supplementary Materials.

This published work and the nomenclatural acts it contains have been registered in ZooBank (http://zoobank.org), the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) for this publication are as follows: urn:lsid:zoobank.org:pub:77314404-726F-4834-9FFA-D1C764B5ECB5. All associated information may be viewed by appending the LSID to the prefix "zoobank.org/".

Genus *Mesalina* Gray, 1838

***Mesalina brevirostris* Blanford, 1874**

Lectotype. BMNH 1946.8.6.25. Designated herein. Type locality: Tumb Island, Arabian/Persian Gulf, Iran. MorphoBank pictures: M407236–M407250.

***Mesalina bernoullii* (Schenkel, 1901) comb. nov.**

Holotype. NMB 4396. Type locality: "Palmyra" (Syria). MorphoBank pictures: M407230–M407235.

***Mesalina microlepis* (Angel, 1936) stat. nov.**

Holotype. MNHN 1935.285. Type locality: "Haouarine" ["à 55 kilomètres au S.-E. de Homs"], (Syria). MorphoBank pictures: M407268–M407305.

***Mesalina saudiarabica* Moravec, Šmíd, Schmitz, Shobrak, Wilms – sp. n.**

ZooBank registration: urn:lsid:zoobank.org:act:8B1926DF-E92A-41FC-B7E6-E15743A0D31C

Holotype (Figure 4). ZFMK 91912, subadult male, Mahazat as-Sayd, Makkah Province, Saudi Arabia, 22.237N, 41.843E, 1,000 m a.s.l., collected in October 2006 by T. Wilms. MorphoBank pictures: M407306–M407312.

Paratype. ZFMK 86583, subadult male, Mahazat as-Sayd, near Al Muwayh, Makkah Province, Saudi Arabia, 22.395N 41.753E, 960 m a.s.l., collected in October 2006 by T. Wilms. MorphoBank picture: M410851.

Diagnosis A species of *Mesalina* and a member of the *M. brevirostris* species complex as revealed by the genetic analyses and characterised by the following combination of characters: (i) genetic (uncorrected) distance of 2.0% from *M. brevirostris*, 2.7% from *M. bernoullii* and 2.8% from *M. microlepis* for the *12S* (after Gblocks); 2.9% from *M. brevirostris*, 3.3% from *M. bernoullii* and 4.0% from *M. microlepis* for the *16S* (after Gblocks); 9.5% from *M. brevirostris*, 7.5% from *M. bernoullii* and 10.8% from *M. microlepis* for the *cytb*; (ii) low number of dorsal scales (41–42); (iii) low number of collar plates (6–8); (iv) low number of preanal scales (2–3); (v) low number of femoral pores in males (12–13); (vi) having 1–2 large semitransparent scales in the lower eyelid window; (vii) in life, dorsum light cinnamon–brown with a pattern of

FIGURE 4 Holotype of *Mesalina saudiarabica* sp. n. (ZFMK 91912). (a) General body habitus; (b) lateral and (c) dorsal view of the head. More photographs of the specimen are available in high resolution at MorphoBank, project 2355, pictures M407306–M407312

small whitish and larger dark cinnamon spots arranged in more or less regular longitudinal rows. Most of the whitish spots are not edged with dark brown colour. The dark cinnamon–brown spots predominate on flanks where they form a characteristic longitudinal lateral row that continues onto the tail. Ventral side is bright white, sharply contrasting with the colouration of the dorsum.

Detailed description of *M. saudiarabica* sp. n. is given in the Supplementary Materials.

4 | DISCUSSION

This study provides a comprehensive assessment of the phylogenetic relationships, morphological and ecological differentiation, and a thorough taxonomic revision of the *Mesalina brevirostris* species complex. With a multilocus data set for 61 individuals covering the entire Middle Eastern part of the complex range we investigated the phylogeny and diversification history of the four newly recognised species. By reconstructing potential distributions of the species we show that they rarely overlap geographically and that there are environmental differences between most of them.

Our study uses the most robust data set ever assembled for deriving the phylogeny of *Mesalina*. The results of the phylogenetic analyses based on three mtDNA and three nDNA markers, and analysed under the multispecies coalescent framework reveal that the mtDNA alone is insufficient for correctly inferring of the phylogenetic relationships within *Mesalina*. While *M. brevirostris* s. s. was reconstructed as sister to *M. saudiarabica* sp. n. with high posterior probability support (pp = 1.0) when only the mtDNA was used, it was recovered as closer to *M. bernoullii* when also nDNA was analysed as a result of shared alleles in all nDNA markers studied. The potential reasons are discussed below. Our results corroborate the general notion that phylogenetic trees based on single genes or mtDNA alone may poorly represent the real species history owing to the stochasticity of the coalescent process, incomplete lineage sorting, potential introgression or effects of selection (Ballard & Whitlock, 2004; Galtier, Nabholz, Glémin, & Hurst, 2009). Given that all but one previous phylogenetic studies of *Mesalina* were mtDNA-based (Joger & Mayer, 2002; Kapli et al., 2008; Šmíd & Frynta, 2012), similar topological discrepancy might as well be found in other closely related species. As exemplified by the results of this study, the phylogeny of the entire genus should be reassessed by analyzing multilocus data preferably in a coalescent-based framework.

4.1 | Cryptic diversification and niche differentiation within *Mesalina*

The existence of possible species complexes of *Mesalina* that are cryptic in their external morphology has already been pointed out. They were first noted by Arnold (1986a, 1986b) in his studies of hemipenial morphology. He found that populations of one species can have obvious differences in the size of the hemipenis and concluded that some species might, in

fact, represent complexes of morphologically cryptic species. One such case was *M. brevirostris*, in which males from the western part of the range possess large hemipenes, whereas males from south-western Iran, Pakistan and India have small hemipenes (Arnold, 1986b). General difference in body habitus was also found between Mesopotamian populations and highland Iranian and Pakistani populations (Arnold, 1986c). Arnold (1986c) assumed either character displacement in sympatric species or poor taxonomy of the genus to be responsible for the morphological variation. Our results confirm the latter to be the case. As demonstrated here by the level of genetic, ecological and morphological differentiations the species complex is in fact formed by four clearly differentiated species, and Arnold's western populations are recognised here as *M. bernoullii* and his southern Iranian and Pakistani populations retain the name *M. brevirostris* s. s.

The position of *M. microlepis* as sister to the other three species of the complex as reconstructed by the species-tree analysis is somewhat surprising given that it was generally considered very closely related or even conspecific with *M. bernoullii* as recognised herein (Anderson, 1999; Haas, 1957). *Mesalina microlepis* is the north-western most of the four species studied here and according to our results it diverged from the clade of *M. bernoullii*, *M. brevirostris* s. s. and *M. saudiarabica* sp. n. in the middle Pliocene (3.7 Myr). The three latter species diversified on the Pliocene/Pleistocene boundary (1.7 Myr). As has been proposed by some authors (Mayer et al., 2006; Moravec, 2004), progressive aridization of the Middle East that started towards the end of the Pliocene and continues to date (Edgell, 2006; Whybrow & McClure, 1980) could have triggered speciation between the three southern species. Similar pattern of increased speciation in response to aridization of the Arabian Peninsula has been reported for other reptile genera (de Pous et al., 2016; Tamar, Carranza, et al., 2016). All three species currently prefer areas with high temperatures and low precipitation as their SDMs suggest (Fig. S2). They could have become isolated in local refugia when the environmental conditions began to change and suitable habitats were not available in the interior of Arabia. This hypothesis assumes that they were present in their current ranges prior to the aridization and did not colonise them more recently.

Despite the general trend of cryptic speciation of *Mesalina* that is not reflected in the morphology, some of the species show considerable intraspecific morphological variation that is not coupled with their genetic diversification. For instance, two morphological forms of *M. bernoullii* differing in size, colouration and scalation have been recorded from Syria and were assumed to be differentiated at a specific or subspecific level (Mayer et al., 2006; Moravec, 2004). Also the Iranian populations described as the subspecies *M. fieldi* (herein synonymised with *M. bernoullii*) differ in dorsal scales size (Haas & Werner, 1969). Nevertheless, our results show that all these forms fall genetically and morphologically within the intraspecific variation range of *M. bernoullii*. Their morphology might be the result of random drift or adaptation to local conditions (Anderson, 1999; Moravec, 2004).

Of particular interest are the niche comparisons of the species. Niche similarities between most species are extremely low, reaching between 0.003 and 0.005, and all but one species pairs do not have identical niches. However, as the alternative analysis (PCA) of the environmental overlap shows, these extremely low *D* values can be merely attributed to the virtual lack of geographic overlap of the species' predicted distributions, and the way Schoener's *D* metric is calculated (Schoener, 1968). According to the equation, when probabilities of occurrence of two species are mutually exclusive, in other words when the probability of occurrence of one species is high in regions where the other species is not likely to occur then the *D* value will be, by definition, close to 0. The *D* values were thus necessarily very low because the modelled ranges were largely allopatric (see also Warren, Cardillo, Rosauer, & Bolnick, 2014). Also, even if species show niche divergence but do not occur in the same area then ecological differentiation had probably a little role in their diversification (Wiens, 2011).

The sole exception was the comparison of *M. microlepis* and *M. bernoullii*, whose niches were found to be very similar ($D = 0.63$) and identical according to the randomisation identity tests. It is important to note that although all SDMs were significantly better than those drawn at random and therefore informative, the potential range of *M. microlepis* may be overpredicted as a result of low number of localities available for that species. This may in turn lead to the observed overlap of potential ranges or suitable conditions with *M. bernoullii*. We therefore presume that segregation between the species is rather a result of geographic isolation than actual disparity of their environmental niches. This assumption is supported by the results of the PCA that show that the environmental spaces occupied by *M. bernoullii* and *M. saudiarabica* sp. n. largely overlap despite the low *D* value of their niche overlap. Furthermore, the background tests did not rule out the possibility that the low similarity is based on the differences in the underlying environmental conditions available in their ranges.

4.2 | Sex-biased gene flow between *M. bernoullii* and *M. brevirostris* s. s

Unlike the species-tree estimation based on all six genes, the analysis of mtDNA did not recover *M. bernoullii* and *M. brevirostris* s. s. to be closely related. However, the nDNA networks show that the two species share alleles in all genes studied. One potential explanation is that the nuclear genes studied are not involved in the speciation process and, by chance, are not variable enough to contribute to the phylogenetic resolution (Nosil & Schluter, 2011). The lack of variance might then be a result of incomplete lineage sorting of ancestral polymorphism. However, under this assumption the lack of variance would then be expected also for *M. microlepis* and

M. saudiarabica sp. n., yet these species have all the alleles private with the exception of one in the *c-mos* (shared *M. microlepis* and *M. bernoullii*). Another plausible explanation is that there is, or has been, ongoing gene flow of nuclear but not mitochondrial DNA between *M. bernoullii* and *M. brevirostris* s. s. that is responsible for the lack of variability in the nDNA, but not in the mtDNA genes. This could be caused by sex-biased dispersal with males of either of the species dispersing and mating with females of the other species while females being more sedentary and not spreading the mitochondrial genomes. Currently there are no data available for *Mesalina* regarding dispersal differences between males and females; however, studies have shown that male-biased dispersal is very widespread among lizards including lacertids (Doughty, Sinervo, & Burghardt, 1994; Johansson, Surget-Groba, & Thorpe, 2008; Massot, Huey, Tsuji, & van Berkum, 2003; Olsson, Gullberg, & Tegelström, 1996; Qi, Yang, Lu, & Fu, 2013; Rassmann, Tautz, Trillmich, & Gliddon, 1997). It can therefore be expected also in the genus *Mesalina*.

The possible contact zone between the two species could be located on either side of the Arabian/Persian Gulf considering their current distributions. Moreover, their contact could have been facilitated by the repeatedly desiccating Arabian/Persian Gulf in the Quaternary, which was a result of the global climatic fluctuations and sea level changes. The Gulf was almost non-existent or, at most, formed by series of lakes during the glacial periods of the late Pleistocene and early Holocene (Kennett & Kennett, 2006; Lambeck, 1996). Such a flat plain could then form the region where *M. bernoullii* and *M. brevirostris* s. s. overlapped. *Mesalina brevirostris* s. s. in particular might have penetrated more northward along the Gulf owing to its current preference for low altitude areas. To properly locate the contact zone between *M. bernoullii* and *M. brevirostris* s. s. and to understand the causes and direction of potential gene flow extensive sampling on both the Iranian and Saudi sides of the Arabian/Persian Gulf is needed. In Iran, it might be somewhere near Bushehr where Arnold (1986a) found both species to occur in sympatry.

Interestingly, very limited allele sharing was detected between *M. bernoullii* and *M. microlepis*, which occur sympatrically in western Syria. With the limited data available it seems that these two species do not hybridise.

4.3 | Taxonomy of *Mesalina*

The taxonomy of the genus *Mesalina* has been relatively stable over the past decades compared to other Middle Eastern Eremiadini (e.g., *Acanthodactylus*, *Eremias*). The last species were described in 2002 (*M. kuri* by Joger & Mayer, 2002; and *M. bahaeldini* by Segoli et al., 2002). The taxonomic adjustments recommended herein emphasise how the diversity of a relatively well-known species may actually be underestimated. *Mesalina saudiarabica* sp. n. described here from western Arabia contributes to the intensively growing knowledge on the evolution and systematics of the pan-Arabian reptile fauna within the last years (Carranza et al., 2016; Kapli et al., 2015; Metallinou et al., 2012, 2015; de Pous et al., 2016; Šmíd, Shobrak, Wilms, Joger, & Carranza, 2017; Šmíd, Carranza, et al., 2013; Šmíd, Moravec, et al., 2013; Šmíd et al., 2015; Tamar, Carranza, et al., 2016; Tamar, Scholz, et al., 2016). As some of the studies show, cryptic and previously unrecognised species are present along the western Arabian mountains, and more species descriptions from there may thus be expected.

For future taxonomic work on *Mesalina,* it is important to note that *M. saudiarabica* sp. n. is not any of Arnold's (1980, 1986c) undescribed south Arabian species (*Mesalina* sp. A from the mountains of Yemen and Saudi Arabia and *M*. sp. B from Dhofar, Oman). Its presence was not recorded until the material for recent phylogenetic studies (Kapli et al., 2015; this study) had become available. Further effort should be dedicated to obtaining genetic data from the two supposedly new species mentioned by Arnold (1980, 1986c) as well as from two narrow-ranging species that have not yet been analysed genetically and placed in a phylogenetic framework, *M. ayunensis* and *M. ercolinii* (Lanza & Poggesi, 1975). Such data may shed new light on the evolutionary history and hopefully help to untangle relationships within some of the other *Mesalina* species complexes.

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ARCHIVED DATA

All alignments, phylogenetic trees, distribution records used for the SDMs, and photographs of all name-bearing type specimens of all the species and of all other examined material were deposited in MorphoBank (project 2355; www.morphobank.org).

REFERENCES

Abukashawa, S., & Hassan, M. (2016). New record of the small-spotted lizard, *Mesalina guttulata* (lichtenstein, 1823) from Dongonab bay, Red sea. *Russian Journal of Herpetology*, *22*, 219–223.

Anderson, S. C. (1999). *The lizards of Iran*. Ithaca, NY: Society for the Study of Amphibians and Reptiles.

Angel, F. (1936). Reptiles et batraciens de syrie et de Mésopotamie récoltés par m. P. Pallary. *Bulletin de L'Institut D'Egypte*, *18*, 107–116.

Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology*, *11*, 1504–1513.

Arnold, E. N. (1980). The reptiles and amphibians of Dhofar, southern Arabia. *Journal of Oman Studies, Special Report*, *2*, 273–332.

Arnold, E. N. (1986a). The hemipenis of lacertid lizards (Reptilia: Lacertidae): Structure, variation and systematic implication. *Journal of Natural History*, *20*, 1221–1257.

Arnold, E. N. (1986b). A key and annotated check-list to the lizards and amphisbaenians of arabia. *Fauna of Saudi Arabia*, *8*, 385–435.

Arnold, E. N. (1986c). Why copulatory organs provide so many useful taxonomic characters: The origin and maintenance of hemipenial differences in lacertid lizards (Reptilia: Lacertidae). *Biological Journal of the Linnean Society*, *29*, 263–281.

Arnold, E. N., Arribas, O., & Carranza, S. (2007). Systematics of the palaearctic and oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*, *1430*, 1–86.

Baha El Din, S. (2006). *A guide to the reptiles and amphibians of Egypt*. Cairo, New York: The American University in Cairo Press.

Ballard, J. W. O., & Whitlock, M. C. (2004). The incomplete natural history of mitochondria. *Molecular Ecology*, *13*, 729–744.

Bischoff, W. (1991). Übersicht der arten und unterarten der familie Lacertidae 4. Die gattunges *Latastia*, *Meroles*, *Mesalina*, *Nucras*, *Ophisops*, *Pedioplanis*, und *Philochortus*. *Die Eidechse*, *4*, 17–25.

Blanford, W. T. (1874). Description of new Reptilia and Amphibia from Persia and Baluchistan. *Annals and Magazine of Natural History*, *4*, 31–35.

Blanford, W. T. (1876). *Eastern Persia. An account of the journeys of the Persian boundary commission 1870-71-72. Volume ii. The zoology and geology*. London: Macmillan and Co.

in den Bosch, H. A. J. (2001). *Mesalina brevirostris* blanford, 1874 in Lebanon, with data on reproduction. *Zoology in the Middle East*, *23*, 31–46.

Bouckaert, R. R. (2010). DensiTree: Making sense of sets of phylogenetic trees. *Bioinformatics*, *26*, 1372–1373.

Boulenger, G. A. (1887). *Catalogue of the lizards in the British Museum (Natural History). Vol. III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae*. London: Trustees of the British Museum.

Boulenger, G. A. (1921). *Monograph of the Lacertidae. II*. London: Longmans, Green & Co. and British Museum (Natural History).

Carranza, S., & Arnold, E. N. (2012). A review of the geckos of the genus *Hemidactylus* (Squamata: Gekkonidae) from Oman based on morphology, mitochondrial and nuclear data, with descriptions of eight new species. *Zootaxa*, *3378*, 1–95.

Carranza, S., Simó-Riudalbas, M., Jayasinghe, S., Wilms, T., & Els, J. (2016). Microendemicity in the northern Hajar Mountains of Oman and the United Arab Emirates with the description of two new species of geckos of the genus *Asaccus* (Squamata: Phyllodactylidae). *PeerJ*, *4*, e2371.

Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, *17*, 540–552.

Clement, M., Posada, D., & Crandall, K. A. (2000). TCS: A computer program to estimate gene genealogies. *Molecular Ecology*, *9*, 1657–1659.

Cox, S. C., Carranza, S., & Brown, R. P. (2010). Divergence times and colonization of the Canary Islands by *Gallotia* lizards. *Molecular Phylogenetics and Evolution*, *56*, 747–757.

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModeltest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772.

Dayrat, B. (2005). Towards integrative taxonomy. *Biological Journal of the Linnean Society*, *85*, 407–415.

Disi, A. M. (1991). A contribution to the herpetofauna of Jordan 4. Lizards of Jordan. *Zoology in the Middle East*, *5*, 25–36.

Disi, A. M. (1996). A contribution to the knowledge of the herpetofauna of Jordan. Vi. The Jordanian herpetofauna as a zoogeographic indicator. *Herpetozoa*, *9*, 71–81.

Disi, A. M., & Amr, Z. S. (1998). Distribution and ecology of lizards in Jordan. *Zoologische Abhandlungen Staatliches Museum fur Tierkunde Dresden*, *21*, 43–66.

Disi, A. M., Modrý, D., Necas, P., & Rifai, L. (2001). *Amphibians and reptiles of the Hashemite Kingdom of Jordan*. Frankfurt am Main: Edition Chimaira.

Doughty, P., Sinervo, B., & Burghardt, G. M. (1994). Sex-biased dispersal in a polygynous lizard, *Uta stansburiana*. *Animal Behaviour*, *47*, 227–229.

Drummond, A. J., & Bouckaert, R. R. (2015). *Bayesian evolutionary analysis with beast*. New York: Cambridge University Press.

Drummond, A., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, *7*, 214.

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973.

Edgell, H. S. (2006). *Arabian deserts: Nature, origin and evolution*. Dordrecht, The Netherlands: Springer.

Elith, J., Graham, H. C., Anderson, P. R., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*, 129–151.

Ezard, T., Fujisawa, T., & Barraclough, T. (2009). SPLITS: Species' limits by threshold statistics. *R package version*, 1.

Flot, J. F. (2010). SeqPHASE: A web tool for interconverting phase input/output files and fasta sequence alignments. *Molecular Ecology Resources*, *10*, 162–166.

Fu, J. (2000). Toward the phylogeny of the family Lacertidae – why 4708 base pairs of mtDNA sequences cannot draw the picture. *Biological Journal of the Linnean Society*, *71*, 203–217.

Galtier, N., Nabholz, B., Glémin, S., & Hurst, G. (2009). Mitochondrial DNA as a marker of molecular diversity: A reappraisal. *Molecular Ecology*, *18*, 4541–4550.

Gardner, A. S. (2013). *The amphibians and reptiles of Oman and the UAE*. Frankurt am Main: Edition Chimaira.

Haas, G. (1957). Some amphibians and reptiles from Arabia. *Proceedings of the California Academy of Sciences, 4th ser*., 29, 47–86 + 12 figs.

Haas, G., & Werner, Y. L. (1969). Lizards and snakes from southwestern Asia, collected by Henry Field. *Bulletin of the Museum of Comparative Zoology*, *138*, 327–406.

Heled, J., & Drummond, A. J. (2010). Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution*, *27*, 570–580.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978.

Hoofien, J. H. (1957). An addition on the fauna of Sinai: *Eremias brevirostris* Blanf. *Annals and Magazine of Natural History*, *12*, 719–720.

Hosseinian Yousefkhani, S. S., Rastegar-Pouyani, E., Rastegar-Pouyani, N., Masroor, R., & Šmíd, J. (2013). Modelling the potential distribution of *Mesalina watsonana* (Stoliczka, 1872) (Reptilia: Lacertidae) on the Iranian Plateau. *Zoology in the Middle East*, *59*, 220–228.

Ilgaz, Ç., Baran, I., Kumlutaş, Y., & Avci, A. (2005). A new record of *Mesalina brevirostris* from southeastern Anatolia. *Russian Journal of Herpetology*, *12*, 230–236.

Jiménez-Valverde, A., & Lobo, J. M. (2007). Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica*, *31*, 361–369.

Joger, U., & Mayer, W. (2002). A new species of *Mesalina* (Reptilia: Lacertidae) from Abd al-Kuri, Socotra archipelago, Yemen, and a preliminary molecular phylogeny for the genus *Mesalina*. *Fauna of Arabia*, *19*, 497–505.

Johansson, H., Surget-Groba, Y., & Thorpe, R. S. (2008). Microsatellite data show evidence for male-biased dispersal in the Caribbean lizard *Anolis roquet*. *Molecular Ecology*, *17*, 4425–4432.

Kamali, K. (2013). Geographic distribution: *Mesalina brevirostris* (Blanford's short-nosed desert lizard). *Herpetological Review*, *44*, 274.

Kapli, P., Lymberakis, P., Crochet, P. A., Geniez, P., Brito, J. C., Almutairi, M., … Poulakakis, N. (2015). Historical biogeography of the lacertid lizard *Mesalina* in north Africa and the Middle East. *Journal of Biogeography*, *42*, 267–279.

Kapli, P., Lymberakis, P., Poulakakis, N., Mantziou, G., Parmakelis, A., & Mylonas, M. (2008). Molecular phylogeny of three *Mesalina* (Reptilia: Lacertidae) species (*M. guttulata, M. brevirostris* and *M. bahaeldini*) from north Africa and the Middle East: Another case of paraphyly? *Molecular Phylogenetics and Evolution*, *49*, 102–110.

Kapli, P., Poulakakis, N., Lymberakis, P., & Mylonas, M. (2011). A reanalysis of the molecular phylogeny of Lacertidae with currently available data. *Basic and Applied Herpetology*, *25*, 97–104.

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, *30*, 772–780.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., … Duran, C. (2012). Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*, 1647–1649.

Kennett, D. J., & Kennett, J. P. (2006). Early state formation in southern Mesopotamia: Sea levels, shorelines, and climate change. *Journal of Island & Coastal Archaeology*, *1*, 67–99.

Kumlutaş, Y., Taskavak, E., Baran, I., Ilgaz, Ç., & Avci, A. (2002). First record of Blanford's short-nosed desert lizard *Mesalina brevirostris* Blanford, 1874, from Anatolia. *Herpetozoa*, *15*, 171–178.

Lambeck, K. (1996). Shoreline reconstructions for the Persian Gulf since the last glacial maximum. *Earth and Planetary Science Letters*, *142*, 43–57.

Martin, D. P., Lemey, P., Lott, M., Moulton, V., Posada, D., & Lefeuvre, P. (2010). RDP3: A flexible and fast computer program for analyzing recombination. *Bioinformatics*, *26*, 2462–2463.

Massot, M., Huey, R. B., Tsuji, J., & van Berkum, F. H. (2003). Genetic, prenatal, and postnatal correlates of dispersal in hatchling fence lizards (*Sceloporus occidentalis*). *Behavioral Ecology*, *14*, 650–655.

Mayer, W., Moravec, J., & Pavlicev, M. (2006). Differentiation within Syrian populations of the lizard *Mesalina brevirostris*. In C. Corti, P. Lo Cascio & M. Biaggini (Eds.), *Mainland and insular lacertid lizards: A Mediterranean perspective* (pp. 125–131). Firenze: Firenze University Press.

Mayer, W., & Pavlicev, M. (2007). The phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: Convergent adaptations to arid habitats within the subfamily Eremiainae. *Molecular Phylogenetics and Evolution*, *44*, 1155–1163.

Metallinou, M., Arnold, E. N., Crochet, P.-A., Geniez, P., Brito, J. C., Lymberakis, P., … Carranza, S. (2012). Conquering the Sahara and Arabian deserts: Systematics and biogeography of *Stenodactylus* geckos (Reptilia: Gekkonidae). *BMC Evolutionary Biology*, *12*(258), 1–17.

Metallinou, M., Červenka, J., Crochet, P.-A., Kratochvíl, L., Wilms, T., Geniez, P., … Carranza, S. (2015). Species on the rocks: Systematics and biogeography of the rock-dwelling *Ptyodactylus* geckos (Squamata: Phyllodactylidae) in North Africa and Arabia. *Molecular Phylogenetics and Evolution*, *85*, 208–220.

Moravec, J. (2004). Distribution and morphological variation of the lizard *Mesalina brevirostris* in Syria. In V. Pérez-Mellado, N. Riera & A. Perera (Eds.), *The biology of lacertid lizards. Evolutionary and ecological perspectives* (pp. 245–257). Maó, Menorca: Institut Menorquí d'Estudis.

Nosil, P., & Schluter, D. (2011). The genes underlying the process of speciation. *Trends in Ecology & Evolution*, *26*, 160–167.

Olsson, M., Gullberg, A., & Tegelström, H. (1996). Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*). *Journal of Evolutionary Biology*, *9*, 229–242.

Padial, J. M., Miralles, A., De la Riva, I., & Vences, M. (2010). The integrative future of taxonomy. *Frontiers in Zoology*, *7*, 16.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259.

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., … Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, *55*, 595–609.

de Pous, P., Machado, L., Metallinou, M., Červenka, J., Kratochvíl, L., Paschou, N., … Carranza, S. (2016). Taxonomy and biogeography of *Bunopus spatalurus* (Reptilia; Gekkonidae) from the Arabian Peninsula. *Journal of Zoological Systematics and Evolutionary Research*, *54*, 67–81.

Qi, Y., Yang, W., Lu, B., & Fu, J. (2013). Genetic evidence for male-biased dispersal in the Qinghai toad-headed agamid *Phrynocephalus vlangalii* and its potential link to individual social interactions. *Ecology and Evolution*, *3*, 1219–1230.

de Queiroz, K. (1998). The general lineage concept of species, species criteria, and the process of speciation. In D. J. Howard & S. H. Berlocher (Eds.), *Endless forms: Species and speciation* (496 pp.). Oxford: Oxford University Press.

de Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology*, *56*(6), 879–886.

Raes, N., & ter Steege, H. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography*, *30*, 727–736.

Rambaut, A., & Drummond, A. (2007). *Tracer v1.4*. Retrieved from http://beast.bio.ed.ac.uk/tracer

Rassmann, K., Tautz, D., Trillmich, F., & Gliddon, C. (1997). The microevolution of the Galápagos marine iguana *Amblyrhynchus cristatus* assessed by nuclear and mitochondrial genetic analyses. *Molecular Ecology*, *6*, 437–452.

Ross, W. (1988). Observation on three species of *Mesalina* from eastern Saudi Arabia. *Fauna of Saudi Arabia*, *9*, 451–456.

dos Santos, A. M., Cabezas, M. P., Tavares, A. I., Xavier, R., & Branco, M. (2015). TCSbu: A tool to extend tcs network layout and visualization. *Bioinformatics*, *btv636*, 1–2.

Schenkel, E. (1901). Achter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, *13*, 142–199.

Schmidt, K. P. (1939). Reptiles and amphibians from southwestern Asia. *Zoological Series of Field Museum of Natural History*, *24*, 49–92.

Schoener, T. W. (1968). The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology*, *49*, 704–726.

Segoli, M., Cohen, T., & Werner, Y. L. (2002). A new lizard of the genus *Mesalina* from Mt. Sinai, Egypt. *Faunistiche Abhandlungen Staatliches Museum für Tierkunde Dresden*, *23*, 157–176.

Sindaco, R., & Jeremčenko, V. K. (2008). *The reptiles of the western Palearctic. 1. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and central Asia*. Latina, Italy: Monografie della Societas Herpetologica Italica - I. Edizioni Belvedere.

Šmíd, J., Carranza, S., Kratochvíl, L., Gvoždík, V., Nasher, A. K., & Moravec, J. (2013). Out of Arabia: A complex biogeographic history of multiple vicariance and dispersal events in the gecko genus *Hemidactylus* (Reptilia: Gekkonidae). *PLoS One*, *8*(5), e64018.

Šmíd, J., & Frynta, D. (2012). Genetic variability of *Mesalina watsonana* (Reptilia: Lacertidae) on the Iranian Plateau and its phylogenetic and biogeographic affinities as inferred from mtDNA sequences. *Acta Herpetologica*, *7*, 139–153.

Šmíd, J., Moravec, J., Kodym, P., Kratochvíl, L., Hosseinian Yousefkhani, S. S., Rastegar-Pouyani, E., & Frynta, D. (2014). Annotated checklist and distribution of the lizards of Iran. *Zootaxa*, *3855*, 1–97.

Šmíd, J., Moravec, J., Kratochvíl, L., Gvoždík, V., Nasher, A. K., Busais, S., … Carranza, S. (2013). Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt. *ZooKeys*, *355*, 79–107.

Šmíd, J., Moravec, J., Kratochvíl, L., Nasher, A. K., Mazuch, T., Gvoždík, V., & Carranza, S. (2015). Multilocus phylogeny and taxonomic revision of the *Hemidactylus robustus* species group (Reptilia, Gekkonidae) with descriptions of three new species from Yemen and Ethiopia. *Systematics and Biodiversity*, *13*, 346–368.

Šmíd, J., Shobrak, M., Wilms, T., Joger, U., & Carranza, S. (2017). Endemic diversification in the mountains: Genetic, morphological, and geographical differentiation of the *Hemidactylus* geckos in southwestern Arabia. *Organisms, Diversity and Evolution*, *17*, 267–285.

Stephens, M., Smith, N. J., & Donnelly, P. (2001). A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics*, *68*, 978–989.

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, *240*, 1285–1293.

Talavera, G., & Castresana, J. (2007). Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology*, *56*, 564–577.

Talavera, G., Dincă, V., & Vila, R. (2013). Factors affecting species delimitations with the GMYC model: Insights from a butterfly survey. *Methods in Ecology and Evolution*, *4*, 1101–1110.

Tamar, K., Carranza, S., Sindaco, R., Moravec, J., Trape, J.-F., & Meiri, S. (2016). Out of Africa: Phylogeny and biogeography of the widespread genus *Acanthodactylus* (Reptilia: Lacertidae). *Molecular Phylogenetics and Evolution*, *103*, 6–18.

Tamar, K., Scholz, S., Crochet, P.-A., Geniez, P., Meiri, S., Schmitz, A., … Carranza, S. (2016). Evolution around the Red Sea: Systematics and biogeography of the agamid genus *Pseudotrapelus* (Squamata: Agamidae) from North Africa and Arabia. *Molecular Phylogenetics and Evolution*, *97*, 55–68.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, *30*, 2725–2729.

Templeton, A. R., Crandall, K. A., & Sing, C. F. (1992). A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics*, *132*, 619–633.

Uetz, P., & Hošek, J. (2017). *The reptile database*. Retrieved from http://www.reptile-database.org/

Warren, D. L., Cardillo, M., Rosauer, D. F., & Bolnick, D. I. (2014). Mistaking geography for biology: Inferring processes from speceis distributions. *Trends in Ecology & Evolution*, *29*, 572–580.

Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution*, *62*, 2868–2883.

Warren, D. L., Glor, R. E., & Turelli, M. (2010). ENMtools: A toolbox for comparative studies of environmental niche models. *Ecography*, *33*, 607–611.

Werner, Y. L. (1971). Lizards and snakes from Transjordan, recently acquired by the British Museum (Natural History). *Bulletin of the British Museum (Natural History)*, *21*, 215–256. + 216 pl.

Whybrow, P. J., & McClure, H. (1980). Fossil mangrove roots and palaeoenvironments of the Miocene of the eastern Arabian Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *32*, 213–225.

Wiens, J. J. (2011). The causes of species richness patterns across space, time, and clades and the role of "ecological limits". *The Quarterly Review of Biology*, *86*, 75–96.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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SUPPLEMENTARY MATERIALS

A detailed taxonomic revision of the *M. brevirostris* species complex.

Genus *Mesalina* Gray, 1838

***Mesalina brevirostris* Blanford, 1874**

Mesalina brevirostris – Blanford (1874)
Eremias brevirostris – Boulenger (1887)
Eremias brevirostris brevirostris – Haas & Werner (1969)
Mesalina brevirostris brevirostris – Szczerbak (1989)

Lectotype. BMNH 1946.8.6.25. Designated herein. Type locality: Tumb Island, Arabian/Persian Gulf, Iran. MorphoBank pictures: M407236–M407250.

Paralectotypes. BMNH 1917.3.6.16–17, same locality as the lectotype; BNHM 1946.8.6.34, Kalabagh, Punjab, Pakistan. MorphoBank pictures: M407251–M407267.

Distribution. Southern Iran, including islands in the Arabian/Persian Gulf, Bahrain, Qatar, United Arab Emirates and adjacent Saudi Arabia (Fig. 1). Apart from the paralectotype BNHM 1946.8.6.34, the species has been reported from Pakistan by some authors (e.g. Haas & Werner 1969; Khan 2006). The Pakistani range seems to be formed by two disjunct populations – (i) coastal, which might represent an eastern continuation of the range of *M. brevirostris* s. s. documented in Iran, and (ii) the Punjab population. Unfortunately, we were not able to obtain any Pakistani material for the genetic analyses and we thus cannot confirm whether the Pakistani populations are conspecific with those from the Arabian/Persian Gulf. Khan (2006) noticed the presence of occipital shield in the Punjab population (found also in the paralectotype) which is usually absent in *M. brevirostris* s. s. and which may indicate a possible distinction of the northern Pakistani population.

Notes. The type locality restriction made by Schmidt (1939) to ‘Kalabagh, Punjab’ without designating a lectotype is *per se* not valid according to the International Code of Zoological Nomenclature, Articles 74.1 and 76.2 (ICZN 1999). The type locality designated herein represents Blanford’s original collection site on the Tumb Island, which is located close to the genetically screened populations (Fig. 1).

***Mesalina bernoullii* (Schenkel, 1901) comb. nov.**

Eremias bernoullii – Schenkel (1901)
Eremias brevirostris – Boulenger (1887)
Eremias brevirostris forma *typica* – Angel (1936)
Eremias brevirostris fieldi – Haas & Werner (1969). Holotype MCZ 56617. Type locality Mahor Birinji, Khuzestan Province, Iran. MorphoBank pictures: M407313–M407317.
Mesalina brevirostris – Szczerbak (1989)
Mesalina brevirostris brevirostris – Szczerbak (1989)

Holotype. NMB 4396. Type locality: ‘Palmyra’ (Syria). MorphoBank pictures: M407230–M407235.

Distribution. Sinai, Jordan, Syria, Iraq, south-western Iran, Kuwait, north-eastern Saudi Arabia (Fig. 1).

Notes. *Mesalina bernoullii* represents a morphologically very variable species (Table S5). Several geographically isolated morphotypes that differ considerably in body size and scalation can be found within its large range. For example, Haas and Werner (1969) assigned a subspecific status (*Eremias brevirostris fieldi*) to the population from south-western Iran characterized by low numbers of dorsal and gular scales and subdigital lamellae and Moravec (2004) described a morphotype from Jabal al Arab, southern Syria, that has unusually high numbers of scales of the same characters. Nevertheless, our results did not show any correlation between this morphological and phylogenetic clustering.

The material analyzed in this study included specimens from the type locality of *Eremias bernoullii* Schenkel, 1901 corresponding morphologically to the holotype of this taxon. It also included a specimen from ca. 40 km of the type locality of *E. brevirostris fieldi* Haas and Werner, 1969 corresponding morphologically to this form, as well as individuals representing the Jabal al Arab morphotype. Based on the results of the phylogenetic and morphological analyses we conclude that the name *Eremias brevirostris fieldi* Haas and Werner, 1969 is a junior subjective synonym of *Eremias bernoullii* Schenkel, 1901.

***Mesalina microlepis* (Angel, 1936) stat. nov.**
Eremias brevirostris – Boulenger (1921)
Eremias brevirostris microlepis – Angel (1936)
Mesalina brevirostris microlepis – Szczerbak (1989)

Holotype. MNHN 1935.285. Type locality: 'Haouarine' ['à 55 kilomètres au S.-E. de Homs'], (Syria). MorphoBank pictures: M407268–M407305.

Distribution. Lebanon, Syria, northern Jordan and southern Turkey (Fig. 1).

Notes. *Mesalina microlepis* is morphologically very similar to *M. bernoullii* and, contrary to what Angel (1936) suggested it cannot be distinguished from it by the numbers of dorsal and gular scales, and subdigital lamellae. The only morphological character that discriminates the species is the structure of the lower eyelid window. All specimens of *M. microlepis* (including the holotype) possess a window consisting of more than three roughly equal semitransparent scales whereas the window of *M. bernoullii*, *M. brevirostris* s. s. and the new Saudi species consists of 1–3 larger semitransparent scales (see Fig. 3 in Mayer *et al*. 2006). *Mesalina microlepis* and *M. bernoullii* have been confirmed to occur syntopically in western Syria (Mayer *et al.* 2006). The presence of *M. microlepis* in Jordan and Turkey is confirmed based on specimens with similar eyelid window structure (Haas & Werner 1969; Kumlutaş *et al.* 2002).

***Mesalina saudiarabica* Moravec, Šmíd, Schmitz, Shobrak, Wilms – sp. n.**
Mesalina brevirostris – Kapli *et al.* (2015)
Mesalina sp. – Kapli *et al*. (2015)

Holotype. ZFMK 91912, subadult male, Mahazat as-Sayd, Makkah Province, Saudi Arabia, 22.237 N, 41.843 E, 1000 m a.s.l., collected in October 2006 by T. Wilms. MorphoBank pictures: M407306–M407312.

Paratype. ZFMK 86583, subadult male, Mahazat as-Sayd, near Al Muwayh, Makkah Province, Saudi Arabia, 22.395 N 41.753 E, 960 m a.s.l., collected in October 2006 by T. Wilms. MorphoBank picture: M410851.

Referred material not included in the type series. NMP6F 29-30 (photovoucher), adult male, observed on the type locality in October 2006 by T. Wilms.

Diagnosis. A species of *Mesalina* and a member of the *M. brevirostris* species complex as revealed by the genetic analyses and characterized by the following combination of characters: (1) genetic (uncorrected) distance of 2.0% from *M. brevirostris*, 2.7% from *M. bernoullii*, and 2.8% from *M. microlepis* for the *12S* (after Gblocks); 2.9% from *M. brevirostris*, 3.3% from *M. bernoullii*, and 4.0% from *M. microlepis* for the *16S* (after Gblocks); 9.5% from *M. brevirostris*, 7.5% from *M. bernoullii*, and 10.8% from *M. microlepis* for the *cytb*; (2) low number of dorsal scales (41–42); (3) low number of collar plates (6–8); (4) low number of preanal scales (2–3); (5) low number of femoral pores in males (12–13); (6) having 1–2 large semitransparent scales in the lower eyelid window; (7) in life, dorsum light cinnamon brown with a pattern of small whitish and larger dark cinnamon spots arranged in more or less regular longitudinal rows. Most of the whitish spots are not edged with dark brown color. The dark cinnamon brown spots predominate on flanks where they form a characteristic longitudinal lateral row that continues onto the tail. Ventral side bright white, sharply contrasting with the coloration of the dorsum.

Comparisons. *Mesalina saudiarabica* sp. n. can primarily be distinguished from other species of the complex by its genetic differentiation at both mtDNA and nDNA level. Genetic distances in the mtDNA genes are given above in the diagnosis and in Table 1. The differentiation in the nDNA is obvious from the allele networks (Fig. 2) that show that the species does not share alleles of any gene with any other species. *Mesalina saudiarabica* sp. n. is also geographically isolated from the rest of the complex. The nearest localities of *M. bernoullii* lie 680 km to the east or 860 to the north. Moreover it can be distinguished morphologically from *M. microlepis* by having 1–2 large semitransparent scales in the lower eyelid (several roughly equal semitransparent scales in the latter), lower number of collar plates (6–8 vs. 10–13; *t*-test t = 5.01, $p < 0.001$), lower number of dorsal scales (41–42 vs. 48–61; *t*-test t = 3.78, $p < 0.005$), lower number of preanal scales (2–3 vs. 4; *t*-test t = 8.14, $p < 0.001$), and lower number of femoral pores in males (12–13 vs. 15–20; *t*-test t = 5.12, $p < 0.001$). The lower number of collar plates differentiates the new species also from *M. bernoullii* (6–8 vs. 8–13; *t*-test t = 3.14, $p < 0.005$) and *M. brevirostris* s. s., although not significantly after Bonferroni correction (6–8 vs. 8–10; *t*-test t = -2.67, $p < 0.05$) (Tables S4, S5).

Description of the holotype. Subadult male (Fig. 4). Body slender, slightly depressed; snout short with prominent elevated nostrils, occipital shield absent, two large semitransparent scales in the lower eyelid; snout-vent length 31.0 mm, tail length 56.0 mm, head length 6.9/8.0 mm (to the anterior/posterior edge of the ear), head width 5.1 mm, head depth 3.5 mm. Upper labials (left/right) anterior the centre of eye 5/5 (smaller fifth upper labial separating the subocular from the mouth included), gulars 25, plates in collar 8, dorsals across midbody 41, ventrals across belly 12, transverse rows of ventrals 32, preanals in straight median series 3, subdigital lamellae 23/24, femoral pores 13/13. In alcohol, dorsum light brown with a pattern of small whitish and larger dark brown spots. Most of the whitish spots are not edged with dark brown color. The spots are arranged in more or less regular longitudinal rows. The dark brown spots predominate on flanks where they form a longitudinal lateral row that continues onto the tail. The lateral row of large brown spots is bordered by a dorsolateral row of small whitish spots and a narrow inconspicuous whitish ventrolateral line. Ventral side white.

Variation. The paratype generally corresponds in morphology with the holotype. Apart from several minute differences in scalation described in the paragraph Diagnosis it differs also in the presence of a distinct occipital shield and the presence of only one large semitransparent scale in the lower eyelid. The paratype lacks the left hind leg and the tail.

Distribution and ecology. All eight so far known localities of *Mesalina saudiarabica* sp. n. as well as its range of suitable conditions are located in central-western Saudi Arabia on the central plateau of the Arabian Peninsula at elevations of 900–1050 m a.s.l. The region is characterized by hot and semi-arid to arid climate with mean summer temperatures up to 30°C and mean annual precipitation of 50–100 mm with rain typically occurring between March and May (Edgell 2006; Shobrak 2011). The terrain consists mostly of flat gravel plains known as 'regs', occasionally intersected by dry sandy wadis and dominated by sparse vegetation of perennial grasses including *Stipagrostis* sp., *Panicum turgidum* and *Lasiurus scindicus* and small trees, mainly *Acacia* sp. (Mandaville 1990).

The type locality is located in the Mahazat as-Sayd Nature Reserve, approximately 170 km E-NE of Taif. The reserve is Saudi Arabia's only completely fenced wildlife reserve and is a reintroduction site for MacQueen's bustard (*Chlamydotis macqueenii*), Arabian oryx (*Oryx leucoryx*) and Sand gazelles (*Gazella subgutturosa*). At the reserve, *Acacia tortilis* is the most common tree species, *Fagonia indica* and *Indigofera spinosa* are the most common herbs, and *Panicum turgidum* and *Stipagrostis* spp. are the prevailing grasses.

Etymology. The specific epithet is derived from the name of the country where the species occurs. Proposed English name – Arabian short-nosed desert lizard.

References to Supplementary Materials

Angel, F. (1936). Reptiles et batraciens de Syrie et de Mésopotamie récoltés par M. P. Pallary. *Bulletin de l'Institut d'Egypte*, 18, 107–116.

Blanford, W. T. (1874). Description of new Reptilia and Amphibia from Persia and Baluchistan. *Annals and Magazine of Natural History*, 4, 31–35.

Boulenger, G. A. (1887). *Catalogue of the lizards in the British Museum (Natural History). Vol. III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae.* London: Trustees of the British Museum.

Boulenger, G. A. (1921). *Monograph of the Lacertidae. II.* London: Longmans, Green & Co. and British Museum (Natural History).

Edgell, H. S. (2006). *Arabian deserts: nature, origin and evolution*. Dordrecht, The Netherlands: Springer.

Haas, G., & Werner, Y. L. (1969). Lizards and snakes from southwestern Asia, collected by Henry Field. *Bulletin of the Museum of Comparative Zoology*, 138, 327–406.

ICZN (1999). *International Code of Zoological Nomenclature*. London, UK: The International Trust for Zoological Nomenclature.

Kapli, P., Lymberakis, P., Crochet, P. A., Geniez, P., Brito, J. C., Almutairi, M., Ahmadzadeh, F., Schmitz, A., Wilms, T., Rastegar-Pouyani, N., & Poulakakis, N. (2015). Historical biogeography of the lacertid lizard *Mesalina* in North Africa and the Middle East. *Journal of Biogeography*, 42, 267–279.

Khan, M. S. (2006). *Amphibians and reptiles of Pakistan*. Malabar, Florida: Krieger Publishing Company.

Kumlutaş, Y., Taskavak, E., Baran, I., Ilgaz, Ç., & Avci, A. (2002). First record of Blanford's Short-nosed desert lizard *Mesalina brevirostris* Blanford, 1874, from Anatolia. *Herpetozoa*, 15, 171–178.

Mandaville, J. P. (1990). Flora of Eastern Saudi Arabia. *London: Kegan Paul Int*.

Mayer, W., Moravec, J., & Pavlicev, M. (2006). Differentiation within Syrian populations of the lizard *Mesalina brevirostris*. In C. Corti, P. Lo Cascio e M. Biaggini (Eds). *Mainland and insular lacertid lizards: a Mediterranean perspective* (pp 125–131). Firenze University Press, Firenze, 218 pp.

Moravec, J. 2004. Distribution and morphological variation of the lizard *Mesalina brevirostris* in Syria. In V. Pérez-Mellado, N. Riera & A. Perera (Eds) *The biology of lacertid lizards. Evolutionary and ecological perspectives.* pp. 245–257): Institut Menorquí d'Estudis. Recerca, 8. Maó, Menorca.

Schenkel, E. (1901). Achter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 13, 142–199.

Schmidt, K. P. (1939). Reptiles and Amphibians from Southwestern Asia. *Zoological Series of Field Museum of Natural History.*, 24, 49–92.

Shobrak, M. (2011). Changes in the number of breeding pairs, nest distribution and nesting trees used by the Lappet-faced Vulture Torgos tracheliotus in the Mahazat As-Sayd protected area, Saudi Arabia. *Journal of the Bombay Natural History Society*, 108, 114–119.

Szczerbak, N. N. (1989). Catalogue of the African Sand Lizards (Reptilia: Sauria: Eremiainae: *Lampreremias*, *Pseuderemias*, *Taenieremias*, *Mesalina*, *Meroles*). *Herpetozoa*, 1, 119–132.

SUPPLEMENTARY FIGURES

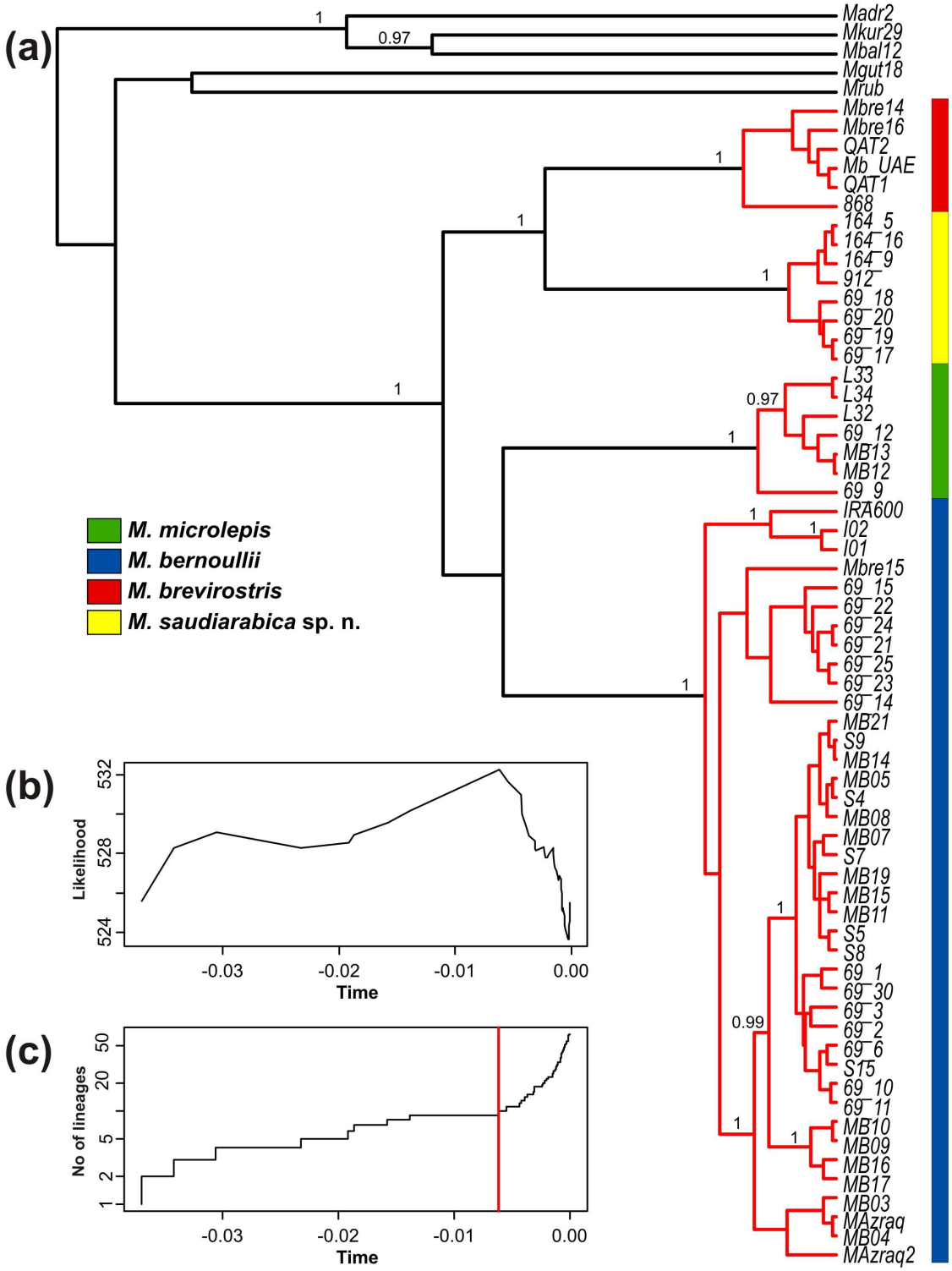

Figure S1. Results of the BI analysis of concatenated mtDNA data and GMYC species delimitation analysis. (a) MCC tree from the mtDNA analysis with posterior probabilities ≥ 0.95 shown by nodes. Sample codes correspond to those in Table S1. Branches colored in red indicate putative species identified by the GMYC species delimitation analysis. (b) Likelihood values produced by GMYC to estimate the transition between cladogenesis and intraspecific coalescence. (c) Lineage-through-time plot based on the depicted tree that shows the transition from interspecific to intraspecific branching events (red line). The time scale in (b) and (c) is relative.

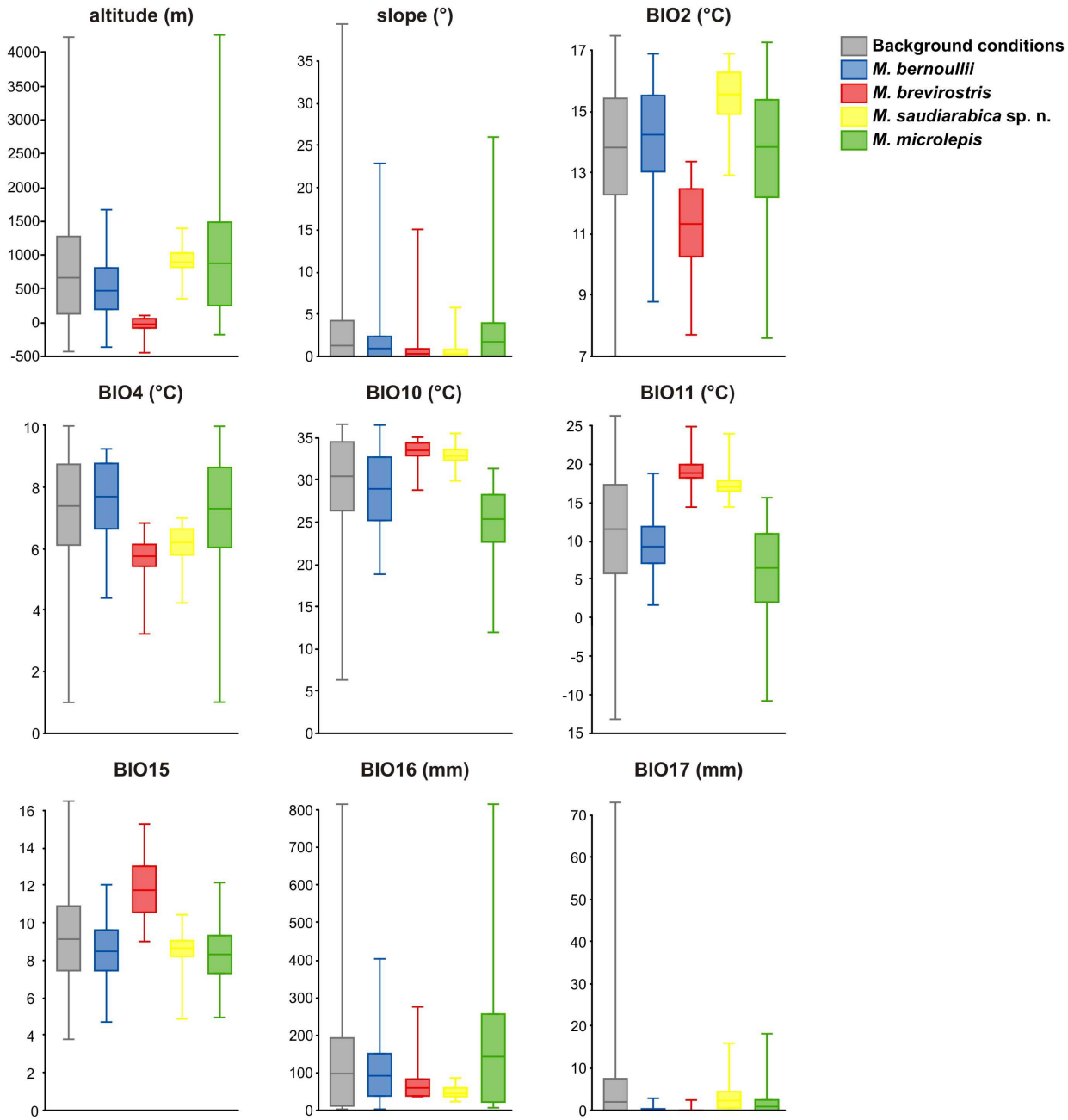

Figure S2. Environmental space of the background used for developing the SDMs (grey box) and its parts occupied by *Mesalina bernoullii*, *M. brevirostris*, *M. saudiarabica* sp. n., *M. microlepis*. Values for the nine non-correlated environmental variables are shown (for abbreviations explanation see Material and methods). The species environmental space is based on their modelled distribution. Mean values (central line), standard deviation (box) and minimum and maximum values (whiskers) are shown.

Table S1. Material used for the genetic analyses. 'Sample' column refers to codes shown in Fig. S1; 'Analyses' indicates what phylogenetic analyses each sample was used for.

Sample	Museum number	Species	Country	Locality	Lat	Long	*12S*	*16S*	*cytb*	MC1R	β-*fibint7*	*c-mos*	Analyses
L32	NMP 74214/1	*M. microlepis*	Lebanon	Hermel	34.366	36.403	KY967184	KY967122	KY967149	KY967105	KY967205	KY967089	mtDNA/*BEAST
L33	NMP 74214/2	*M. microlepis*	Lebanon	Hermel	34.366	36.403	KY967184	KY967123	KY967150	KY967106	KY967206	KY967089	mtDNA/*BEAST
L34	NMP 74214/3	*M. microlepis*	Lebanon	Hermel	34.366	36.403	KY967184	KY967123	KY967150	KY967107	KY967207	KY967089	mtDNA/*BEAST
MB12	NMP 70439/4	*M. microlepis*	Syria	3 km W of Sadad	34.311	36.907	KY967184	KY967124	KY967151				mtDNA
MB13	NMP 70439/5	*M. microlepis*	Syria	3 km W of Sadad	34.311	36.907	KY967184	KY967125	KY967151				mtDNA
69_9	NHMC 80.3.69.9	*M. microlepis*	Syria	10-17 km NE of Deir ez-Zur	35.417	40.32	KY967183	EF555306	EF555264			KY967088	mtDNA
69_12	NHMC 80.3.69.12	*M. microlepis*	Syria	40 km S of Homs	34.293	36.766	KY967184	EF555309	EF555267		KM411259	KY967089	mtDNA/*BEAST
S4	NMP 73984/1	*M. bernoullii*	Syria	3 km W of Sadad	34.311	36.907	KY967189	KY967133	KY967160	KY967115	KY967214	KY967096	mtDNA/*BEAST
S5	NMP 73984/2	*M. bernoullii*	Syria	3 km W of Sadad	34.311	36.907	KY967189	KY967133	KY967173	KY967115	KY967215	KY967096	mtDNA/*BEAST
S7	NMP 73984/3	*M. bernoullii*	Syria	3 km W of Sadad	34.311	36.907	KY967189	KY967142	KY967174	KY967111	KY967216	KY967097	mtDNA/*BEAST
S8	NMP 73984/4	*M. bernoullii*	Syria	3 km W of Sadad	34.311	36.907	KY967189	KY967143	KY967175	KY967115	KY967217	KY967098	mtDNA/*BEAST
S9	-	*M. bernoullii*	Syria	3 km W of Sadad	34.311	36.907	KY967189	KY967133	KY967164	KY967110	KY967218	KY967096	mtDNA/*BEAST
S15	NMP 73983	*M. bernoullii*	Syria	Palmyra	34.525	38.286	KY967189	KY967141	KY967172	KY967114	KY967213	KY967095	mtDNA/*BEAST
I01	-	*M. bernoullii*	Iran	Chosrevi	34.389	45.471	KY967190	KY967134	KY967154	KY967112	KY967208	KY967091	mtDNA/*BEAST
I02	-	*M. bernoullii*	Iran	Chosrevi	34.389	45.471	KY967191	KY967135	KY967155	KY967113	KY967209	KY967092	mtDNA/*BEAST
IRA600	CUP REPT\IRA\600	*M. bernoullii*	Iran	SE of Haft Tappe	32.033	48.5	KY967192	KY967136	KY967156				mtDNA
MB03	NMP 70224/2	*M. bernoullii*	Jordan	10 km SW of Azrag	31.833	36.817		KY967132	KY967159				mtDNA
MB04	NMP 71120	*M. bernoullii*	Jordan	S of Amman, road Azraq - Al - Jafr	30.923	36.569	KY967193	KY967132	KY967159				mtDNA
MB05	NMP 71527	*M. bernoullii*	Jordan	E Jordan	32.458	38.037		KY967133	KY967160				mtDNA
MB07	NMP 70305/1	*M. bernoullii*	Syria	28 km N of Palmyra	34.628	38.561	KY967189	KY967133	KY967162		KY967210		mtDNA
MB08	NMP 70305/2	*M. bernoullii*	Syria	28 km N of Palmyra	34.628	38.561	KY967194	KY967133	KY967161				mtDNA
MB09	NMP 70211/2	*M. bernoullii*	Syria	9 km SW of Rashiedeh	32.722	36.938	KY967195	KY967137	KY967165				mtDNA
MB10	NMP 70211/3	*M. bernoullii*	Syria	9 km SW of Rashiedeh	32.722	36.938	KY967195	KY967137	KY967166			KY967093	mtDNA
MB11	NMP 70439/3	*M. bernoullii*	Syria	3 km W of Sadad	34.311	36.907	KY967189	KY967133	KY967167				mtDNA
MB14	NMP 70440/7	*M. bernoullii*	Syria	Hawarin	34.267	37.067	KY967189	KY967133	KY967163				mtDNA
MB15	NMP 70440/8	*M. bernoullii*	Syria	Hawarin	34.267	37.067	KY967189	KY967133	KY967168				mtDNA
MB16	NMP 70629/1	*M. bernoullii*	Jordan	Amman	31.967	35.967	KY967195	KY967138	KY967169				mtDNA
MB17	NMP 70629/2	*M. bernoullii*	Jordan	Amman	31.967	35.967	KY967195	KY967139	KY967170		KY967211	KY967094	mtDNA/*BEAST
MB19	NMP 33079/2	*M. bernoullii*	Iraq	SW of Ar Rutbah	33.021	40.277	KY967189	KY967133					mtDNA
MB21	NMP 33079/4	*M. bernoullii*	Iraq	SW of Ar Rutbah	33.021	40.277		KY967133					mtDNA
MB_Azraq	NMP 70224/1	*M. bernoullii*	Jordan	10 km SW of Azrag	31.833	36.817			KY967157				mtDNA
MB_Azraq2	NMP 70224/3	*M. bernoullii*	Jordan	10 km SW of Azrag	31.833	36.817			KY967158				mtDNA
Mbre15	SMB 10708	*M. bernoullii*	Egypt	Sinai, Ras Mohamed	27.747	34.229	KY967196	KY967140	KY967171		KY967212		mtDNA

Sample	Museum number	Species	Country	Locality	Lat	Long	*12S*	*16S*	*cytb*	MC1R	β-*fibint7*	*c-mos*	Analyses
69_1	NHMC 80.3.69.1	*M. bernoullii*	Syria		34.362	38.174		EF555302	EF555260				mtDNA
69_2	NHMC 80.3.69.2	*M. bernoullii*	Syria		34.6	37.832		EF555303	EF555261		KM411250		mtDNA
69_3	NHMC 80.3.69.3	*M. bernoullii*	Syria		34.6	37.832	KY967189	KY967131	EF555262		KM411252	KY967090	mtDNA/*BEAST
69_6	NHMC 80.3.69.6	*M. bernoullii*	Syria		34.814	38.79		EF555305	EF555263				mtDNA
69_10	NHMC 80.3.69.10	*M. bernoullii*	Syria		35.427	40.028	KY967189	EF555307	EF555265				mtDNA
69_11	NHMC 80.3.69.11	*M. bernoullii*	Syria		35.427	40.028		EF555308	EF555266				mtDNA
69_14	NHMC 80.3.69.14	*M. bernoullii*	Saudi Arabia		26.418	47.479		KM411038	KM411190		KM411277		mtDNA
69_15	NHMC 80.3.69.15	*M. bernoullii*	Saudi Arabia		26.415	47.477		KM411039	KM411191		KM411278		mtDNA
69_21	NHMC 80.3.69.21	*M. bernoullii*	Kuwait		29.368	47.81		KM411083	KM411234				mtDNA
69_22	NHMC 80.3.69.22	*M. bernoullii*	Kuwait		29.014	47.977		KM411084	KM411235				mtDNA
69_23	NHMC 80.3.69.23	*M. bernoullii*	Kuwait		29.845	48.113		KM411085	KM411236		KM411302		mtDNA
69_24	NHMC 80.3.69.24	*M. bernoullii*	Kuwait		29.379	47.842		KM411086	KM411237				mtDNA
69_25	NHMC 80.3.69.25	*M. bernoullii*	Kuwait		29.824	47.25		KM411031	KM411183				mtDNA
69_30	NHMC 80.3.69.30	*M. bernoullii*	Syria		33.683	36.495		KM410995	KM411142				mtDNA
Mbre14	-	*M. brevirostris*	Bahrain		26.135	50.535	KY967186	KY967127	KY967152	KY967108	KY967203	KY967087	mtDNA/*BEAST
Mbre16	-	*M. brevirostris*	UAE	Jabal Dannah	24.158	52.633	KY967187	KY967128	KY967153	KY967109	KY967204	KY967087	mtDNA/*BEAST
Mb_UAE	NHMW 32326:10	*M. brevirostris*	UAE	Abu Dhabi	24.387	54.547	AY035831	AY035841					mtDNA
QAT1	QM Q201376	*M. brevirostris*	Qatar	Fuwairit	26.011	51.39	KY967188	KY967129					mtDNA
QAT2	QM Q201371	*M. brevirostris*	Qatar	Ras Laffan	25.823	51.574	KY967188	KY967130					mtDNA
868	SUHC 868	*M. brevirostris*	Iran	Bandar-e Lengeh	26.688	54.422	KY967185	KY967126					mtDNA
69_20	NHMC 80.3.69.20	*M. saudiarabica* sp. n.	Saudi Arabia		23.511	41.422		KM411043	KM411195				mtDNA
69_19	NHMC 80.3.69.19	*M. saudiarabica* sp. n.	Saudi Arabia		24.253	41.154		KM411042	KM411194				mtDNA
69_18	NHMC 80.3.69.18	*M. saudiarabica* sp. n.	Saudi Arabia		23.504	41.347		KM411041	KM411193				mtDNA
69_17	NHMC 80.3.69.17	*M. saudiarabica* sp. n.	Saudi Arabia		23.539	40.589		KM411040	KM411192		KM411279		mtDNA/*BEAST
164_9	NHMC 80.3.164.9	*M. saudiarabica* sp. n.	Saudi Arabia		22.252	41.88		KM411054	KM411206				mtDNA
164_5	NHMC 80.3.164.5	*M. saudiarabica* sp. n.	Saudi Arabia		22.4	41.733		KM411046	KM411198				mtDNA
164_16	ZFMK 86583	*M. saudiarabica* sp. n.	Saudi Arabia	near Al Moiyah	22.395	41.753	KY967181	KY967121	KM411151				mtDNA/*BEAST
912	ZFMK 91912	*M. saudiarabica* sp. n.	Saudi Arabia	Mahazat-as-Sayd	22.237	41.843	KY967182			KY967104	KY967202	KY967086	mtDNA/*BEAST
Madr2	IBES 2807	*M. adramitana*	Oman	16 km S of Duqm	19.563	57.623	KY967176	KY967116	KY967144	KY967099	KY967197	KY967081	mtDNA
Mbal12	IBES 5650	*M. balfouri*	Yemen		12.363	53.933	KY967178	KY967118	KY967146	KY967101	KY967199	KY967083	mtDNA
Mgut18	TAU 16256	*M. bahaeldini*	Israel	Zomet Ha'nokdim (Ohalim)	31.19	34.805	KY967177	KY967117	KY967145	KY967100	KY967198	KY967082	mtDNA
Mkur29	IBES 5368	*M. kuri*	Yemen	Abd al Kuri	12.2	52.266	KY967179	KY967119	KY967147	KY967102	KY967200	KY967084	mtDNA
Mrub	NMP 74765/1	*M. rubropunctata*	Sudan	Wadi Halfa	21.801	31.349	KY967180	KY967120	KY967148	KY967103	KY967201	KY967085	mtDNA

Table S2. List of collections and their acronyms from which material was examined both genetically and morphologically.

Acronym	Collection
BMNH	Natural History Museum, London, UK
CUP	Charles University, Prague, Czech Republic
IBES	Institute of Evolutionary Biology Collection, Barcelona, Spain
MCZ	Museum of Comparative Zoology, Cambridge, USA
MNHN	Muséum National d'Histoire naturelle, Paris, France
NHMC	Natural History Museum of Crete, Greece
NHMW	Museum of Natural History, Vienna, Austria
NMB	Naturhistorisches Museum Basel, Switzerland
NMP	National Museum Prague, Czech Republic
QM	Qatar Museum, Doha, Qatar
SMB	Sherif Baha El Din private collection, Cairo, Egypt
SUHC	Sabzevar University Herpetological Collection, Khorasan Razavi, Iran
TAU	Tel Aviv University Zoological Museum, Tel Aviv, Israel
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

Table S3. Genetic markers amplified for this study with corresponding primer details, fragment length (before and after being trimmed by Gblocks), PCR annealing temperature, and original source.

Gene	Primer name	Primer sequence (5´- 3´)	Fragment length (before/after Gblocks)	Annealing T	Primer source
12S	12Sa 12Sb	AAACTGGGATTAGATACCCCACTAT GAGGGTGACGGGCGGTGTGT	392/383 bp	48°C	Kocher *et al*. 1989
16S	16SL1 16SH1	CGCCTGTTTAACAAAAACAT CCGGTCTGAACTCAGATCACGT	543/487 bp	47°C	Palumbi *et al*. 1991 (modified)
cytb (partial)	GLUDG CYTB2	TGACTTGAARAACCAYCGTTG CCCTCAGAATGATATTTGTCCTCA	425 bp	49°C	Palumbi *et al*. 1991 Kocher *et al*. 1989
cytb (complete)	L14910 H16064	GACCTGTGATMTGAAAACCAYCGTTGT CTTTGGTTTACAAGAACAATGCTTTA	1137 bp	46°C	Burbrink *et al*. 2000
MC1R	MC1RF MC1RR	AGGCNGCCATYGTCAAGAACCGGAACC CTCCGRAAGGCRTAAATGATGGGGTCCAC	663 bp	56°C	Pinho *et al*. 2009
β-*fibint7*	Mes_fib7_F Mes_fib7_R	AGAGACAATGATGGCTGGTATG TGGAACACTGTTTCTTTGGGTC	550/540 bp	50°C	Kapli *et al.* 2014
c-mos	Cmos-FUF Cmos-FUR	TTTGGTTCKGTCTACAAGGCTAC AGGGAACATCCAAAGTCTCCAAT	394 bp	53°C	Gamble e*t al.* 2008

References to Table S3 not cited in the text

Burbrink, F. T., Lawson, R., & Slowinski, J. B. (2000). Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution*, 54(6), 2107–2118.

Gamble, T., Bauer, A. M., Greenbaum, E., & Jackman, T. R. (2008). Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *Journal of Biogeography*, 35(1), 88–104.

Kocher, T. D., Thomas, W. K., Meyer, A., Edwards, S. V., Pääbo, S., Villablanca, F. X., et al. (1989). Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences*, 86(16), 6196–6200.

Palumbi, S., Martin, A., Romano, S., McMillan, W. O., Stice, L., & Grabowski, G. (1991). *Simple fool's guide to PCR*. Honolulu: Department of Zoology and Kewalo Marine Laboratory, University of Hawaii, 45 pp.

Pinho, C., Rocha, S., Carvalho, B. M., Lopes, S., Mourao, S., Vallinoto, M., et al. (2010). New primers for the amplification and sequencing of nuclear loci in a taxonomically wide set of reptiles and amphibians. *Conservation Genetics Resources*, 2(1), 181–185.

Table S4. Material examined for morphological comparisons and original measurements for each specimen. For details on the morphological character acronyms see Material and methods.

Species	Type specimen	Museum number	Country	Locality	sex	SVL	TL	HL	HW	HD	Upper labials.L	Upper labials.R	gulars	collar	dorsals	ventrals	praeanals	Subdigital lamellae.L	Subdigital lamellae.R	pores.L	pores.R	Data source
Mesalina microlepis	Holotype	MNHN 1935.285	Syria	Hawarin	m	55.0		11.6	8.5	6.7	6	6	26	11	61	36	4	24	24	18	20	this study
Mesalina microlepis		NMP 74214/1	Lebanon	Hermel	m	50.0	91.0	12.3	8.9	6.8	5	5	26	11	51	31	4	21	21	17	17	this study
Mesalina microlepis		NMP 74214/2	Lebanon	Hermel	m	50.0	91.0	11.4	8.1	6.5	5	5	24	10	52	30	4	21	22	18	18	this study
Mesalina microlepis		NMP 74214/3	Lebanon	Hermel	f	50.0	91.0	11.5	8.4	5.9	5	6	28	13	55	33	4	20	21	17	17	this study
Mesalina microlepis		NMP 70439/4	Syria	3 km W of Sadad	m	52.0	98.0	11.0	8.2	6.1	5	5	26	10	52	33	4	23	23	18	17	this study
Mesalina microlepis		NMP 70439/5	Syria	3 km W of Sadad	m	52.0		11.3	9.1	6.4	5	5	23	11	48	30	4	22	22	17	16	this study
Mesalina microlepis		NMP 70439/6	Syria	3 km W of Sadad	m	51.0	105.0	11.6	9.0	6.6	5	5	27	11	59	33	4	23	23	18	19	this study
Mesalina microlepis		NHMC 80.3.69.9	Syria	10-17 km NE of Deir ez-Zur	m	54.0	113.0	12.6	9.5	7.0	5	5	27	10	50	29	4	23	23	16	16	this study
Mesalina microlepis		NHMC 80.3.69.12	Syria	40 km S of Homs	m	51.0		11.5	8.6	6.6	5	5	24	11	52	29	4	22	22	15	16	this study
Mesalina bernoullii	Holotype	NMB 4396	Syria	Palmyra	m	44.0	82.0	9.2	7.0	4.8	5	5	24	9	45	32	3	22	23	15	14	this study
Mesalina bernoullii		NHMC 80.3.69.2	Syria		f	53.0		11.6	8.4	6.2	5	5	25	10	48	32	4	24	25	15	15	this study
Mesalina bernoullii		NHMC 80.3.69.3	Syria		f	47.0	47.0	9.7	7.6	5.0	4	4	26	11	50	33	3	24	25	15	14	this study
Mesalina bernoullii		NHMC 80.3.69.10	Syria		f	42.0	42.0	9.5			5	5	25	10	46	33	3	23	24	15	15	this study
Mesalina bernoullii		NMP 33079/1	Iraq	SW of Ar Rutbah	m	47.0	78.0	9.8	7.7		5	5	23	11	41	29	4	21	21	14	14	this study
Mesalina bernoullii		NMP 33079/2	Iraq	SW of Ar Rutbah	f	46.0		8.7	7.4		5	5	26	10	51	31	3	23	23	15	15	this study
Mesalina bernoullii		NMP 33079/3	Iraq	SW of Ar Rutbah	m	44.0	89.0	9.4			5	5	22	10	48	29	3	22	21	12	13	this study
Mesalina bernoullii		NMP 33079/4	Iraq	SW of Ar Rutbah	f						5	5	23	10	44	33	3	22	22		14	this study
Mesalina bernoullii		NMP 33096	Iraq	50 km SE of Ar Rutbah	m	46.0	89.0	9.6	7.4		5	5	24	8	45	29	3	22	22	13	13	this study
Mesalina bernoullii		NMP 34774/1	Syria	Dayr az Zawr	m	45.0		9.5	7.4	5.0	5	5	24	8	46	32	3	27	26	15	15	this study
Mesalina bernoullii		NMP 34774/2	Syria	Dayr az Zawr	m	43.0		9.1	7.4	5.5	5	5	25	8	43	31	3	22	22	14	15	this study
Mesalina bernoullii		NMP 34783/1	Syria	Abu Kamal	m	39.0					5	6	23	10	44	33	3	22	22		15	this study
Mesalina bernoullii		NMP 34876/1	Syria	Palmyra	m	44.0	84.0	9.1	7.7	5.4	5	5	22	10	48	29	3	23	22	13	12	this study
Mesalina bernoullii		NMP 34876/2	Syria	Palmyra	m	44.0		10.2	8.2	5.5	5	5	24	11	48	31	3	23	22	14	14	this study
Mesalina bernoullii		NMP 34876/3	Syria	Palmyra	f	47.0	92.0	8.3	7.0	4.8	4	3	24	8	44	36	3	21	21	14	14	this study
Mesalina bernoullii		NMP 34876/4	Syria	Palmyra	f	48.0	82.0	9.1	7.1	5.1	5	5	23	9	50	33	3	23	23	13	13	this study
Mesalina bernoullii		NMP 34876/5	Syria	Palmyra	f	42.0	79.0	8.8	6.8	4.5	5	5	23	8	48	33	3	22	22	14	13	this study
Mesalina bernoullii		NMP 34558	Iran	15 km NE Bandar Lengeh	m	44.0		9.7	7.0	5.2	5	4	28	9	37	29	3	21	21	15	15	this study
Mesalina bernoullii		NMP 34877	Syria	Al Salhyeh	f	48.0	83.0	8.7	7.4	5.0	6	6	25	9	46	34	3	21	25	13	12	this study
Mesalina bernoullii		NMP 34878/1	Syria	Abu Kamal	m	43.0	84.0	9.3	7.3	5.1	5	5	25	9	51	34	3	22	22	12	13	this study
Mesalina bernoullii		NMP 34878/2	Syria	Abu Kamal	m	44.0		9.1	7.3	4.8	5	5	26	8	48	31	3	25	25	14	14	this study
Mesalina bernoullii		NMP 34879/1	Syria	4 km E of Abu Kamal	f	48.0		9.2	7.1	5.0	5	5	23	10	48	34	3	21	21	12	13	this study
Mesalina bernoullii		NMP 34879/2	Syria	4 km E of Abu Kamal	f	42.0		9.1	7.8	4.7	5	5	24	10	51	34	4	22	23	14	14	this study
Mesalina bernoullii		NMP 34879/4	Syria	4 km E of Abu Kamal	f	48.0	90.0	9.2	7.2	4.9	5	5	23	10	44	35	3	23	24	13	13	this study
Mesalina bernoullii		NMP 34880	Syria	10 km of Rashiedeh	m	57.0	113.0	13.7	9.6	6.6	5	5	27	9	55	32	4	22	22	16	16	this study
Mesalina bernoullii		NMP 34881	Syria	15 km NE of Rashiedeh	f	54.0	94.0	11.1	8.2	5.2	5	6	29	8	64	33	5	21	22	16	15	this study
Mesalina bernoullii		NMP 70211/1	Syria	9 km SW of Rashiedeh	m	56.0		12.7	9.7	6.4	5	5	29	12	62	33	5	21	20	14	14	this study

Species	Type specimen	Museum number	Country	Locality	sex	SVL	TL	HL	HW	HD	Upper labials.L	Upper labials.R	gulars	collar	dorsals	ventrals	praeanals	Subdigital lamellae.L	Subdigital lamellae.R	pores.L	pores.R	Data source
Mesalina bernoullii		NMP 70211/2	Syria	9 km SW of Rashiedeh	m	51.0		12.5	9.4	5.9	6	5	31	11	62	35	5	22	21	15	14	this study
Mesalina bernoullii		NMP 70211/3	Syria	9 km SW of Rashiedeh	m	56.0	110.0	12.4	9.5	6.0	5	5	32	13	59	34	5	22	21	14	14	this study
Mesalina bernoullii		NMP 70224/1	Jordan	10 km SW of Azrag	m						4	3	20	10	49	31	3	22	23	11	12	this study
Mesalina bernoullii		NMP 70224/2	Jordan	10 km SW of Azrag	f						5	5	23	10	53	33	3	21	21	13	13	this study
Mesalina bernoullii		NMP 70224/3	Jordan	10 km SW of Azrag	m						5	5	28	10	59	33	4	24	24	12	13	this study
Mesalina bernoullii		NMP 70225	Jordan	Schauamari	m	40.0		9.2	6.9		5	5	25	8	49	33	3	22	23	12	12	this study
Mesalina bernoullii		NMP 70305/1	Syria	28 km N of Palmyra	m	47.0	90.0	10.3	7.8	5.2	5	5	25	11	44	33	3	23	23	13	14	this study
Mesalina bernoullii		NMP 70305/2	Syria	28 km N of Palmyra	m	43.0		10.3	7.7	5.1	4	4	23	11	47	30	3	23	23	15	15	this study
Mesalina bernoullii		NMP 70305/3	Syria	28 km N of Palmyra	f	48.0	88.0	10.1	7.5	5.2	5	5	26	10	45	31	2	23	22	13	13	this study
Mesalina bernoullii		NMP 70305/4	Syria	28 km N of Palmyra	m	43.0		9.5	7.2	4.8	4	4	23	11	41	30	3	22	21	13	13	this study
Mesalina bernoullii		NMP 70313	Syria	5 km SW of Abu Kemal	f	40.0	69.0	8.0	6.0	4.1	5	5	24	9	42	34	4	24	24	14	13	this study
Mesalina bernoullii		NMP 70439/3	Syria	3 km W of Sadad	m	48.0	97.0	10.4	8.2	5.4	5	5	24	10	52	33	4	24	24	18	18	this study
Mesalina bernoullii		NMP 70440/7	Syria	Hawarin	f	52.0		10.4	8.2	5.4	5	5	27	11	55	34	4	23	23	15	16	this study
Mesalina bernoullii		NMP 70440/8	Syria	Hawarin	f	48.0	91.0	10.0	7.2	5.1	4	4	29	11	52	34	4	25	25	14	14	this study
Mesalina bernoullii		NMP 70629/1	Jordan	Amman	f	56.0	100.0	10.9	8.5	6.0	4	4	26	8	52	34	4	21	23	12	13	this study
Mesalina bernoullii		NMP 70629/2	Jordan	Amman	f	56.0	96.0	11.7	9.6	6.6	4	4	28	9	53	34	3	21	22			this study
Mesalina bernoullii		NMP 70629/3	Jordan	Amman	m	52.0		11.2	9.3	5.9	4	5	24		49	30	4	22	21	14	13	this study
Mesalina bernoullii		NMP 71540	Iraq	Bagdad	f	54.0		10.4	8.3	6.4	4	4	25	9	45	33	3	21	21	15	14	this study
Mesalina bernoullii		NMP 73984/1	Syria	3 km W of Sadad	m	48.0	91.0	11.3	8.4	6.1	5	5	27	11	55	31	3	22	22	13	13	this study
Mesalina bernoullii		NMP 73984/2	Syria	3 km W of Sadad	m	46.0	90.0	10.9	8.1	5.8	5	5	28	11	47	33	3	22	23	14	16	this study
Mesalina bernoullii		NMP 73984/3	Syria	3 km W of Sadad	f	48.0		9.9	7.9	5.5	5	6	33	12	56	36	3	24	24	14	14	this study
Mesalina bernoullii		NMP 73984/4	Syria	3 km W of Sadad	m	45.0	92.0	10.0	8.2	5.6	4	4	24	12	52	31	3	22	23	13	13	this study
Mesalina bernoullii		CUP REPT\IRA\600	Iran	SE of Haft Tappe	m	44.0		9.5	7.6	5.5	4	4	21	10	36	32	3	20	19	15	16	this study
Mesalina saudiarabica sp. nov.	Paratype	ZFMK 86583	Saudi Arabia	Al Moiyah	m subad	32.5		7.5	5.6	3.7	5	6	26	6	42	32	2		23		12	this study
Mesalina saudiarabica sp. nov.	Holotype	ZFMK 91912	Saudi Arabia	Mahazat-as-Sayd	m subad	31.0	56.0	6.9	5.1	3.5	5	5	25	8	41	32	3	23	24	13	13	this study
Mesalina brevirostris	Paralectotype	BNHM 1946.8.6.34	Pakistan	Kalabagh	f	44.0					7	5	28	9	46	33		24		14	15	Boulenger (1921)
Mesalina brevirostris		?	Iran	Dasht	f	41.0					4	4	28	10	42	30		22		15	16	Boulenger (1921)
Mesalina brevirostris	Lectotype	BMNH 1946.8.6.25	Iran	Tumb Island	f	40.0					5	5	25	9	46	32		21		16	16	Boulenger (1921)
Mesalina brevirostris	Paralectotype	BMNH 1917.3.6.16	Iran	Tumb Island	f	40.0					4	4	26	8	45	32		22		15	15	Boulenger (1921)
Mesalina brevirostris	Paralectotype	BMNH 1917.3.6.17	Iran	Tumb Island	f	36.0					4	4	25	9	47	30		20		14	14	Boulenger (1921)

Table S5. Morphological comparison of *Mesalina saudiarabica* sp. n. with the other species formerly included under *M. brevirostris*. Values marked by asterisk indicate subadult specimens.

n **Mean ± SD** **Min – Max**	***M. brevirostris*** **data from (Blanford 1876)**	***M. brevirostris*** **data from (Boulenger 1921)**	***M. brevirostris fieldi*** **data from (Haas & Werner 1969)**	***M. bernoullii***	***M. microlepis***	***M. saudiarabica* sp. n.**
Dorsal scales	? 43–45	5 42–47	22 31–39	50 49.0 ± 5.99 36–64	9 53.3 ± 4.24 48–61	2 41–42
Gular scales	- -	5 25–28	22 20–25	50 25.2 ± 2.70 20–33	9 25.7 ± 1.66 23–28	2 25–26
Collar scales	- -	5 8–10	22 8–9	49 9.9 ± 1.26 8–12	9 10.9 ± 0.93 10–13	2 6–8
Ventral scales (♂)	? 30–33	- -	22 28–35	28 31.5 ± 1.73 29–35	8 31.4±2.45 29–36	2 32
Ventral scales (♀)		5 30–33		22 33.5 ± 1.26 31–36	1 33	2 -
Preanal scales	- -	- -	-	50 3.4 ± 0.66 2–5	9 4.0 ± 0.0	2 2–3
Lamellae under 4th toe	- -	5 20–24	44 16–20	100 22.5 ± 1.34 19–27	18 22.2 ± 1.11 20–24	3 23–24
Femoral pores (♂)	? 13–16	- -	44 12–15	55 13.9 ± 1.43 11–16	16 17.3 ± 1.29 15–20	3 12–13
Femoral pores (♀)		5 14–16		41 13.9 ± 1.03 12–16	2 17	- -
SVL (♂)	- -	- -	- -	26 46.3 ± 4.65 39.0–57.0	8 51.9 ± 1.81 50.0–55.0	2 31.0–32.0*
SVL (♀)	- -	5 36.0–44.0	- -	20 48.4 ± 4.68 40.0–55.0	1 50	- -
HW*100/HL (♂)	- -	- -	- -	24 77.4 ± 3.47 70,1–84.6	8 75.0 ± 2.98 71.1–80.5	3 73.9–74.7*
HW*100/HL (♀)	- -	- -	- -	19 78.9 ± 4.20 72.4–85.7	1 73	- -
HD*100/HL (♂)	- -	- -	- -	21 52.6 ± 3.49 48.2–60.4	8 56.5 ± 0.94 55.3–57.8	3 49.3–50.7*
HD*100/HL (♀)	- -	- -	- -	18 52.9 ± 3.39 46.8–61.5	1 51.3	- -