Šmíd *et al. BMC Zoology* (2025) 10:11
https://doi.org/10.1186/s40850-025-00233-3

BMC Zoology

RESEARCH **Open Access**

Phylogeny and systematics of Arabian lacertids from the *Mesalina guttulata* species complex (Squamata, Lacertidae), with the description of a new species

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Abstract

Background The lacertid genus *Mesalina* has been the subject of several phylogenetic and biogeographic studies as well as taxonomic revisions within the last decade. The genus is partitioned into seven main clades, some of which represent species complexes of morphologically very similar species. The *Mesalina guttulata* species complex is one such case. This complex currently comprises four described species that occur through Arabia and northern Africa, however, the presence of a cryptic species in Saudi Arabia, Kuwait, and Jordan was pointed out recently. For this study, we collected new material of the various species of the *M. guttulata* complex, including the undescribed lineage from across Saudi Arabia. We carried out multilocus phylogenetic analyses using three mitochondrial and three nuclear markers and analysis of morphological data to verify whether the undescribed lineage deserves a species rank.

Results The results show that the lineage is clearly genetically separated from the other species of the complex and shows morphological differentiation from the other species. Therefore, we describe it herein as a new species, *Mesalina cryptica* sp. nov.

Conclusions We contribute to the taxonomy of Arabian lacertid lizards by describing a new species distributed in central Saudi Arabia, with isolated populations occurring in Kuwait and Jordan. Despite its large range, the species is genetically and morphologically homogeneous. The gap in its distribution between the Jordan and Saudi Arabia populations is ascribable to the paucity of sampling along the Saudi/Iraqi border.

Keywords Lizards, Mesopotamia, Middle East, Sauria, Squamates, Reptiles, Taxonomy

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Background

Our knowledge of the diversity and distribution of the Arabian reptile fauna has been growing steadily over the past decades. The phylogeny and systematics of many reptile groups have been resolved [1–3], biogeographic scenarios that explain the history of the Arabian fauna have been put forward [4–10], and new species have been discovered and described [11–20]. Quite naturally, most scientific attention has historically been attracted by the most species-rich regions of Arabia, which are the mountainous parts along the peninsula's western, southern, and eastern coasts [21]. In this respect, the interior central and northern Arabia, which do not harbor such rich reptile communities, rank among the least studied regions. This is, however, slowly changing lately, as more field surveys are conducted in these previously neglected outback regions and new important findings are being made [22–28].

Central Saudi Arabia, in the surroundings of the capital Riyadh is geomorphologically characterized by the Tuwaiq Escarpment, a tall vertical edge that extends north/south for approximately 800 km and is surrounded by a mosaic of rock outcrops, stone and gravel plains, and sand dunes [29]. This variety of habitats supports a rich interconnected community of species with differing habitat preferences. The rocky outcrops are home to two endemic reptiles that are known only from the vicinity of the Tuwaiq Escarpment in central Saudi Arabia: the gecko *Tropiocolotes wolfgangboehmei* [30] and the agamid *Pseudotrapelus tuwaiqensis* [17]. Additionally, an undescribed species of the lacertid genus *Mesalina* had been discovered in the area, however, its taxonomy has not yet been resolved [31].

The genus *Mesalina* of Arabian mainland (not counting the Socotra Archipelago) is represented by nine described species, plus the undescribed potential species mentioned above. Three of these species – *M. bernoullii, M. brevirostris,* and *M. saudiarabica* – belong to the *M. brevirostris* complex that occurs in northern Arabia, Mesopotamia, and the Levant [20]. Four species – *M. arnoldi, M. austroarabica, M. bahaeldini*, and the undescribed species from central Saudi Arabia that was formerly referred to as lineage 4 – belong to the *M. guttulata* complex whose distribution stretches from western Africa across the entire Sahara to Arabia where it occurs primarily in the northwest, and in the western and southern mountains [31]. Two species – *M. adramitana* and *M. ayunensis* – belonging to the *M. adramitana* complex inhabit eastern and southern Arabia [32]. The last species, *M. martini*, represents an isolated evolutionary lineage within the genus' phylogeny and ranges on the African side of the Red Sea and marginally in southwestern Arabia [21].

The systematics of the *M. guttulata* complex was recently revised [31]. The study concluded that the complex includes five species: *M. austroarabica* from Yemen and the Dhofar Mountains of Oman, *M. arnoldi* from the highlands of Yemen and southwestern Saudi Arabia, *M. bahaeldini* from the Sinai Peninsula of Egypt, Israel, Jordan, and northwestern Saudi Arabia, *M. guttulata* from northern Africa, and another genetically deeply diverged lineage that was not described by the authors due to the lack of voucher specimens. We use the term "lineage 4" that was coined by the authors for this candidate species. Motivated by this sampling gap, we conducted targeted field trips to central and northern Saudi Arabia between 2019–2024 intending to collect additional specimens that would allow us to morphologically diagnose this lineage and conduct morphological and genetic comparisons with the other species of the complex.

In this study, we present new genetic, morphological, ecological, and distribution data for species of the *M. guttulata* complex in Arabia, with the aim to test whether the undescribed lineage 4 ref [31]. represents a distinct species. We conduct phylogenetic analyses of three mitochondrial and three nuclear markers to assess the level of genetic isolation of the lineage from the other species of the complex. We compare morphological variation between and within the species of the complex. We conclude that lineage 4 represents an evolutionarily unique entity that we describe herein as a new species.

Methods

Sample and specimen collection

New samples and specimens were collected during targeted field trips to Saudi Arabia and Jordan between 2019 to 2024. The trips to Saudi Arabia were conducted under the collaboration with National Centre for Wildlife (formerly Saudi Wildlife Authority) as part of the joint projects 'Systematics and biodiversity of the reptiles of southwestern Saudi Arabia' and 'Biodiversity and systematics of the reptiles of western Saudi Arabia'; with King AbdulAziz Royal Reserve Development Authority as part of the project 'King AbdulAziz and Al Summan Royal Nature Reserves Project'; with University of Ha'il as part of the joint project 'Diversity of reptiles and amphibians of northern Arabia'; with Royal Commission for AlUla as part of the project 'The biodiversity of Wadi Ashar' led by The Centre for Middle Eastern Plants. Field work in Tabuk Province carried out between 2021–2024 was part of projects developed by NEOM Nature Reserve and the Prince Mohammed bin Salman Royal Reserve Development Authority. Field work in Jordan was arranged in collaboration with the University of Jordan, Amman.

Taxon sampling for genetic analyses

In the genetic analyses, we included five samples of *M. arnoldi*, 21 samples of *M. austroarabica*, 19 samples of *M. bahaeldini*, 14 samples of *M. guttulata*, 35 samples of lineage 4, and six samples of other *Mesalina* species that are not part of the *M. guttulata* species complex, which were used as outgroups (two samples of *M. adramitana*, and one sample of each *M. balfouri, M. bernoullii, M. brevirostris*, and *M. kuri*).We downloaded all available sequence data from GenBank or generated new genetic data for each species. A total of 38 individuals were sequenced *de novo* for this study (four of *M. austroarabica*, four of *M. bahaeldini*, six of *M. guttulata*, and 21 of lineage 4). For two samples of *M. arnoldi* that were included in the study of ref [31]. we generated new sequences of two nuclear loci to complete the genetic matrix (Table S1).

In addition to the samples that were used for the phylogenetic analyses, we sequenced the 12S rRNA mitochondrial gene for 46 additional samples from Saudi Arabia

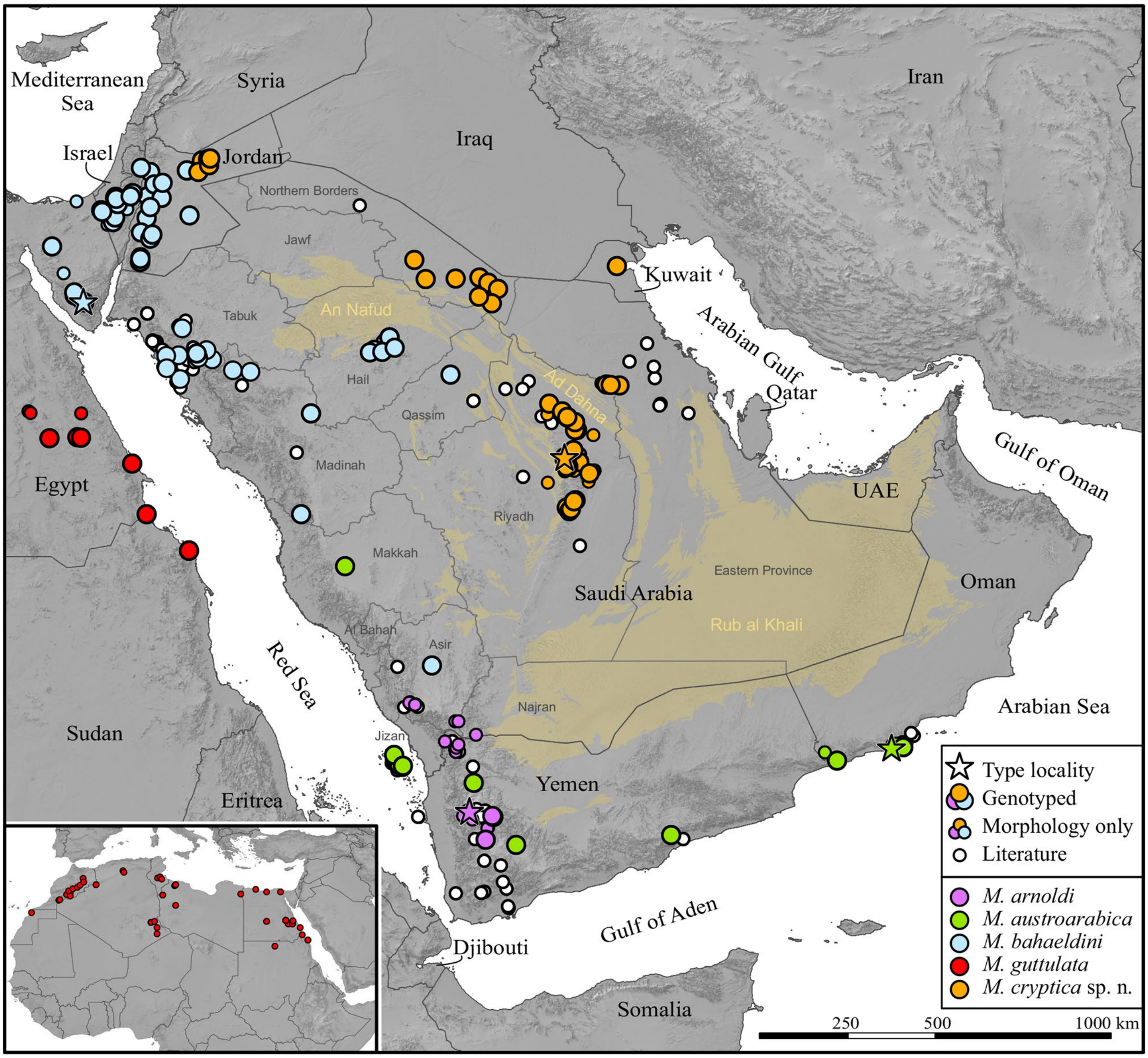

Fig. 1 Distribution of the species of the *M. guttulata* complex in Arabia and northern Africa. The color of circles indicates species assignment. Records shown as large circles are of genotyped specimens/samples, specimens shown as small circles were determined based on morphology. Small white circles are published records or observations that were neither genotyped nor examined morphologically. Stars indicate type localities; the type locality of *M. guttulata* is 'Lower Egypt (near Alexandria or Siwa)' [33] and is not shown in the map. The borders of Saudi provinces are in grey, and their names are in small font. Areas and their respective names marked in yellow are major sand dune deserts of Arabia (the yellow layer is the Arabian sand Desert ecoregion from ref [34]).

(Table S1; Fig. 1). The 12S rRNA is a suitable candidate gene for DNA barcoding of Arabian lizards, including lacertids, since most Arabian species have been sequenced for this gene [21], making the reference library, which the barcodes are compared to, nearly complete.

DNA extraction and sequencing

Each sample included in the phylogenetic analyses was sequenced for up to three mitochondrial and three nuclear genes. These were the 12S rRNA (*12S*), 16S rRNA (*16S*), and cytochrome b (*cytb*) from the mitochondrial DNA, and the acetylcholine receptor M4 (*ACM4*), oocyte maturation factor MOS (*CMOS*), and melanocortin 1 receptor (*MC1R*) from the nuclear DNA. We extracted genomic DNA from pieces of muscle or tail tip samples preserved in 96% ethanol using the Qiagen Blood and Tissue kit following the manufacturer's protocol. Primers and PCR conditions followed ref [32]. Both strands of the PCR products were sequenced at Macrogen (the Netherlands). The quality of raw sequence data was checked using the Geneious Prime software [35], which was also used for sequence editing and the assembly of contigs.

Phylogenetic analyses

We used the MAFFT plugin of Geneious with default settings to align all genes independently. The alignment lengths of the genes were 399 base pairs (bp) for *12S*, 534 bp for *16S*, 1,125 bp for *cytb*, 423 bp for *ACM4*, 393 bp for *CMOS*, and 665 bp for *MC1R*. We concatenated the alignments and inferred phylogenetic relationships by means of Maximum Likelihood (ML) and Bayesian Inference (BI).

The ML analysis was conducted in the online interface of IQ-Tree [36, 37; https://iqtree.cibiv.univie.ac.at/]. The concatenated alignment was partitioned by gene, and the best-fit substitution model was selected automatically for each partition during the analysis. Branch support was assessed using the Shimodaira-Hasegawa-like approximate likelihood ratio test [SH-aLRT; 38] and ultrafast bootstrap [UFBoot; 39], both with 1,000 replicates.

The BI analysis was run in MrBayes 3.2 [40]. The alignment was also partitioned by gene. The best substitution model of each partition was determined using PartitionFinder 1.1 [41]. The resulting models were GTR + I + G for the *12S, 16S, ACM4*, and *MC1R* partitions; GTR + G for *cytb*; and HKY + I for *CMOS*. To avoid overparameterization, we excluded the + I parameter of the GTR + I + G as it is accounted for by the + G of the model. We ran three independent MrBayes runs, each for 20^6 generations and sampled every 2,000 generations. Stationarity was determined by the standard deviations of the split frequencies being lower than 0.01. Convergence of the three runs and the effective sample sizes of all estimated parameters was inspected using Tracer 1.5 [42]. The initial 10% of posterior trees were discarded as burnin; the remaining trees were used to generate a 50% majority-rule consensus tree. Branches with SH-aLRT ≥ 80, UFBoot ≥ 95, and a Bayesian posterior probability ≥ 0.95 were considered strongly supported. Phylogenetic trees were visualized with FigTree 1.4 (https://tree.bio.ed.ac.uk/software/figtree/). Uncorrected genetic distances (*p*-distances) for the three mitochondrial markers were calculated in MEGA X [43].

We further evaluated the relationships within the *M. guttulata* species complex at the level of individual nuclear loci by reconstructing their allele networks. Because the alignments of all three nuclear loci contained ambiguous heterozygous nucleotide positions, we resolved their haplotypes in PHASE 2.1 [44], applying the phase probability threshold of 0.7 and using SeqPHASE [45] to convert input and output files. Outgroup taxa were not included in the phasing process. The networks were reconstructed using the TCS algorithm [46] as implemented in PopART [47].

To assess the degree of reticulation in the evolutionary history of the *M. guttulata* species complex, we reconstructed phylogenetic networks using the neighbor-net algorithm [48] implemented in SplitsTree v. 4 [49]. The outgroup species were excluded from this analysis, and we used the phased alignments of the nuclear markers. We inferred the phylogenetic networks with two input datasets: one that included all the genetic markers (mitochondrial and nuclear), and one of the nuclear markers only. Support of the networks was assessed with 1,000 bootstrap replicates. We tested for recombination in the nuclear dataset using the ϕ statistic implemented in SplitsTree [50].

Species delimitation

To assess whether the species of the *M. guttulata* complex indeed represent independently evolving lineages and to confirm if lineage 4 deserves the status of a species, we conducted a multilocus coalescent-based species delimitation analysis using the software Bayesian Phylogenetics and Phylogeography [BP&P; 51, 52]. The phased alignments of the nuclear loci were included in the analysis. We only included samples that had at least two of the three nuclear markers sequenced, of which there were 90 phased sequences (i.e. 45 individuals) in total. The tree topology was fixed to the one that resulted from the ML and BI analyses, and we calculated speciation probabilities at each node of that tree. We run the analysis six different times with different combinations of parameter settings to account for varying ancestral population sizes and divergence depths. We tested the following combinations of gamma-distributed priors (with shape parameters α and β) for the population size (θ) and divergence depth (τ) parameters: large ancestral population size

($\alpha = 1$, $\beta = 10$) and deep divergences among species ($\alpha = 1$, $\beta = 10$); large ancestral population size ($\alpha = 1$, $\beta = 10$) and shallow divergences ($\alpha = 2$, $\beta = 2000$); small ancestral population size ($\alpha = 2$, $\beta = 2000$) and shallow divergences ($\alpha = 2$, $\beta = 2000$). Each analysis was run twice, with the reversible-jump algorithm 0 (with parameter $\varepsilon = 2$) and 1 (with parameters $\alpha = 2$, $m = 1$) [52]. Rates were set to vary among loci, with the locus rate parameter generated form a Dirichlet prior distribution ($\alpha = 2$). No variation in locus heredity was assumed. The optimal acceptance proportions were controlled to fall in the interval (0.15–0.7) [53].

Sampling of morphological data

The dataset for the morphological analyses was built on data presented by ref [31]., which included 44 specimens of *M. arnoldi*, 18 specimens of *M. austroarabica*, 11 specimens of *M. bahaeldini*, and 18 specimens of *M. guttulata*. We complemented this dataset by adding six specimens of *M. austroarabica* from Farasan Islands, Saudi Arabia, 15 specimens of *M. bahaeldini* from Israel, and 18 specimens of lineage 4, of which four were from Jordan and 14 from Saudi Arabia. The specimens examined are housed in herpetological collections whose acronyms are given in Table S2.

In accordance with previous taxonomic studies on *Mesalina* [20, 31, 33, 54], we scored the following metric and meristic characters using a digital caliper with accuracy to the nearest 0.1 mm and a dissecting microscope: Snout to vent length (SVL) – distance from the tip of the snout to the cloaca; Head length 1 (HL1) – distance from the tip of the snout to the posterior edge of the ear; Head length 2 (HL2) – distance from the anterior margin of the eye to the tip of the snout; Head length 3 (HL3) – distance from the posterior margin of the eye to the anterior margin of the ear; Head width (HW) – maximum head width; Head depth (HD) – maximum head depth; Forelimb length – from the axilla to the tip of the distal claw; Hind limb length – from the groin to the tip of the distal claw; Length of the 4th toe from the insertion of the 5th toe including the claw (Toe4); Tail length (TL) – from the cloaca to the tip of the tail, if original. The meristic (pholidotic) characters were: Supralabials – the number of supralabials from the rostral to the most posterior clearly enlarged plate on the upper lip; Suboculars – the number of supralabials from the subocular (included) to the rostral (excluded); Gulars – the number of gular scales in a straight median series from the collar scales to the contact of the chin-shields; Plates in collar – the number of enlarged scales in the collar; Dorsals – the number of dorsal scales across midbody; Ventrals across belly – the number of ventral scales in the longest row across belly; Transverse rows of ventrals – the number of transverse series of ventral scales, counted to the level of the femoral pores; Femoral pores – the number of femoral pores; Subdigital lamellae under the 4th toe – the number of lamellae along the underside of the 4th toe. Juveniles were used only for comparisons of meristic characters. Original morphological data are presented in Table S3. High-resolution photographs of most examined specimens were uploaded to MorphoBank (https://morphobank.org; Project number 5392) where they are available for free download. MorphoBank accession numbers for each specimen are provided in Table S4.

Morphological data analyses

To test if the morphological characters show signs of sexual dimorphism, we used paired *t*-tests with the significance level (α) of 0.05. Males and females were treated separately in analyses of the dimorphic traits. We then examined whether the distribution of each character values was normal using D'Agostino normality test implemented in the *fBasics* R package [55]. Traits that did not show sexual dimorphism were analyzed for both sexes pooled together; normality of the other traits was tested separately for males and females. Pairwise between-species differences in the normally distributed traits were then tested using one-way ANOVA with the Tukey post-hoc test. Interspecific differences in the traits that did not follow a normal distribution were tested with the nonparametric Kruskal–Wallis test, and the Wilcoxon rank-sum test was used to calculate the significance of pairwise comparisons. Given that detailed pairwise comparisons between *M. arnoldi, M. austroarabica, M. bahaeldini*, and *M. guttulata* were provided by ref [31]., we here focused primarily on the differences between lineage 4 to the remaining species of the *M. guttulata* species complex.

Results

Phylogenetic analyses

The ML and BI analyses of the concatenated dataset resulted in largely similar topologies. Both approaches supported the monophyly of the *M. guttulata* species complex (Fig. 2; SH-aLRT = 99.8/ UFBoot = 100/ Bayesian posterior probability = 1.0; support values are given in the same order hereafter). Monophyly of all species of the complex was strongly supported (*M. arnoldi*: 96.8/100/1.0; *M. austroarabica*: 99.9/100/1.0; *M. bahaeldini*: 100/100/1.0; *M. guttulata*: 98.2/100/1.0; lineage 4: 100/100/1.0). The northwestern species *M. bahaeldini* was recovered as sister to the African *M. guttulata* (87.3/93/0.99), and the southern Arabian *M. austroarabica* was sister to the lineage 4 (91.5/97/1.0). The position of the last species, *M. arnoldi,* was in both analyses inferred as sister to the latter pair (*M. austroarabica* + lineage 4), however, the topology was not strongly supported in any of the branch support tests

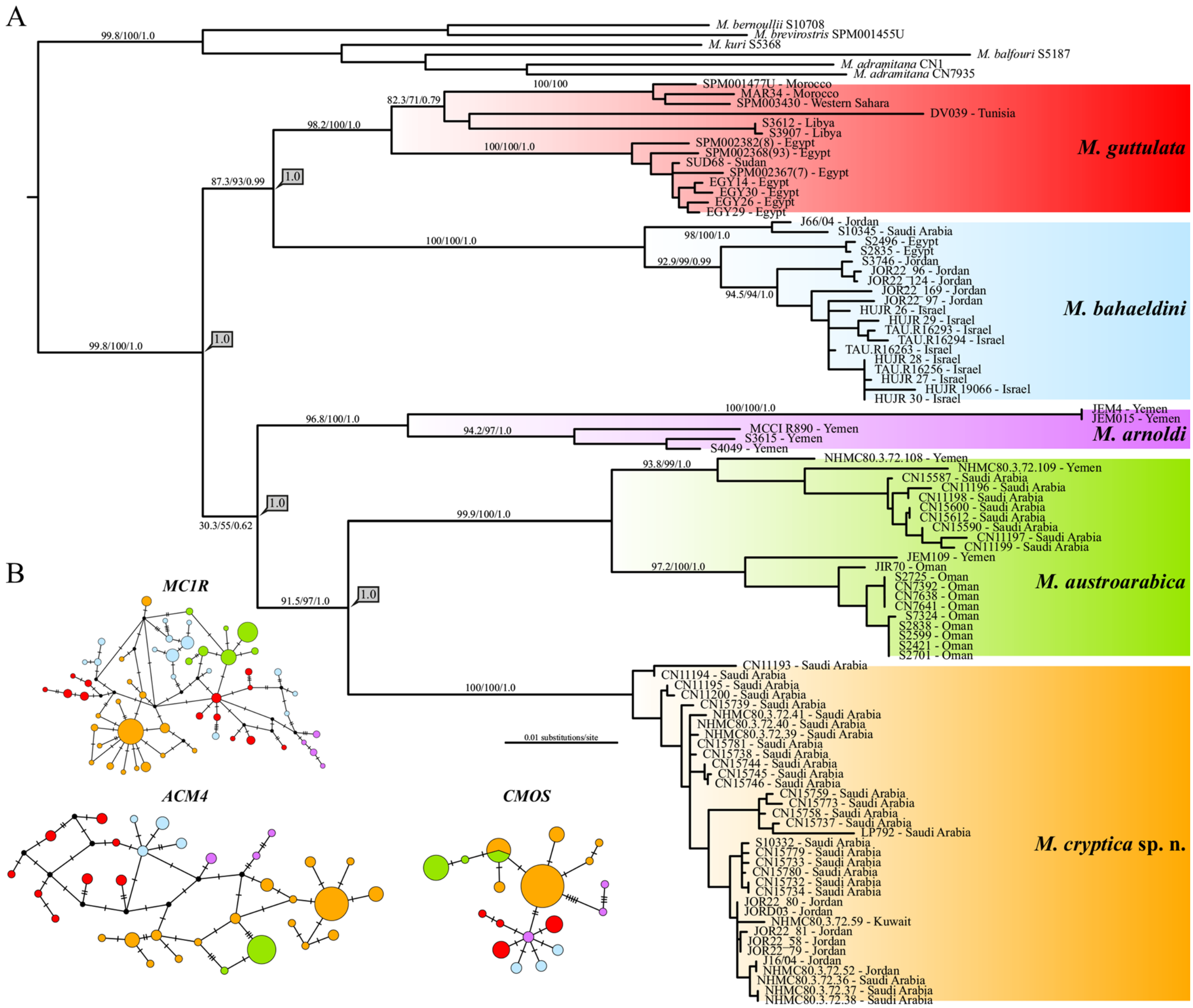

Fig. 2 Phylogenetic relationships within the *M. guttulata* species complex. **A)** Maximum likelihood tree of the complex (species highlighted in color) and outgroup taxa. Numbers above branches indicate support values in the following order: SH-aLRT, UFBoot, posterior probability resulting from the Bayesian analysis. Numbers in grey boxes that point at the nodes connecting species are speciation probabilities as inferred by the species delimitation analyses. All iterations of the delimitation analysis with different prior and parameter settings resulted in speciation probabilities equaling 1.0 for all nodes. **B)** Allele networks for the three nuclear markers analyzed in this study. Colors in the networks correspond to those in the tree. Circle sizes are proportional to the number of samples sharing that haplotype. Transverse bars on the connecting lines show the number of mutations separating each unique haplotype

(30.3/55/0.62). Lineage 4 showed shallow levels of genetic differentiation across its relatively large range from central Arabia to Jordan, with the geographically outlying samples from Jordan nested within the Saudi samples.

At the level of individual nuclear markers, the five species showed no sharing of alleles, with each species having its own private alleles in all three nuclear loci (Fig. 2B). The only exception was *CMOS*, in which *M. austroarabica* and lineage 4 shared one common allele. Nonetheless, each of these species possessed other alleles that were unique to them and not shared with any other species. It should be mentioned that *CMOS* was the least variable of the loci, with most species being differentiated by a single substitution along the 393 bp alignment.

The phylogenetic networks inferred with SplitsTree showed that the deep evolutionary history within the *M. guttulata* species complex was, to some degree, reticulated (Fig. 3). This was particularly apparent in the network of the nuclear loci. The ϕ test did not find statistically significant evidence for recombination in the nuclear dataset (p = 0.09263).

Species delimitation

Regardless of the prior and parameter settings, all iterations of the species delimitation analysis strongly

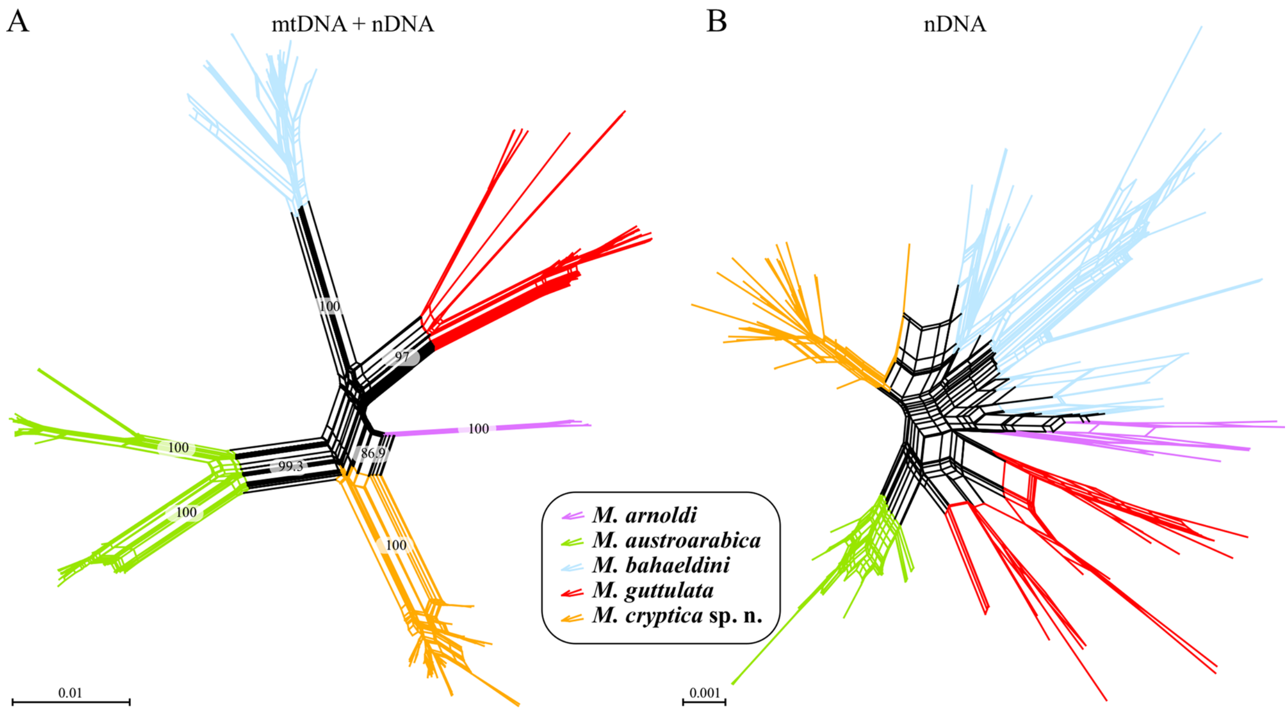

Fig. 3 Phylogenetic network resulting from the SplitsTree analysis of **A)** the combined mitochondrial and nuclear dataset and **B)** the nuclear markers alone. Bootstrap values are shown for major clades in the network based on the combined dataset. The network that was based only on the nuclear data had no clusters supported, likely as a result of the high degree of ancestral reticulation

supported that speciation occurred in all nodes of the input tree, with all nodes receiving posterior support of 1.0 (Fig. 2).

Morphological analyses

Many of the characters were sexually dimorphic for many species (Table S5), we thus analyzed them separately for both sexes. In fact, sexual dimorphism was not confirmed for only five traits: SVL, Supralabials, Gulars, Plates in collar, and Dorsals. Pairwise morphological comparisons of lineage 4 with the other species of the *M. guttulata* complex are detailed in Table S6 and Figs. S1–S5.

Taxonomic implications

The clade that was until now referred to as *Mesalina* lineage 4 bears a unique combination of genetic and morphological characteristics that differentiate it from the described species of the *M. guttulata* complex. Specifically, the clade's genetic differentiation is similar to that of the other species of the complex. It also possesses unique alleles in all three analyzed nuclear markers that separate it from the other species, indicating that there is no recent introgression between the species of the complex. Furthermore, the species delimitation analysis supports that speciation has taken place between *Mesalina* lineage 4 and its sister clade, *M. austroarabica*. Also, the distribution of the clade does not overlap with any of the described species, although the distance to the nearest confirmed records of the geographically closest *M. bahaeldini* is only about 30 km in a straight line in northern Jordan, indicating a possible presence of a contact zone between the two species in the region. In light of this evidence, we conclude that it represents an independent species which we proceed to describe it as new.

Systematics

Lacertidae Oppel, 1811

Mesalina Gray, 1838

Mesalina cryptica sp. nov.

English name: Arabian small-spotted lizard

Arabic name: البرص العربي المنقط الصغير

Chresonymy.

Mesalina guttulata in refs. [56–61]

Mesalina guttulata guttulata in ref [62].

Mesalina sp. in refs. [31, 32, 63]

Mesalina lineage 4 in refs. [17, 21, 28, 31]

Mesalina sp. 4 in ref [64].

Holotype. NMP6V 76,937 (sample code CN15773; MorphoBank accessions: M908788–M908801; Figs. 4A, and 5), adult male; Saudi Arabia, Riyadh Province, about 7 km N of Hadlulah Al Muzahimeyah (24.561°N, 46.307°E (datum WGS84; Fig. 4B), 750 m a.s.l., collected by J. Šmíd, S. Carranza, M. Shobrak on 14 June 2019.

Paratypes. NMP6V 76941 (sample code CN11194), adult male; NMP6V 76940 (sample code CN11193), adult female; NMP6V 76938 (sample code CN11195), adult female; all three from Saudi Arabia, Riyadh Province, Sha'Ib Luha, about 15 km South of Riyadh (24.444°N,

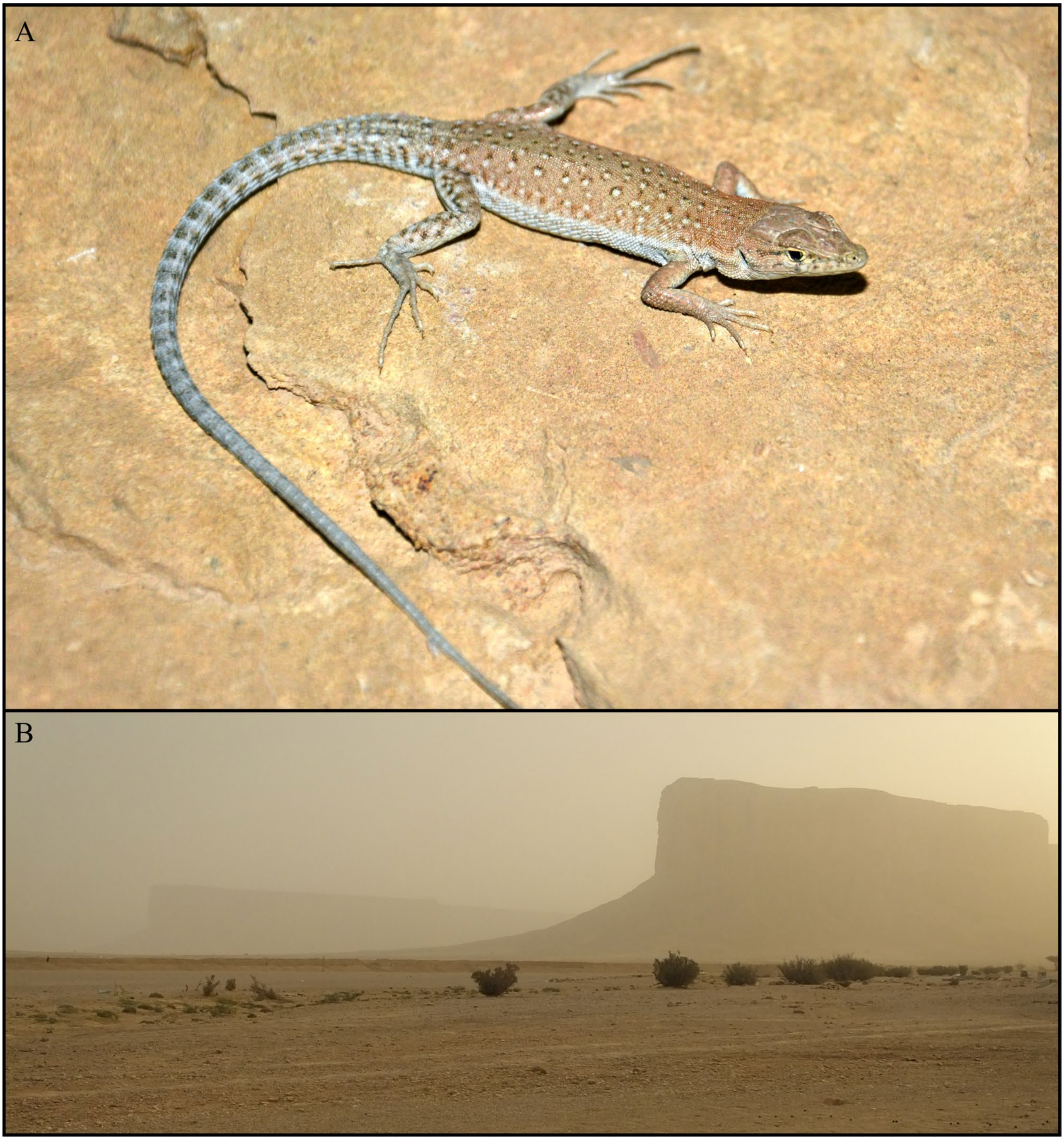

Fig. 4 **A)** Holotype (NMP6V 76937) of *M. cryptica* sp. nov. in life (photo by Al Faqih Ali Salim). **B)** The species type locality about 7 km N of Hazlulah, west of Riyadh, Saudi Arabia (24.561°N, 46.307°E), with the abrupt vertical cliffs of the Tuwaiq Escarpment visible in the background (photo by Jiří Šmíd)

Fig. 5 Details of preserved holotype of *M. cryptica* sp. nov. (NMP6V 76937, sample code CN15773). Dorsal **(A)** and ventral **(B)** view of the body; dorsal **(C)**, left lateral **(D)**, and ventral **(E)** view of the head; detail of the cloacal region with the femoral pores **(F)**. The grid in the background is 1 × 1 cm

46.676° E, 660 m a.s.l.), collected by L. Chirio on 17 January 2015; NMP6V 76939 (sample code CN11200), adult female; Saudi Arabia, Riyadh Province, Wadi Hanifa, about 5 km Southwest of Al Awsat (24.324°N, 46.396° E, 810 m a.s.l., collected by L. Chirio on 10 April 2015).

Other specimens examined. In addition to the holotype and paratypes, 30 additional samples were included in the genetic analysis, ten of which were also examined morphologically, and 20 other samples were DNA-barcoded. Nine specimens were included in the morphological analyses but were not sequenced.

Diagnosis

A medium-sized species of *Mesalina*, member of the *M. guttulata* species complex with the following combination of morphological characters: 1) SVL up to 47 mm in both sexes (the character is not sexually dimorphic; adult males: 43.5–47.0 mm, adult females: 41.8–46.1 mm); 2) well-developed occipital scale in contact with the interparietal; 3) lower eyelid with a transparent window made up of two large scales; 4) 8–10 supralabials; 5) four upper labials in front of the subocular; 6) 9–12 plates in collar; 7) 21–29 gulars; 8) ventral plates in eight straight longitudinal rows; 9) 36–48 dorsal scales across midbody; 10) 24–29 femoral pores in males, 25–33 in females (the character is not sexually dimorphic); 11) 19–22 lamellae under 4th toe; 12) dorsal coloration of adults beige to dark brown, with black-and-white ocelli (the white dots are flanked but not completely surrounded by black specks); the ocelli are arranged in irregular longitudinal and transverse rows; 13) adult males with orange flanks; 14) juveniles sometimes with pale dorsolateral stripes that start at the level of the eye and extend all the way down on the tail; 15) juveniles with a bluish tail.

Genetic diagnosis

Mesalina cryptica sp. nov. may be differentiated by genetic characters in the mitochondrial genes that are unique to the species and not shared with the other species of the *M. guttulata* complex. These are, in the *12S* alignment: nucleotide C present in position 607 (*vs.* A in *M. austroarabica* and T in *M. arnoldi, M. bahaeldini*, and *M. guttulata*); C in position 784 (*vs.* T in the other species). In the *16S* alignment: AA in positions 1106–1107 (*vs.* TT or CT in the other species), A in position 1123 (*vs.* G in the other species). In the *cytb* alignment: T in position 99 (*vs.* C in the other species), A in position 231 (*vs.* C or T in the other species), T in position 364 (*vs.* C in the other species). The position numbers are given as absolute values and indicate the position of the nucleotide in the complete gene (aligned to the mitogenome of *M. guttulata* [PQ390636]), not relative to the gene fragments amplified with the primers used here. Genetic distances between *M. cryptica* sp. nov. and the other species of the *M. guttulata* complex ranged between 4.0–5.2% in *12S*, 4.5–6.3% in *16S*, and 11.8–13.3% in *cytb*. Distances between and within all the species of the complex are detailed in Table S7.

Comparisons

Several key characters may be used to differentiate *M. cryptica* sp. nov. from each of the other species of the *M. guttulata* complex (see also Table S6 and Figs. S1–S5).

Compared to *M. arnoldi, M. cryptica* sp. nov. is smaller (SVL: mean 47.4 mm, range 40.0–56.0 mm in the former *vs.* mean 43.9 mm, range 41.8–47.0 mm in the latter), has a shorter head (HL3: mean 4.8 mm, range 3.9–5.4 mm in males and mean 4.1 mm, range 3.4–4.8 mm in females *vs.* mean 3.9 mm, range 2.8–4.9 mm in males and mean 3.4 mm, range 2.7–3.9 mm in females), has fewer dorsal midbody scales (mean 46.3, range 38–57 *vs.* mean 42.3, range 36–48), females have a lower number of transverse series of ventral scales (mean 31.9, range 29–37 *vs.* mean 27.6, range 25–31), and males have a lower number of femoral pores (mean 30.0, range 25–34 *vs.* mean 26.8, range 24–29).

Compared to *M. austroarabica, M. cryptica* sp. nov. is larger (SVL: mean 40.4 mm, range 38.0–47.0 mm, *vs.* 43.9 mm, range 41.8–47.0 mm), males have broader heads (HW: mean 6.6 mm, range 6.1–7.0 mm *vs.* mean 7.1 mm, range 6.9–7.3 mm),, and females have shorter heads (HL3: mean 3.9 mm, range 2.9–5.3 mm *vs.* mean 3.6 mm, range 2.7–4.5 mm).Compared to *M. bahaeldini, M. cryptica* sp. nov. has more gular scales (mean 22.4, range 19–27 *vs.* mean 25.2, range 21–29), less dorsal midbody scales (mean 47.3, range 43–55 *vs.* mean 42.3, range 36–48), and females have longer forelimbs (mean 14.3 mm, range 12.3–16.1 mm *vs.* mean 15.7, range 13.6–17.6 mm),fewer transverse series of ventral scales (mean 30.2, range 28–36 *vs.* mean 27.4, range 24–31), longer heads (HL1: mean 9.9 mm, range 9.3–11.2 mm *vs.* mean 11.0 mm, range 9.8–12.6 mm), and broader heads (HW: mean 6.2 mm, range 5.8–6.8 mm *vs.* mean 6.8 mm, range 5.8–7.1 mm).

Compared to *M. guttulata, M. cryptica* sp. nov. is smaller (SVL: mean 46.0 mm, range 42.0–50.0 mm *vs.* mean 43.9 mm, range 41.8–47.0 mm), females have shorter heads (HL3: mean 4.1 mm, range 4.0–4.2 mm *vs.* mean 3.4 mm, range 2.7–3.9 mm), females have a lower number of transverse series of ventral scales (mean 30.8, range 29–33 *vs.* mean 27.6, range 25–31), females have more femoral pores (mean 21.1, range 18–26 *vs.* mean 27.6, range 25–31), broader heads (HW: mean 6.2 mm, range 5.6–6.6 mm *vs.* mean 6.8 mm, range 5.8–7.1 mm), and a lower number of subdigital lamellae under the 4th toe (mean 21.4, range 21–22 *vs.* mean 20, range 19–22).

Although a number of traits present statistically significantly differentiation of *M. cryptica* sp. nov. from the other species of the complex, we must note that many of these characters are of little practical use in the field or when trying to key out specimens in herpetology collections. No single trait is unique to *M. cryptica* sp. nov. Therefore, the best way to identify this species is through genetic tools (e.g., DNA barcoding) or by considering the geographic origin of the specimens.

Etymology

The species epithet "cryptica" is derived from the Latin word for "concealed" or "hidden", and refers to that the species had been overlooked for its morphological similarity with the other species of the *M. guttulata* complex, which were considered conspecific prior to the taxonomic revision by ref [31].

Description of the holotype

Adult male with an original tail (Fig. 5A) and with the following metric and meristic characteristics: SVL: 44.5 mm, HL1: 12.3 mm, HL2: 5.1 mm, HL3: 4.2 mm, HW: 7.2 mm, HD: 5.2 mm, forelimb length: 15.7 mm, hindlimb length: 27.2 mm, supralabials: 9/9 (left/right; Fig. 5D), suboculars: 5/5, gulars: 25, plates in collar: 10, dorsal midbody scales: 41, ventrals across belly: 8 (Fig. 5B), transverse rows of ventrals: 29, femoral pores: 24 (12 + 12; Fig. 5F), subdigital lamellae under the 4th toe: 20/21, well-developed occipital scale in contact with the interparietal (Fig. 5C), five pairs of postmental scales following the mental that gradually increase in size until the 4th pair, the 5th pair being considerably smaller, the first three pairs of postmentals in contact (Fig. 5E).

Coloration in life (Fig. 4A). Dorsal color light brown with numerous ocelli formed by round white spots incompletely surrounded by dark brown granules. The ocelli form irregular rows that start on the nape and run down to the level of cloaca. Head is uniformly light brown with faint irregular darker markings dorsally and with two parallel dark brown stripes laterally running from the eye to the tympanum, the upper one that goes from the mid-line of the eye to the upper margin of the tympanum being more pronounced than the lower one that borders the supralabials. Forelimbs are uniformly light brown. Hind limbs have a reticulated pattern of dark brown, light brown, and white; the anterior side of the hind limbs with enlarged scales that are all uniformly light brown. Head, body and limbs are white ventrally. Flanks are also white. The tail has a faint bluish hue both from the top and ventrally.

Variation

Original morphological data for each specimen of *M. cryptica* sp. nov. are given in Table S3. The number of supralabials varies between 8 and 10, with the majority of specimens (14 out of 18) having 9. Gulars vary between 21 and 29, plates in collar between 9 and 12, transverse rows of ventrals between 24 and 31, with most specimens (14 out of 17) having between 26 and 29.

Habitat and distribution

All individuals of *M. cryptica* sp. nov. were observed or captured in rocky or gravely habitats from barren flat plains to rocky outcrops and scree slopes (Fig. 6). The species is typically encountered in flat areas of hard gravel with sparse shrubby vegetation and scattered rocks of varying sizes, using rock crevices for shelter. Along the Tuwaiq Escarpment of central Saudi Arabia, specimens were found climbing steep scree slopes up to the point where the scree meets the vertical wall of the escarpment (Fig. 6). In Jordan, the species lives in flat deserts of volcanic black basalt rocks in the east of the country (Fig. 6). It has been reported from localities ranging from 99 m in elevation (Kuwait) to 913 m (south of Riyadh, Saudi Arabia). *Mesalina cryptica* sp. nov. avoids loose soft sands, which contrasts with the habitat preference of species of the *M. brevirostris* complex, some of which also occur in central Arabia [28]. Practically speaking, the habitat inhabited by species of the *M. guttulata* complex, including *M. cryptica* sp. nov., is typically very difficult to drive through because of the large and often sharp rocks, while the species of the *M. brevirostris* complex live on finer gravel usually without large rocks that can be driven through with ease.

In the central Saudi Arabian part of its range, *M. cryptica* sp. nov. has been found to live sympatrically with *Pseudotrapelus tuwaiqensis, Trapelus ruderatus, Uromastyx aegyptia* (Agamidae), *Bunopus tuberculatus, Cyrtopodion scabrum, Hemidactylus granosus, Stenodactylus doriae, Tropiocolotes wolfgangboehmei* (Gekkonidae), *Ptyodactylus hasselquistii* complex (Phyllodactylidae), *Acanthodactylus boskianus, A. opheodurus, A. schmidti, Mesalina brevirostris* (Lacertidae), *Diplometopon zarudnyi* (Trogonophidae), *Varanus griseus* (Varanidae), *Malpolon moilensis, Psammophis schokari* (Psammophiidae), *Spalerosophis diadema* (Colubridae), *Echis coloratus* (Viperidae). It should be noted that given the close association of *M. cryptica* sp. nov. to rocky and gravely habitats, most of the species it may be found with either share the same specialization (e.g., *Pseudotrapelus, Tropiocolotes*) or are habitat generalists (e.g., *Bunopus, Varanus*). The co-occurrence with the psammophilous species (e.g., *Diplometopon, Stenodactylus*) is usually enabled by heterogeneous habitats formed by a mosaic of gravel plains or rocky outcrops interspaced with sandy patches.

In Jordan, *M. cryptica* sp. nov. was found with *Pseudotrapelus sinaitus, Trapelus agnetae, Uromastyx aegyptia* (Agamidae), *Bunopus tuberculatus, Cyrtopodion scabrum, Hemidactylus lavadeserticus, Stenodactylus grandiceps* (Gekkonidae), *Ptyodactylus puiseuxi* (Phyllodactylidae), *Ophisops elegans* (Lacertidae), *Psammophis schokari* (Psammophiidae), and *Platyceps rogersi* (Colubridae).

Biology. Not much is known about the species' ecology and behavior. It is active during the day at relatively high ambient temperatures (30–41 C) and low relative air humidity (20–33%). Males in nuptial coloration with orange flanks were observed in March (e.g., see MorphoBank picture M908995). Juveniles (SVL ~ 30 mm) were abundant and largely outnumbered adults in mid-June.

Conservation status recommendation. Until now, *Mesalina cryptica* sp. nov. has been confirmed from 43 unique localities, most of which lie in Saudi Arabia (36 localities), six are from Jordan, and one from Kuwait. The extent of occurrence (EOO) of the species is 424,000 km^2, and the area of occupancy (AOO) is 164 km^2 [calculated using the GeoCAT online tool; 65]. Following the IUCN Red List criteria (https://www.iucnredlist.org/) and based on these two criteria alone, the species would be considered Least Concern (based on EOO) or Endangered (based on AOO). However, we must consider that the low AOO is caused by low survey density in northern Saudi Arabia and southern Iraq where the species likely occurs. Should these regions be more thoroughly explored, new localities of *M. cryptica* sp. nov. may likely pop up, which would then increase the species' AOO. Also, considering that the species does not seem to suffer from a small population size and that the habitat it occupies is widespread in northern Arabia, we are inclined not to consider the species to be under a direct threat and recommend categorizing it as Least Concern.

Discussion

In this study, we contribute to the knowledge of the systematics, taxonomy, and distribution of the reptile fauna of the Arabian Peninsula by describing a new species of lacertid lizard from central and northern Saudi Arabia, Kuwait, and Jordan. The existence of the species as an evolutionarily distinct lineage was first hinted at by ref [61]., who included in their phylogenetic analysis several

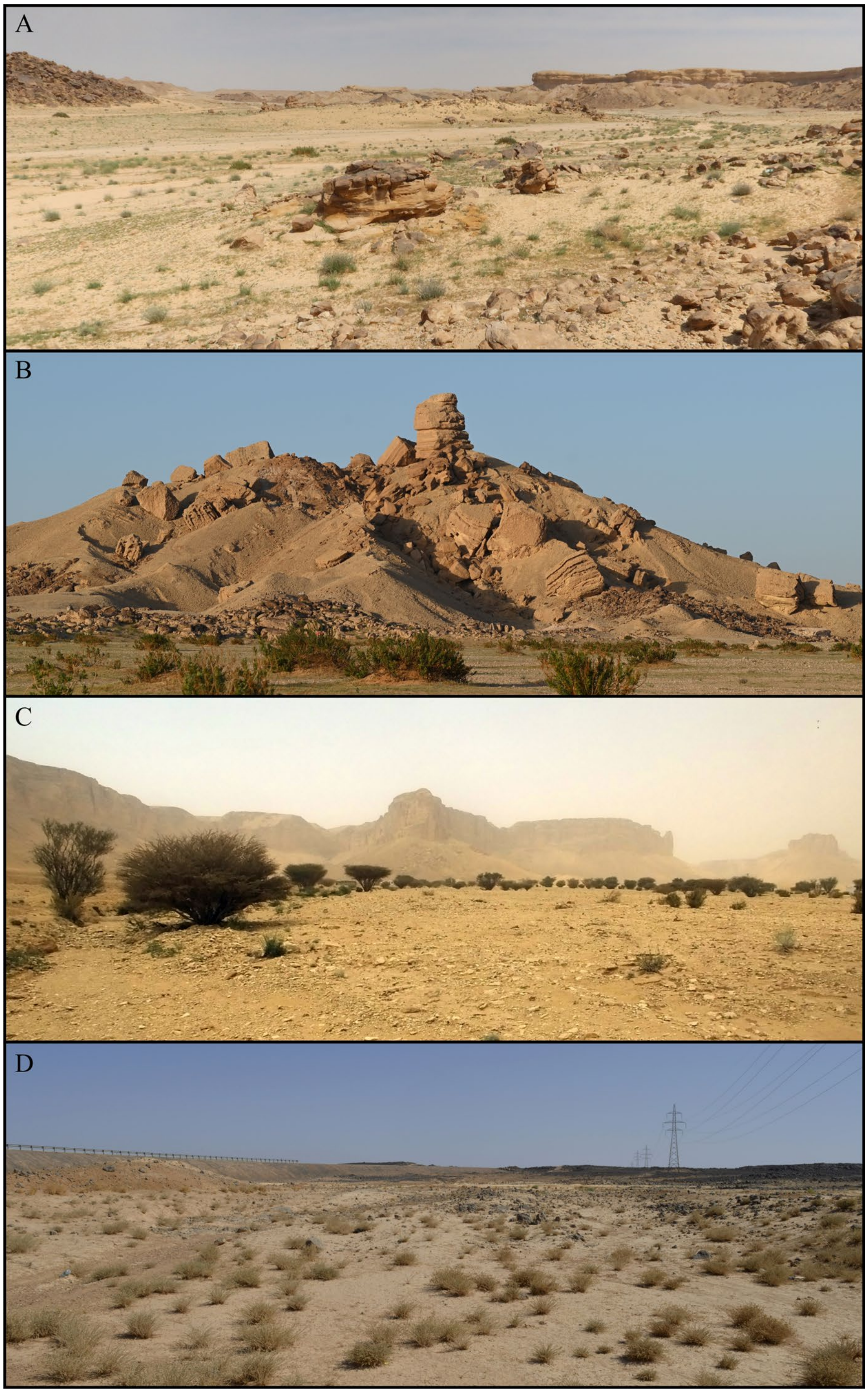

Fig. 6 Habitat of *M. cryptica* sp. nov. in Saudi Arabia and Jordan. **A)** and **B)** Ruwayghib area, around 100 km North of Riyadh, Saudi Arabia (25.589°N, 46.384°E), photo by Jiří Šmíd **(A)** and Marius Burger **(B); C)** Al Awsat, about 55 km Southwest of Riyadh, Saudi Arabia (24.332°N, 46.345°E), photo by Jiří Šmíd; **D)** 10 km East of Safawi, Jordan (32.226°N, 37.22°E), photo by Vojtěch Hejduk

samples from central, southern and northern Arabia and also pointed to the paraphyly of *M. guttulata* with respect to *M. bahaeldini*. Later on, two new species in the *M. guttulata* complex were described from southern Arabia, *M. arnoldi* and *M. austroarabica*, which resolved some of the issues within the complex [31]. The fifth species of the complex, however, was left undescribed for the lack of enough voucher specimens available at that time. Nonetheless, the authors laid the groundwork for future research on the *M. guttulata* complex, which could be further developed once enough specimens have been collected. During our extensive field work that covered nine provinces of Saudi Arabia (Fig. 1), we collected additional material to be able to delimit the species morphologically and genetically from its congeners.

The topology of the *M. guttulata* complex inferred in our phylogenetic study matches the results of ref [31]. in that *M. cryptica* sp. nov. was recovered sister to *M. austroarabica*, and *M. bahaeldini* sister to *M. guttulata*. The mutual position of these groups with respect to each other and to the last species of the complex, *M. arnoldi*, could not be resolved due to the low support of the topology. Given the close relationships between the species of this complex, it may be necessary to utilize genome-wide data to untangle their mutual relationships (e.g., SNPs).

In terms of biogeography, the ancestor of the *M. guttulata* complex most likely originated in Arabia, from where *M. guttulata*, the only African species of the complex, colonized Africa about 8–10 million years ago [32, 61]. It has been hypothesized that *M. austroarabica* and *M. cryptica* sp. nov. separated during the formation of the Rub al Khali Desert of southern Arabia, the largest continuous sand desert in the world [31]. However, based on current knowledge and the new distribution data presented here, it appears more likely that *M. austroarabica* colonized southern Arabia via the chain of mountain ranges in the western part of the peninsula. The Rub al Khali undoubtedly forms an obstacle to dispersal for these saxicolous lizards, but the mountains that surround it from the north, west, and south enabled colonization of eastern Arabia through this continuous corridor. This distribution pattern is shared with other squamate groups that avoid loose sand and are known to have dispersed throughout Arabia, such as the gecko genera *Hemidactylus* [4], *Tropiocolotes* [66] and *Ptyodactylus* [3], the agamid genus *Pseudotrapelus* [17, 26, 67], and the viperid genus *Echis* [68].

The geographic distribution of localities, from where *M. cryptica* sp. nov. has so far been confirmed, clearly implies that our understanding of the species' real range is far from complete. Most confirmed records originate from the vicinity of the Tuwaiq Escarpment around the city of Riyadh and from northern Saudi Arabia. The populations around Riyadh are separated from the more northerly lying localities by the An Nafud sand fields of northern Saudi Arabia and the dunes of Ad Dahna that connects An Nafud in the north and Rub al Khali in the south (Fig. 1). This effective geographic isolation however contrasts with the low genetic variability observed across the species range. In fact, the phylogenetic structure shows that *M. cryptica* sp. nov. is the least variable of all the species of the *M. guttulata* complex (Fig. 2). Although the sand barrier between the central Saudi and northern populations may seem insurmountable, the sand dunes of Ad Dahna date back to only about 40k years ago [29, 69]. This means that gene flow between the populations was readily feasible until very recently. Considering that the Jordanian samples are nested deep in the *M. cryptica* sp. nov. tree, it is very likely that the range of the species is continuous all the way from Jordan to Kuwait. As a result, new records are to be expected from future explorations of extreme northern Saudi Arabia and southern Iraq.

In addition to the description of the new species provided herein, we also record important range extensions for some other species of the *M. guttulata* complex. *Mesalina austroarabica* was until now known only from the mountains of southwestern Oman and Yemen, although its presence in Saudi Arabia was suspected [31]. We here confirm this prediction by reporting the species form Makkah Province (voucher NMP6V 76845, sample code JIR1073) which extends the range of *M. austroarabica* by more than 700 km to the north along the Asir Mountains from the nearest confirmed mainland Arabian locality in northern Yemen.

Since its description in 2002, *M. bahaeldini* has been considered to be endemic to the Sinai Peninsula, Egypt [33, 61, 70]. The presence of the species further east in Israel, Jordan, and Saudi Arabia was confirmed only relatively recently [20, 31]. The Saudi record (voucher IBE-S10345, sample code S10345) was made fairly inland in Hail, suggesting that the species would likely range all over northwestern Saudi Arabia. However, since then, no further sightings or specimens have been documented in this region. The only evidence for the *M. guttulata* complex to occur in northwestern Saudi Arabia was published by ref [71]., who, however, still referred to the species as *M. guttulata*. For this study, we genotyped 25 *M. bahaeldini* specimens from 21 unique localities within Saudi Arabia. We show that the species occurs throughout the highlands of the Tabuk, Madinah, Hail, and Qassim Provinces in northwestern Saudi Arabia. Additionally, one record (unvouchered specimen, sample code DJ13220) was collected further south in Asir Province, 550 km from the nearest record in Madinah Province (voucher NMP6V 76844, sample code JIR1166).

Our work contributes to the taxonomy and understanding of the distribution of species within the *M. guttulata* complex in Arabia, however, further questions arise. Our results indicate that most species in the complex are more widespread than previously thought. While there is currently no evidence of sympatric species, is it possible that some species' ranges overlap? For example, the Asir and Hejaz Mountains of western Arabia remain very poorly sampled, yet our results suggest that the ranges of three species – *M. arnoldi, M. austroarabica*, and *M. bahaeldini* - may intersect in this region. Do these species form hybrid zones where their ranges overlap? *Mesalina bahaeldini* and *M. cryptica* sp. nov. occur only about 30 km from each other in eastern Jordan, and likely come into contact in northern Saudi Arabia as well. Are there mechanisms that prevent these species from interbreeding? Additionally, what is the exact distribution of all the species, especially *M. cryptica* sp. nov., in northern Saudi Arabia and Iraq? These and other questions will need to be addressed in future studies.

Supplementary information

The online version contains supplementary material available at https://doi.org/10.1186/s40850-025-00233-3.

Supplementary Material 1

Supplementary Material 2

Acknowledgements

We are indebted to the National Center for Wildlife (NCW) for organizing field trips and arranging collection and export permits. Denis Hlaváč eagerly helped in the field in 2023. We thank Jerome Gaugris (Flora, Fauna & Man, Ecological Services Limited) and the King Abdulaziz Royal Nature Reserve Development Authority for arranging and conducting fieldwork in King AbdulAziz Royal Reserve in 2023. Raquel Vasconcelos organized field work in AlUla County in 2022, and Mohammed Darwish and Catarina Pinho helped in the field. The fieldwork in Tabuk Province was part of projects developed and funded by NEOM Nature Reserve and the Prince Mohammed bin Salman Royal Reserve Development Authority. Additional samples were kindly provided by Daniel Jablonski, Petr Velenský and Tomáš Mazuch.

Authors' contributions

JŠ, KT, SC conceptualized the study. DV, LP, KT conducted lab work. JŠ conducted genetic analyses. JŠ, DV, KT collected morphological data. JŠ, MS, MA, ROR, DO, JS provided resources and secured funding necessary to conduct the study. All the authors collected data in the field and contributed to the writing of the manuscript.

Funding

JŠ was supported by the Czech Science Foundation (GACR, project number 25-17736S) and by the Ministry of Culture of the Czech Republic (DKRVO 2024–2028/6.I.b, 00023272). DV and LP were supported by Charles University grant no. SVV260792/2025. SC was supported by grant PID2021-128901NB-I00 funded by MCIN/AEI/10.13039/501,100,011,033 and by ERDF, a way of making Europe.

Data availability

Genetic data generated for this study are available on GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Original morphological data of all specimens examined for this study are appended to the paper as supplementary Table S3. Original high-resolution photographs are available on MorphoBank (http://www.morphobank.org; project number 5392).

Declarations

Ethics approval and consent to participate

Most of the material examined comes from various museum collections (Table S2). Specimens and/or tissue samples were provided with the consent of the respective curators. New specimens and samples were collected with appropriate collecting and export permits (permit numbers 22IACUC02 and--23-0091) approved by the Institutional Animal Care and Use Committee (the IACUC). No endangered or protected species were collected, and no samples from private areas were used for this study. Research was conducted with the approval of the Central Commission for Animal Welfare, the Czech Republic, accreditation no. 1090/2012–MZE–17,214. Specimens were euthanized by an overdose of anesthesia (Alfaxan®). All efforts were made to minimize animal suffering.

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests

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Received: 9 April 2025 / Accepted: 11 June 2025

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