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Systematics of the *Mesalina guttulata* species complex (Squamata: Lacertidae) from Arabia with the description of two new species

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Abstract

Mesalina are small diurnal lacertid lizards inhabiting arid areas from North Africa to northwestern India. Previous phylogenetic studies have shown the existence of several species complexes within the genus, some of them with high levels of undiscovered diversity. In the present study, we carry out an integrative systematic revision of the *Mesalina guttulata* species complex using both molecular and morphological data from across its entire distribution range in North Africa, the Middle East and Arabia. The results of the genetic analyses indicate that *M. guttulata* and *M. bahaeldini* are two allopatric sister taxa separated by the Suez Canal and that the species complex includes a further three unnamed deep phylogenetic lineages, two of them restricted to southern and southwestern Arabia and described herein as *Mesalina austroarabica* **sp. nov.** and *Mesalina arnoldi* **sp. nov.**, respectively. As a result of the lack of enough material, the third deep lineage, distributed across Kuwait, Saudi Arabia and Jordan, is provisionally left undescribed. The two newly described species are characterized by their size, scale counts and tail coloration, as well as differences at the three mitochondrial and one nuclear gene analyzed in the present study.

Key words: biogeography, endemicity, highlands, lacertid lizards, southern Arabia, taxonomy

Introduction

Mesalina Gray, 1838 is a member of the Saharo-Eurasian clade of the tribe Eremiadini, subfamily Lacertinae, family Lacertidae (Arnold *et al.* 2007; Mayer & Pavlicev 2007). The genus is currently comprised by 17 species distributed from coastal West Africa, across the arid areas of North Africa, Middle East, Arabia and eastwards to Pakistan and northwestern India (Sindaco & Jeremcenko 2008; Uetz *et al.* 2017). As a result of its wide distribution and its relative abundance in arid areas, the group has been the subject of several systematic and biogeographic studies using both morphological (Anderson 1999; Arnold 1980, 1986a,b,c; Moravec 2004; Segoli *et al.* 2002; Szczerbak 1974, 1989) and molecular (Joger & Mayer 2002; Kapli *et al.* 2008, 2015; Šmíd *et al.* 2017a; Šmíd & Frynta 2012) data. The most complete molecular study of *Mesalina* so far (Kapli *et al.* 2015), placed the origin of the genus in the east, during the early Miocene (c. 22 Mya) and identified several well-defined species including the eastern *M. wastonana* (Stoliczka, 1872), a sister taxon to all the other species, *M. martini* (Boulenger, 1897) and *M. rubropunctata* (Lichtenstein, 1823) of uncertain phylogenetic position, and the monophyletic assemblage formed by *M. adramitana* (Boulenger, 1917) and the Socotra Archipelago endemics *M. balfouri* (Blanford, 1881) and *M. kuri* Joger & Mayer, 2002. More importantly, the study also uncovered very high levels of undiscovered diversity and taxonomic confusion within what has been considered the *M. olivieri* (Audouin, 1829), *M. guttulata* (Lichtenstein, 1823) and *M. brevirostris* Blanford, 1881 species complexes (see also Kapli *et al.* 2008). The study , highlighting the need for a detailed systematic revision of the genus *Mesalina* in order to assess its real diversity as a first step to being able to properly interpret its biogeography and evolution.

The polyphyly of *M. olivieri*, *M. pasteuri* (Bons, 1960) and *M. simoni* (Boettger, 1881) and the existence of

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several highly divergent mitochondrial lineages (Kapli *et al.* 2015) suggest that the taxonomy of the *M. olivieri* species complex is in need of a thorough taxonomic revision, combining morphological and molecular data across its mainly North African range. A recent taxonomic revision of the *M. brevirostris* species complex by Šmíd *et al.* (2017a) using an integrative approach including molecular, morphological and ecological data confirmed the preliminary findings by Kapli *et al.* (2008, 2015), supporting the presence of four species within the complex that started diversifying approximately 3.7 Ma. The main taxonomic changes by Šmíd *et al.* (2017a) included the designation of a lectotype for *M. brevirostris*, the recognition of *M. microlepis* (Angel, 1936) at the species level, the resurrection of the name *M. bernoullii* (Schenkel, 1901) from the synonymy of *M. brevirostris* and the description of a new species endemic to Saudi Arabia, *M. saudiarabica* Moravec, Šmíd, Schmitz, Shobrak, Wilms, 2017.

Like in the previous two cases, the taxonomic history of the *M. guttulata* species complex is troubled. The species was originally described by Lichtenstein (1823) as *Lacerta guttulata* on the basis of several specimens heterogeneous in coloration and geographical origin collected by Hemprich and Ehrenberg during their expedition to northeast Africa in 1819–1826 (Stresemann 1954). After Lichtenstein (1823), *M. guttulata* was considered part of the genus *Eremias*, a genus that Boulenger (1921) divided into five sections, one of them (section four) being *Mesalina*. Within *Mesalina*, Boulenger (1921) recognized several species (some of them now members of different genera) including *M. guttulata* Gray, 1838, for which he listed five varietiesother than the "forma typica": "*olivieri*", "*martini*", "*balfouri*", "*latastii*" (Boulenger, 1918) and "*susana*" (Boulenger, 1918), none of them currently part of the *M. guttulata* species complex (Arnold 1986b; Kapli *et al.* 2015; Uetz *et al.* 2017). Half a century later, Szczerbak (1974) (see also Szczerbak 1989) gave generic status to *Mesalina* and recognized three subspecies within *M. guttulata*: the nominate, *M. g. watsonana*, and *M. g. susana*, the latter two now not members of the *M. guttulata* species complex. Arnold (1986b) raised to the species rank *M. watsonana* on the basis of hemipenial morphology and Anderson (1999) assigned all Iranian *M. guttulata* that he examined to *M. watsonana*, restricting the distribution of *M. guttulata* to North Africa, the Middle East and Arabia. Arnold (1986a) recognized a form of *M. guttulata* from the highlands of southwestern Arabia as a distinct, undescribed species – *Mesalina* sp. A. This taxon was named by Fritz (1985) as *Mesalina montana* (Type locality: between 36 to 38 km west of Sanaa at 2,800 m on the Sanaa – al-Hudaidah road) but, as pointed out by Schätti & Gasperetti (1994) (page 371, footnote 4), this name is unavailable due to the form of publication (a diploma thesis), and therefore *Mesalina* sp. A is still undescribed.

More recently, Segoli *et al.* (2002) studied in detail the nine syntypes of *Lacerta guttulata* deposited in the Museum für Naturkunde Berlin, Germany (formerly Zoologisches Museum der Humboldt-Universität zu Berlin), collected by Hemprich and Ehrenberg in Egypt and Nubia and found that only six specimens fitted the species' description. As a result of that, Segoli *et al* (2002) designated a specimen from "lower Egypt (near Alexandria or Siwa)" as the lectotype of *M. guttulata* and redescribed the species. In the same study, Segoli *et al* (2002) described the populations of *M. guttulata* from southern Sinai as a new species, *M. bahaeldini* Segoli, Cohen and Werner 2002. A few years later, Werner & Ashkenazi (2010) described the subspecies *M. bahaeldini curatorum* from Suez, Egypt, on the basis of two of the original syntypes of the type series of *M. guttulata* collected during 1820-1821 in "Suez" by the Hemprich and Ehrenberg's expedition to the Near East. These specimens had been excluded from the redescription of *M. guttulata* by Segoli *et al*. (2002) due to their deviant coloration.

The recent molecular study by Kapli *et al*. (2015) identified four deep mitochondrial lineages within the *M. guttulata* species complex and showed that, as currently defined, *M. bahaeldini* makes *M. guttulata* paraphyletic. Finally, as part of recent fieldwork in southeastern Arabia, some isolated populations of a new species resembling *M. guttulata* were discovered that differed morphologically from "true" *M. guttulata* from around the type locality in "lower Egypt (near Alexandria or Siwa)", suggesting the existence of yet a new unnamed species of the *M. guttulata* species complex in southern Arabia (referred to it as *Mesalina* sp. 1 by Carranza *et al.* 2018).

In the present study, we carry out an integrative systematic revision of the *Mesalina guttulata* species complex using both molecular and morphological data from across its entire distribution range in North Africa, the Middle East and Arabia. The results indicate that the species complex includes five deep phylogenetic lineages. Two allopatric sister lineages distributed to the west and east of the Suez Canal corresponding to *M. guttulata* and *M. bahaeldini*, respectively, and a further three unnamed deep phylogenetic lineages: 1) the highland form of southwestern Arabia (*M.* sp. A in Arnold 1986a) described as a new species herein, 2) the southern Arabian populations (*M.* sp. 1 in Carranza *et al.* 2018) also described as a new species herein, and 3) a deep lineage

distributed across Kuwait, Saudi Arabia and Jordan that, as a result of the lack of enough material, is provisionally left undescribed.

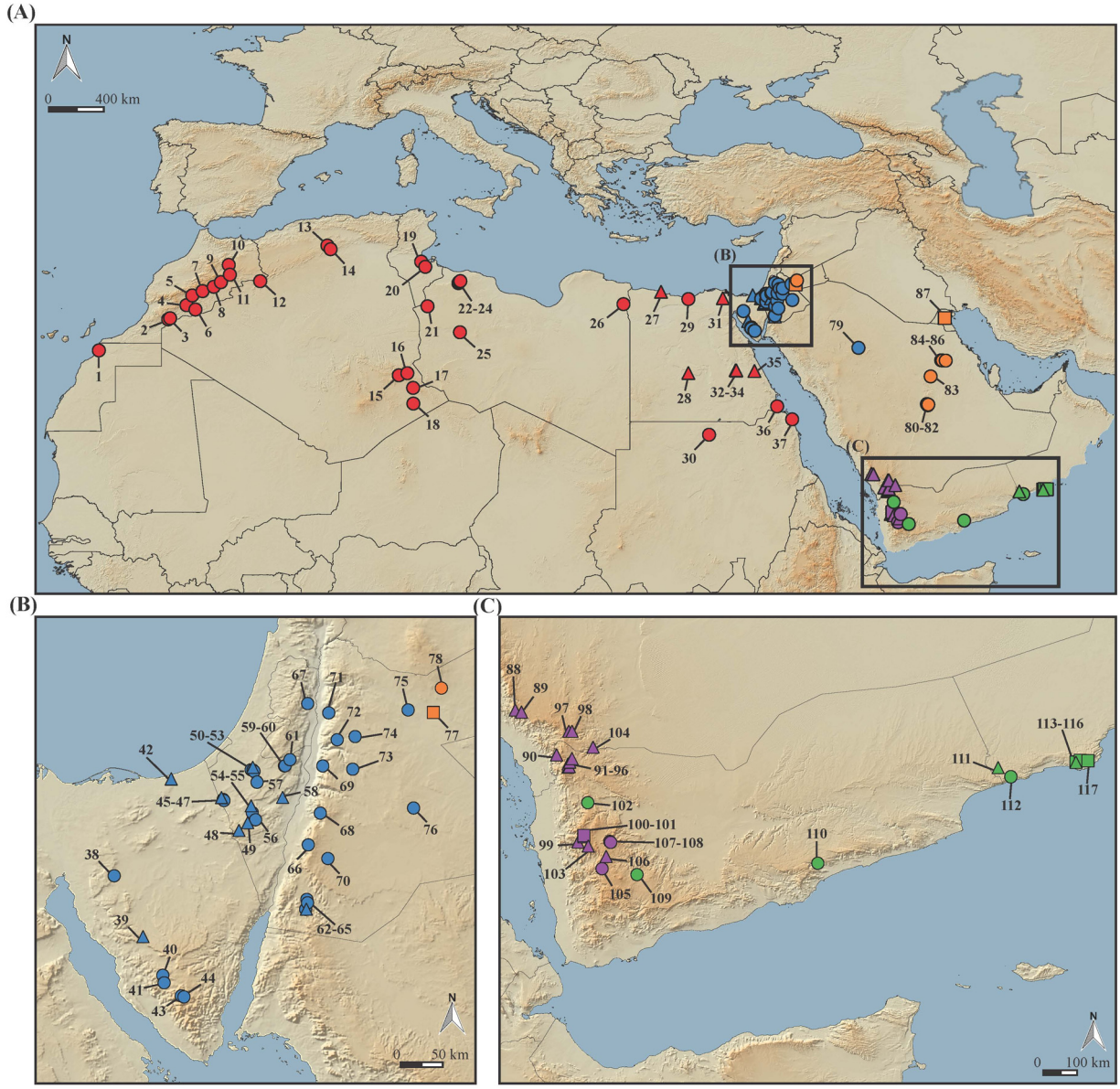


FIGURE 1. Sampling localities of the *Mesalina* specimens used in this study. Circles indicate samples used only in the molecular analyses, triangles indicate specimens examined and included in the morphological analyses only, and squares indicate individuals used in both molecular and morphological analyses. Colors and locality numbers correspond to Figure 2 (see also Appendix I).

Material and methods

Molecular analyses

DNA extraction, amplification and sequence analysis. A total of 119 individuals of *Mesalina* plus two outgroups were included in the phylogenetic analyses. Locality data, sample and voucher codes, taxonomic identification and GenBank accession numbers are listed in Appendix I. The geographical distribution of all the specimens of the *M. guttulata* species complex included in the molecular and morphological analyses (see below) is shown in Fig. 1. In order to include samples from the entire range of our study group, apart from our sequences we also downloaded from GenBank the corresponding 16S rRNA and Cytochrome *b* sequences of all individuals

belonging to this complex from Kapli *et al.* (2008, 2015). For clarity, the number of specimens included in the molecular analyses is listed below based on their lineage assignment in Fig. 2. At the same time, the different lineages correspond to the accepted species in the present work (see also Appendix I). In total, the phylogenetic dataset included 110 representatives of the *M. guttulata* species complex: 43 of lineage 1 (including seven specimens from the mountains of southern Sinai, in the immediate vicinity of the type locality of *M. bahaeldini*), 39 of lineage 2, 13 of lineage 3, 10 of lineage 4, and five of lineage 5. Moreover, the analyses included one specimen of each of the following eight species of *Mesalina*: *M. watsonana*, *M. martini, M. olivieri, M. brevirostris, M. kuri, M. balfouri, M. adramitana* and *M. rubropunctata*, plus two members of the genus *Acanthodactylus* that were used as outgroups in the ML analyses: *A. longipes* (Boulenger, 1918) and *A. scutellatus* (Audouin, 1827) based on published evidence (see Tamar *et al.* 2016).

Genomic DNA was isolated from ethanol-preserved tissue samples using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA) or the SpeedTools Tissue DNA Extraction kit (Biotools, Madrid, Spain). Partial sequences of three mitochondrial markers (12S rRNA - *12S*, 16S rRNA - *16S* and Cytochrome b - *cytb*) and one nuclear gene (melanocortin 1 receptor - *MC1R*) were PCR-amplified and sequenced in both directions for 48 new specimens (a total of 180 new sequences). Primers, PCR conditions and source references for the amplification are detailed in Appendix II. Geneious v. R6 (Kearse *et al.* 2012) was used for assembling and manually editing the chromatographs. All coding fragments were translated into amino acids and no stop codons were observed. Heterozygous positions for the *MC1R* nuclear gene fragment were identified and coded according to IUPAC ambiguity codes. DNA sequences were aligned using MAFFT v.7 (Katoh & Standley 2013) applying parameters by default (Auto strategy, Gap opening penalty: 1.53, Offset value: 0.0). For the ribosomal fragments, we applied the Q-INS-i strategy, in which information on the secondary structure of the RNA was considered. Phased sequences of the *MC1R* fragment were used for the network analysis and also for specific ML analyses. SEQPHASE (Flot 2010) was used to convert the input files, and the software PHASE v.2.1.1 to resolve phased haplotypes (Stephens *et al.* 2001). Default settings in PHASE were used except for phase probabilities that were set as ≥ 0.7 (see Harrigan *et al.* 2008). Uncorrected *p*-distances with pairwise deletion of the mitochondrial fragments were calculated for all *Mesalina* species pairs in MEGA v.6 (Tamura *et al.* 2013).

Phylogenetic and network analyses. Phylogenetic analyses were performed using maximum-likelihood (ML) and Bayesian (BI) methods. Best-fit partitioning scheme and models of molecular evolution were inferred with PartitionFinder v.1.1.1 (Lanfear *et al.* 2012) with the following settings: branch lengths linked, only models available in BEAST evaluated, initial partitions by gene, BIC model selection criterion applied and all partition schemes analyzed. The partition scheme and models of sequence evolution selected were *12S+16S,* GTR+I+G; *cytb,* GTR+I+G and *MC1R,* HKY+I+G. For each gene partition, we performed a Likelihood-ratio test implemented in MEGA v.6 (Tamura *et al.* 2013) to test whether a strict molecular clock or a relaxed clock fit our data best. The hypothesis that the sequences evolve in a clock-like manner could not be rejected at a 5% significance level for the *MC1R* nuclear gene fragment, while it was rejected for the mitochondrial genes. ML analyses were performed in RAxML v.7.4.2 (Stamatakis 2006) as implemented in raxmlGUI (Silvestro & Michalak 2012) with 100 random-addition searches. A GTR+G model of sequence evolution was used with all parameters estimated independently for each partition. Reliability of the ML tree was assessed by bootstrap analysis (Felsenstein 1985) including 1,000 replications. BEAST v.1.8.0 (Drummond *et al.* 2012) was used for BI analyses. Analyses were run three times for $5x10^7$ generations with sampling frequency of 10,000 generations. Models and prior specifications were applied as follows (otherwise by default): models of sequence evolution for each partition as selected by PartitionFinder (see above); Coalescent Constant Size process of speciation; uncorrelated lognormal clock for mitochondrial genes and strict clock for the nuclear one (see above); random starting tree; base substitution prior Uniform (0,100); alpha prior Uniform (0, 10); fix mean rate of molecular clock model of the first partition to 1. Substitution and clock models were unlinked and the xml file was manually modified to set "Ambiguities=TRUE" for the *MC1R* partition to account for variability in the heterozygous positions, instead of treating them as missing data. Posterior trace plots and effective sample sizes (ESS) of the runs were monitored in Tracer v1.5 (Rambaut & Drummond 2013) to ensure convergence. The results of the individual runs were combined in LogCombiner discarding 10% of the samples and the ultrametric tree was produced with TreeAnnotator (both provided with the BEAST package). Nodes in the phylogenetic tree were considered strongly supported if they received ML bootstrap values ≥ 70% and posterior probability (pp) support values ≥ 0.95 (Huelsenbeck & Rannala 2004; Wilcox *et al.* 2002).

With the aim of exploring the patterns of haplotype sharing within the *M. guttulata* species complex, the

genealogical relationships of the *MC1R* nuclear gene fragment were assessed with a haplotype network, inferred using statistical parsimony as implemented in the program TCS v.1.21 (Clement *et al.* 2000). Phased sequences were used (see above) and a connection limit of 95% was applied.

Morphological analyses

Morphological samples, museum acronyms and variables. In order to simplify, the number of specimens included in the morphological analyses are listed below based on the corresponding lineage numbers from Fig. 2, which correspond to the accepted species in the present work (see also Appendix I). The morphological dataset included 83 specimens: 11 of lineage 1 (6 females and 5 males), 18 of lineage 2 (7 females and 11 males), 9 of lineage 3 (3 females and 6 males), 2 of lineage 4 (1 female and 1 male), and 43 specimens of lineage 5 (17 females and 26 males). All vouchers were obtained from the following collections: Laboratoire de Biogéographie et Écologie des Vertébrés de l'École Pratique des Hautes Etudes, Montpellier, France (BEV), Natural History Museum, London, UK (BM), The Hebrew University of Jerusalem, Israel (HUJR), Institute of Evolutionary Biology (CSIC-UPF), Barcelona, Spain (IBE), Museo Civico di Storia Naturale, Carmagnola, Turin, Italy (MCCI), Università di Firenze, Museo Zoologico "La Specola", Firenze, Italy (MZUF), Oman Natural History Museum (ONHM); The Steinhardt Museum of Natural History, Tel Aviv, Israel (TAU), Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK), National Museum Prague, Czech Republic (NMP). The geographical distribution of all the samples used in the morphological (and molecular) analyses are shown in Fig. 1 and locality data, sample and voucher codes, taxonomic identification, and other relevant data are presented in Appendix I.

The following measurements were taken on both sides of each specimen by the same person (R.Si.) using a digital caliper with accuracy to the nearest 0.1 mm: 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, taken at the place of maximum head width; Head depth, taken at the place of maximum head depth; Forelimb length, from the axilla to the tip of the distal claw; Hind limb length, taken from the groin to the tip of the distal claw; 4th toe length, taken from the insertion of the 5th toe including the claw; Tail length, from the cloaca to the tip of the tail, if original. In addition to these mensural (morphometric) variables, eight meristic (pholidotic) characters were also collected using a dissecting microscope: Supralabials, number of supralabials from the most posterior clearly enlarged plate, to the rostral (excluded), including the Subocular, number of supralabials, number of gular scales in a straight median series, from the plates of the collar (excluded) to the point of contact of the two series of chin-shields; Plates in collar, number of enlarged scales in the collar; Dorsals, number of dorsal scales across midbody; Ventrals across belly, number of ventral scales in longest row across belly; Transverse rows of ventrals, number of transverse series of ventral scales, counted along the ventral side to (and excluding) the level of the femoral pores; Femoral pores, number of femoral pores; Subdigital lamellae, number of lamellae along the underside of the 4th toe, defined by their width (the one touching the claw included).

Based on the study by Segoli *et al.* (2002), three morphometric indexes were calculated: Head index, 100 × Head length 1 divided by Head width; Toe index, 100 × 4th toe length divided by total hindlimb length; Lamellae percSVL, 4th toe length as a percentage of SVL and divided by the number of subdigital lamellae under that toe.

Univariate and multivariate analyses. Statistical analyses were performed separately for males and females in order to control for possible confounding effects of sexual dimorphism. In order to compare our results with those reported by Segoli *et al*. (2002), morphological characters (i.e., Head length (HL1), Head width, Head depth, Forelimb length, Hindlimb length, 4th toe length and Tail length) were expressed as a percentage of SVL. First, we used a one-way Analysis of Variance (ANOVA) with Tukey post hoc tests in order to check for differences in morphological traits among species. Then we used multivariate analyses to check whether species could be actually separated on the basis of morphology, and which traits best characterized the morphology of each species.

Multivariate analyses were performed including 33 females and 48 males (81 specimens). Since we had only two adult specimens belonging to lineage 4, we decided to exclude them from the multivariate analyses, pending the incorporation of more specimens in a future study in which the relationships between lineages 3 and 4 will be analyzed in depth. Since original tails were found in only 45 specimens, the character tail length was excluded from the multivariate analyses. We used a non-parametric Multivariate Analysis of Variance (MANOVA) (Anderson 2001) on the matrix of standardized Euclidean distances between specimens in order to check if the morphology

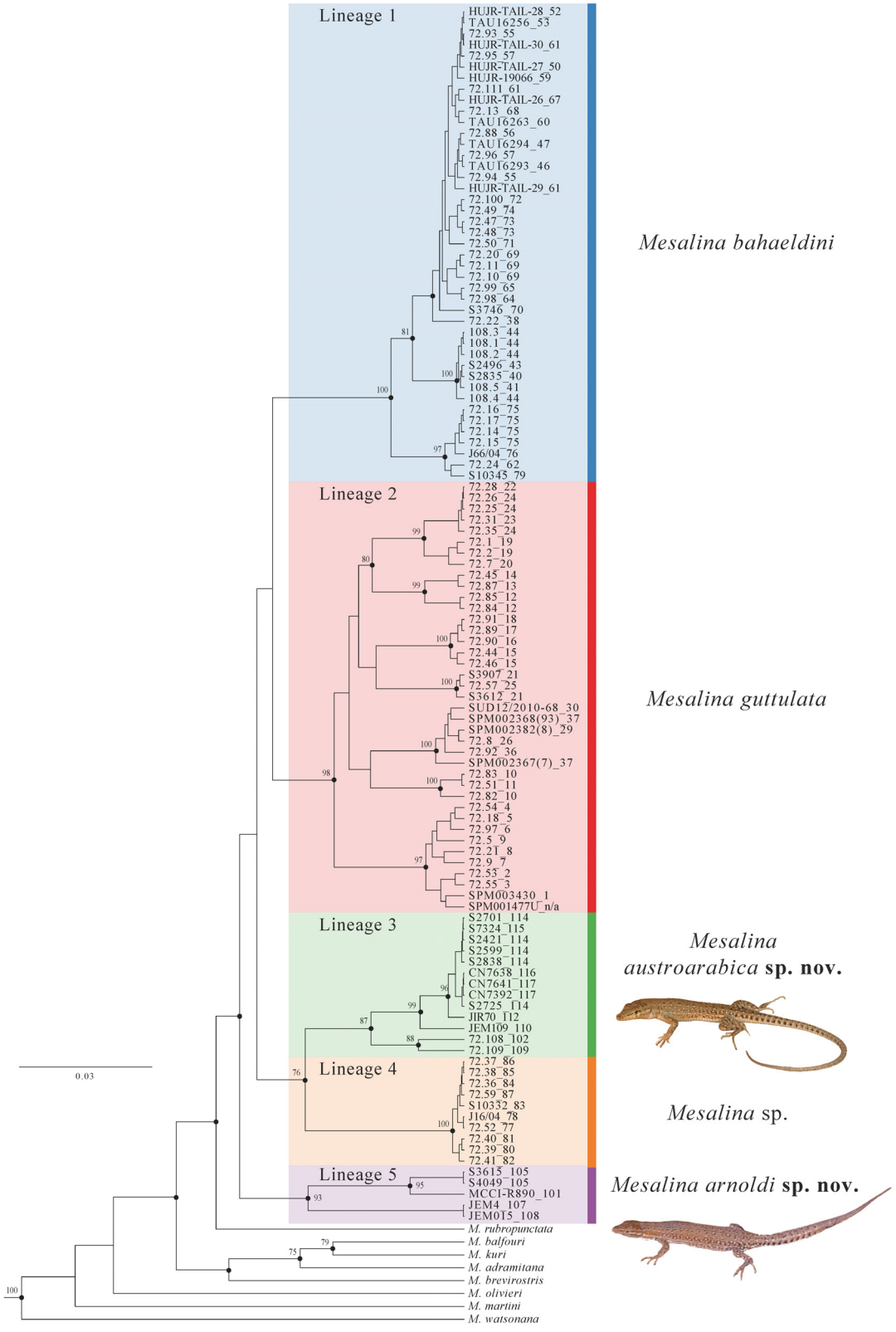


FIGURE 2. Bayesian phylogenetic tree of the genus *Mesalina* based on concatenated sequences of three mitochondrial markers (*12S*, *16S* and *cytb*) and one nuclear gene (*MC1R*). Black dots indicate posterior probability values ≥0.95 and bootstrap values ≥70% are shown next to the nodes. Color bars correspond to the five lineages recognized within the *M. guttulata* complex. Sample codes are followed by locality numbers (see Figure 1 and Appendix I). Taxon names correspond to changes proposed in this study and inset pictures show specimens of the two new species described (not to scale).

differed among sites. The number of permutations was set to 999. Then, a constrained correspondence analysis (CCA) was used to visualize the results and detect the variables that separate the groups better. The effect of variables on specimens' ordination was evaluated by fitting morphological vectors onto the first two CCAs; these vectors point to the direction of most rapid change in the morphological variables, while their length is proportional to the correlation between groups and morphological variables. All tests were performed using the package *vegan* in R 3.3.2 (R Development Core Team 2016), and unless otherwise stated, values reported are means ± standard errors.

Results

Molecular analyses. The dataset used for the phylogenetic analyses consisted of a concatenated alignment of 1,916 base pairs (bp) for 120 individuals (118 *Mesalina* and two outgroups) with 537 variable (*V*) and 424 parsimony informative (*Pi*) positions, including the mitochondrial genes *12S* (398 bp), *16S* (453 bp), *cytb* (402 bp), and the nuclear gene fragment *MC1R* (663 bp).

The results of the phylogenetic analyses using BI and ML analyses produced similar trees differing mostly in the less supported nodes at the intraspecific level (Fig. 2). *Mesalina watsonana* branched as a sister taxon to all the other *Mesalina* species included in the analysis. The *Mesalina guttulata* species complex is divided into five well-supported deep lineages with a mainly allopatric distribution (see Fig. 1): lineage 1.—a genetically very uniform lineage restricted to the Middle East that includes seven specimens from the southern Sinai Mountains, in the vicinity of the type locality of *M. bahaeldini* (locs. 40-41, 43-44), plus 36 other specimens from localities east of the Suez Canal; lineage 2.—a genetically variable and widely distributed lineage that includes all the samples of *M. guttulata* from the area west of the Suez Canal from Egypt to Mauritania; lineage 3.—a genetically variable and widely distributed lineage that includes samples from southern Arabia, between the Dhofar and the Yemen Mountains, that is described as a new species herein (*M.* sp. 1 in Carranza *et al*. 2018); lineage 4.—a genetically very uniform lineage that includes specimens from Jordan, Saudi Arabia and Kuwait and that is left undescribed in the present work (*M.* sp.); and lineage 5.—a highly variable lineage restricted to the highlands of southwestern Arabia that is described as a new species herein (*M.* sp. A in Arnold 1986a). The phylogenetic relationships between the different lineages are not very well supported but the trees suggest that lineage 5 is the first species to branch out of the *M. guttulata* species complex. Lineages 1 and 2 form an unsupported clade, sister group to a well-supported clade formed by lineages 3 and 4.

The results of the haplotype network analyses are presented in Fig. 3. A total of 35 haplotypes were found in the *M. guttulata* species complex: 15 in lineage 1, eight in lineage 2, five in lineage 3, three in lineage 4, and four in lineage 5. Interestingly, despite the relatively high number of specimens analyzed from all five lineages (37 specimens; 74 alleles) all 35 haplotypes are private to each lineage, so there is a complete lack of allele sharing, even between closely related sister lineages, such as lineages 1 and 2 and lineages 3 and 4, respectively (see Fig. 2). The results of the ML analysis of the *MC1R* phased dataset is presented in Appendix III. These results indicate that there is a high degree of genetic isolation between the five lineages of the *Mesalina guttulata* species complex in the nuclear gene *MC1R.*

Inter-specific genetic distances for all the species of *Mesalina* analyzed in the present study are presented in Table 1. Uncorrected genetic distances between the five lineages of the *M. guttulata* species complex range between 3.6–6.6% in the *12S*, 4.3–7.1% in the *16S* and 11.7–15.7% in the *cytb* genes. These values fall within the level of genetic variability observed between the eight species of *Mesalina* included in our study, which ranges between 2.9–10.6% in the *12S*, 5.3–14.5% in the *16S* and 11.4–21.6% in the *cytb*.

Morphological analyses

Mensural (morphometric) characters and indexes. The one-way ANOVA on male measurements showed that six traits (i.e., SVL, Head depth, Forelimb length, 4th toe length, Tail length, and Lamellae percSVL) significantly differed between lineages, while three others (i.e., Head length 1, Head width, and Toe index) where close to the significant threshold (Table 2). Tukey post hoc tests showed that males from lineage 3 had a smaller size than males from lineages 1 and 2, and also had a relatively shorter head, although this latter difference was relevant only with respect to lineage 2. Males of lineage 5 significantly differed from males of lineage 2 in having

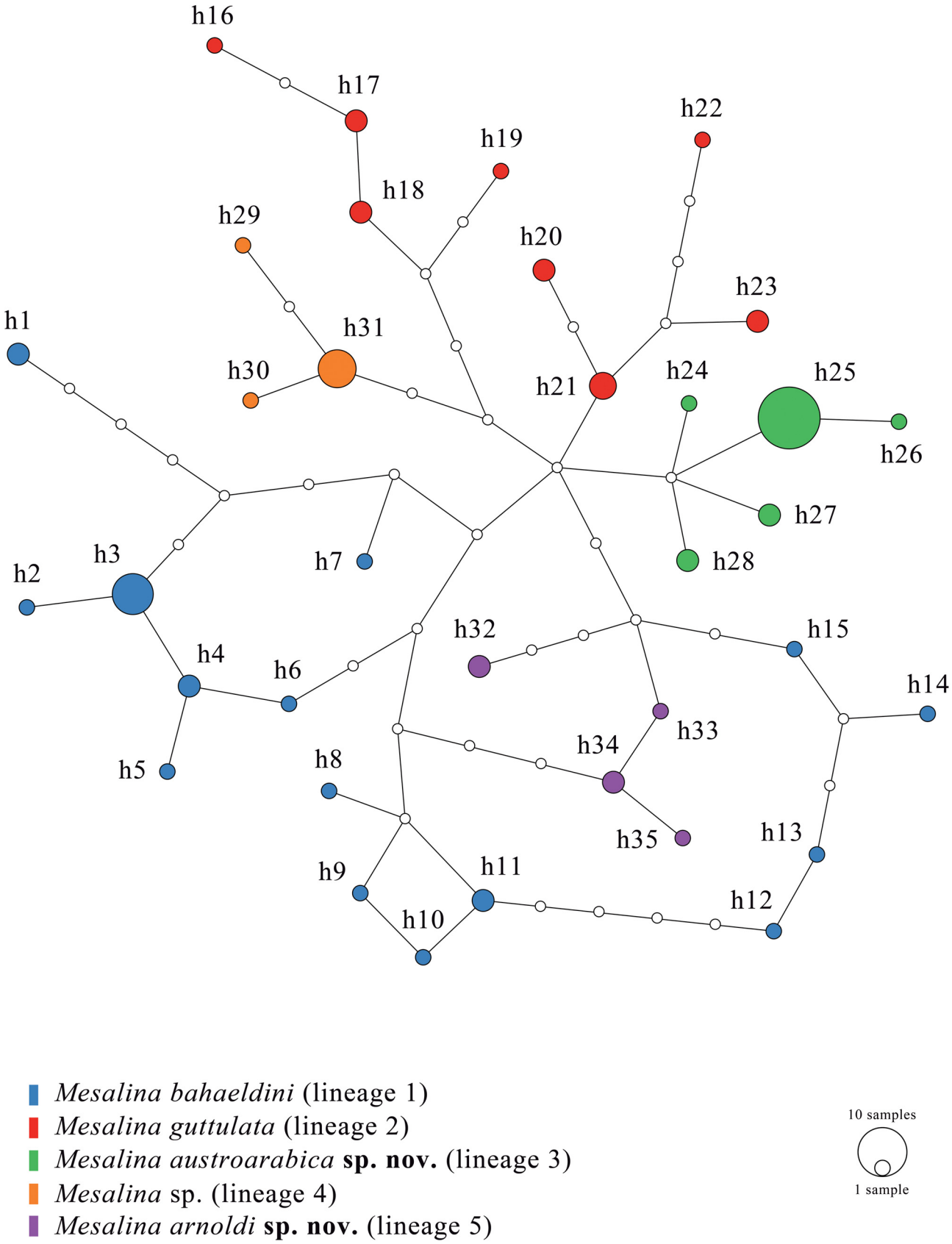


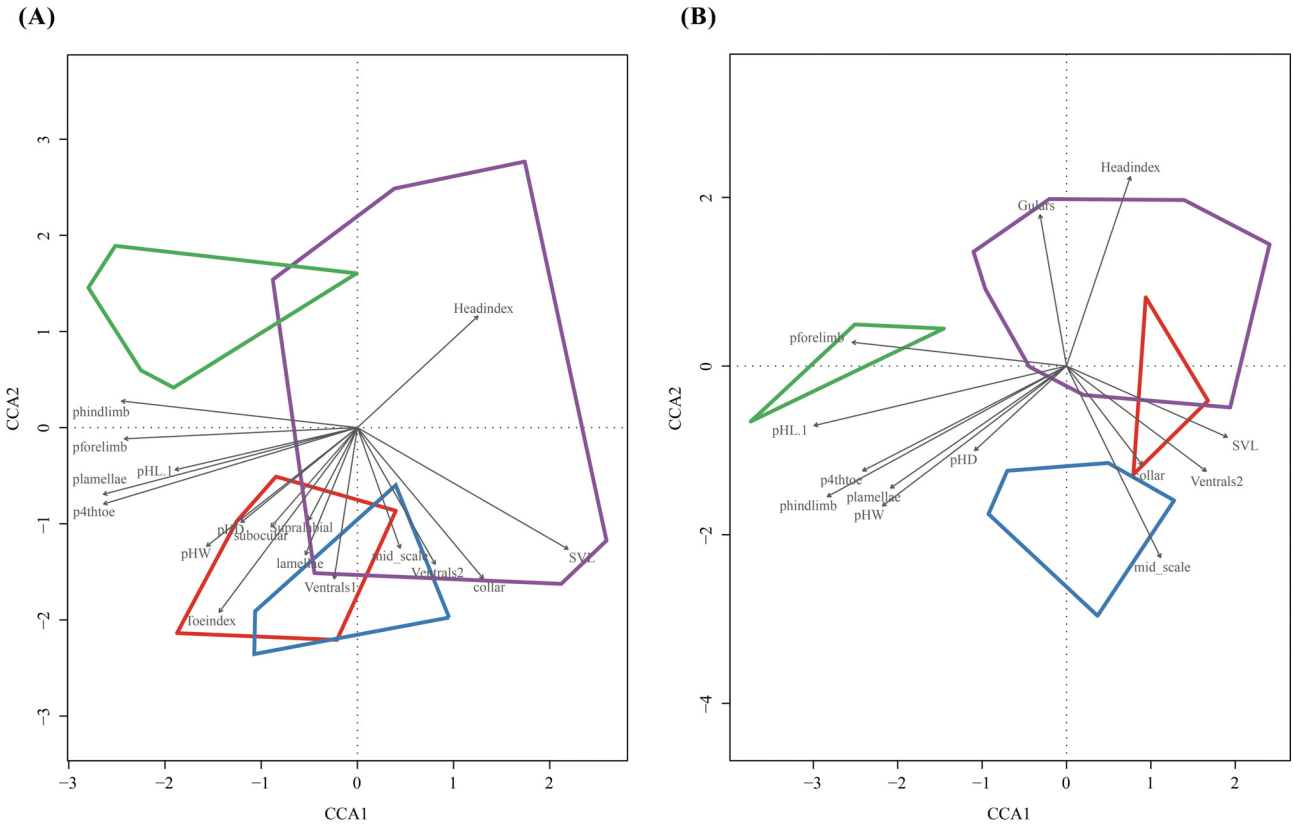
FIGURE 3. Unrooted haplotype network of the *MC1R* nuclear gene. Circle sizes are proportional to the number of individuals that present that particular haplotype (see Appendix I for details). White dots represent mutational steps. Colors correspond to the five lineages recognized within the *M. guttulata* complex.

a thinner head, shorter 4th toe with lower values of Lamellae percSVL and a relatively longer tail and, with respect to lineage 1, in having a relatively longer tail. Furthermore, males of lineage 5 had a significantly larger size, but a relatively narrower head, shorter forelimbs, and lower values of Lamellae percSVL than males of lineage 3.

The same analyses on female measurements revealed significant differences among species in head length and head width, forelimb and hindlimb length, 4th toe length, and Lamellae percSVL (Table 3). However, Tukey post hoc tests highlighted significant differences only concerning lineage 3, which had a relatively longer and wider head than lineage 2, a relatively longer head and forelimbs than lineage 1, and a relatively longer and wider head, longer hindlimbs, a longer 4th toe with higher values of Lamellae percSVL than lineage 5.

Meristic (pholidotic) characters. The one-way ANOVA for males found significant differences among species in five pholidotic characters (i.e., gulars, plates in collar, dorsals, number of transverse rows of ventrals, and femoral pores; Table 4). Tukey post hoc showed that males of lineage 3 had less dorsals than males of lineage 1, while males of lineage 5 had more gulars and femoral pores than males of lineages 1 and 2. Additionally, males of lineage 5 had more dorsal scales than males of lineage 2. Marked differences were found between males of lineages 3 and 5, with males of lineage 5 having more plates in the collar, more dorsals, higher number of transverse rows of ventrals and also more femoral pores.

The one-way ANOVA for females found significant interspecific differences for three pholidotic characters (i.e., supralabials, gulars, and femoral pores), and two other characters (i.e., dorsals and subdigital lamellae) were close to the significant threshold (Table 5). Nearly all differences concerned females of lineage 5, which had significantly more supralabials and gulars, femoral pores and lamellae than females from lineage 1. Females of lineage 3 differed significantly from females of lineage 1 in having more dorsal scales.



Mesalina bahaeldini (lineage 1)
Mesalina guttulata (lineage 2)
Mesalina austroarabica **sp. nov.** (lineage 3)
Mesalina arnoldi **sp. nov.** (lineage 5)

FIGURE 4. Results of constrained correspondence analyses (CCA) for males (A) and females (B). This plot shows the position of each species included in the multivariate analyses on the first two axes of morphological space. See material and methods for details.

TABLE 1. Uncorrected genetic distances (*p*-distances in percentage) between all *Mesalina* species included in the molecular study using the *12S / 16S* (lower-left) and *cytb* (upper-right) mitochondrial gene fragments. Distances among the *M. guttulata* species complex are highlighted in bold.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1. *M. bahaeldini*		**11.4**	**13.7**	**12.4**	**15.2**	13.7	16.2	15.9	15.4	15.4	15.9	17.7	20.4
2. *M. guttulata*	**5.2 / 6.4**		**13.9**	**13.2**	**13.8**	13.4	15.4	13.7	15.2	12.4	17.4	19.4	19.2
3. *M. austroarabica* **sp. nov.**	**6 / 5.5**	**5.7 / 6.4**		**11.7**	**15.7**	15.4	14.9	17.4	16.9	16.2	19.9	17.7	18.9
4. *M.* sp.	**4.2 / 5.7**	**4.2 / 6.4**	**3.6 / 4.3**		**11.9**	12.4	15.2	14.2	14.4	12.4	17.9	17.2	18.2
5. *M. arnoldi* **sp. nov.**	**5.6 / 5.9**	**5.2 / 7.1**	**6.6 / 6.1**	**5.3 / 6.2**		13.3	15.2	14.7	14.2	14.2	16.5	18.7	19.2
6. *M. rubropunctata*	5.5 / 10.4	5.7 / 9.6	5.4 / 10.6	4.4 / 8.7	5.8 / 10		15.9	16.7	14.9	13.4	15.2	18.4	19.2
7. *M. balfouri*	5.7 / 8.6	6 / 8.3	6.5 / 7.7	4.9 / 8.2	5.8 / 8.1	5.5 / 11.1		12.7	13.4	16.7	15.7	15.9	18.2
8. *M. kuri*	5.7 / 8.2	5.2 / 8.3	7.3 / 9.1	4.4 / 7.3	5.8 / 8.4	6.2 / 10.4	2.9 / 7.4		11.4	12.7	15.2	18.4	17.2
9. *M. adramitana*	4.7 / 7.3	5.5 / 7	6.2 / 7.6	4.9 / 6.1	5.4 / 7.5	5.7 / 8.8	4.9 / 6.2	4.4 / 5.3		11.7	15.9	14.9	16.4
10. *M. brevirostris*	7.3 / 7.7	7.8 / 7.6	7.5 / 7.2	4.9 / 6.6	7.4 / 7.3	6.5 / 9.5	6 / 7.1	5.7 / 7.1	7.3 / 7.2		16.7	20.4	17.9
11. *M. olivieri*	7.5 / 8.5	8.3 / 9.4	8.5 / 8.6	5.2 / 7.7	7.4 / 8.8	6.7 / 9.5	7.8 / 8.3	6 / 8.5	7 / 8.5	7 / 8.8		18.7	21.6
12. *M. martini*	9.4 / 8.6	10.9 / 10	10.9 / 9.1	9.1 / 8.2	9.7 / 9.2	9.8 / 10.6	9.1 / 9.4	9.1 / 9.7	9.3 / 9	10.4 / 8.3	10.6 / 8.9		17.4
13. *M. watsonana*	7.3 / 13.4	8.1 / 12.9	7.8 / 14.4	6.7 / 14.3	7.3 / 14.5	8 / 13.5	7.8 / 13.7	7 / 11.4	6 / 14	8.3 / 12.1	8.5 / 12.5	9.6 / 11.8	

TABLE 2. Comparison of mensural characters (means ± SE; min. and max. between brackets) among male *Mesalina austroarabica* **sp. nov.** (n = 6; 6 for tail length); *M.* sp. (n = 1); *M. arnoldi* **sp. nov.** (n = 26; 14 for tail length); *M. guttulata* (n = 11; 8 for tail length) and syntypes of *M. guttulata* (n = 3*;* 0 for tail length; after Segoli *et al.* 2002); *M. bahaeldini* (n = 5; 4 for tail length). Measurements are in percent of SVL (except SVL, head index and toe index). *Maus/Mg, Maus/Mb, Ma/Mg, Ma/Mb, Maus/Ma* = significance of the difference between species pairs. *Maus = M. austroarabica* **sp. nov.**, *Mg = M. guttulata, Mb = M. bahaeldini*, *Ma = M. arnoldi* **sp. nov.**

Character	***M. bahaeldini*** **(lineage 1)**	***M. guttulata*** **(lineage 2)**	***M. austroarabica*** **sp. nov. (lineage 3)**	***M.*** **sp. (lineage 4)**	***M. arnoldi*** **sp. nov. (lineage 5)**	**F**	**df**	***P***	***Maus / Mg***	***Maus/ Mb***	***Ma / Mg***	***Ma/ Mb***	***Maus/ Ma***
SVL (mm)	45.8 ± 1.2 (43-50)	45.5 ± 0.5 (42-48)	38.9 ± 2.4 (31-47)	52.0	47.9 ± 0.7 (40-56)	11.479	3.44	<0.001	0.002	0.009	ns	ns	<0.001
Head length	25.7 ± 0.2 (25.1-26.4)	25.3 ± 0.3 (23.8-26.8)	27.0 ± 0.8 (25.2-30.8)	23.8	25.9 ± 0.2 (22.9-27.5)	2.247	3.44	0.096	0.063	ns	ns	ns	ns
Head width	15.5 ± 0.3 (14.7-16.3)	15.3 ± 0.2 (14.5-16.5)	16.0 ± 0.4 (14.5-17.1)	14.6	14.9 ± 0.2 (11.7-16.4)	2.357	3.44	0.084	ns	ns	ns	ns	0.071
Head depth	9.9 ± 0.2 (9.3-10.8)	10.5 ± 0.2 (9.3-11.7)	10.6 ± 0.3 (10.0-12.1)	10.0	9.8 ± 0.1 (7.7-11.5)	3.073	3.44	0.037	ns	ns	0.089	ns	ns
Head index	166 ± 3 (160-173)	166 ± 3 (145-184)	169 ± 6 (153-188)	163.2	174 ± 3 (149-220)	1.502	3.44	0.23	ns	ns	ns	ns	ns
Forelimb length	33.8 ± 0.7 (31.6-35.4)	36.1 ± 0.8 (32.4-41.1)	37.3 ± 0.9 (35.1-40.5)	29.4	34.5 ± 0.5 (27.3-38.4)	3.275	3.44	0.029	ns	ns	ns	ns	0.067
Hindlimb length	63.1 ± 1.0 (60.5-65.8)	64.3 ± 0.9 (58.5-68.6)	67.7 ± 1.8 (62.5-75.7)	51.9	62.7 ± 1.3 (50.2-72.4)	1.517	3.44	0.22	ns	ns	ns	ns	ns
4^{th} toe length	20.1 ± 0.9 (17.4-22.7)	22.4 ± 0.6 (18.9-25.0)	22.1 ± 0.7 (19.4-23.9)	14.6	20.1 ± 0.4 (16.6-23.3)	4.247	3.44	0.010	ns	ns	0.012	ns	ns
Toe index	32.8 ± 1.2 (28.8-36.1)	34.8 ± 0.9 (30.0-38.7)	32.6 ± 1.0 (29.6-35.7)	28.1	32.1 ± 0.5 (26.7-36.4)	2.659	3.44	0.059	ns	ns	0.035	ns	ns
Tail length	182 ± 12 (160-211)	222 ± 6 (198-260)	213 ± 6 (187-232)	(-)	217 ± 4 (188-255)	3.796	3.31	0.021	ns	ns	ns	0.026	ns
Lamellae percSVL	0.98 ± 0.04 (0.83-1.10)	1.04 ± 0.04 (0.8-1.27)	1.06 ± 0.02 (0.97-1.14)	0.8	0.92 ± 0.02 (0.75-1.08)	4.860	3.44	0.0053	ns	ns	0.015	ns	0.031

TABLE 3. Comparison of mensural characters (means ± SE; min. and max. between brackets) among female *Mesalina austroarabica* **sp. nov.** (n = 3, 1 for tail length), *M.* sp. (n = 1), *M. arnoldi* **sp. nov.** (n = 17; 6 for tail length), *M. guttulata* (n = 7*;* 3 for tail length) and syntypes of *M. guttulata* (n = 2; 1 for tail length; after Segoli *et al.* 2002), and *M. bahaeldini* (n = 6; 3 for tail length). Measurements are in percent of SVL (except SVL, head index and toe index). *Maus/Mg, Maus/Mb, Ma/Mg, Ma/Mb, Maus/Ma* = significance of the difference between species pairs. *Maus* = *M. austroarabica* **sp. nov.**, *Mg* = *M. guttulata, Mb* = *M. bahaeldini*, *Ma* = *M. arnoldi* **sp. nov.**

Character	*M. bahaeldini* (lineage 1)	*M. guttulata* (lineage 2)	*M. austroarabica* sp. nov. (lineage 3)	*M.* sp. (lineage 4)	*M. arnoldi* sp. nov. (lineage 5)	F	df	*P*	*Maus/ Mg*	*Maus/ Mb*	*Ma / Mg*	*Ma/ Mb*	*Maus/ Ma*
SVL (mm)	43.2 ± 1.3 (40-47.5)	46.8 ± 1.2 (42-50)	42.8 ± 1.6 (40-45.5)	41	45.2 ± 1.2 (36-55)	1.005	3.29	0.41	ns ns	ns	ns	ns	ns
Head length	23.3 ± 0.5 (21.1-24.2)	23.1 ± 0.2 (22.3-23.6)	26.5 ± 1.1 (24.6-28.5)	25.4	23.2 ± 0.4 (19.8-25.4)	5.021	3.29	0.006	0.008	0.015	ns	ns	0.004
Head width	14.2 ± 0.3 (13.2-15.2)	13.3 ± 0.4 (12.4-15.7)	15.7 ± 0.7 (14.5-17.0	15.1	13.6 ± 0.2 (10.8-15.4)	4.586	3.29	0.009	0.009	ns	ns	ns	0.012
Head depth	9.2 ± 0.2 (8.5-10.0)	9.1 ± 0.2 (8.4-10.0)	9.8 ± 0.5 (9.0-10.7)	10.7	9.4 ± 0.2 (8.0-10.6)	1.029	3.29	0.39	ns	ns	ns	ns	ns
Head index	164 ± 2 (158-172)	175 ± 5 (147-189)	169 ± 1 (168-170)	167.7	171 ± 3 (142-187)	0.926	3.29	0.44	ns	ns	ns	ns	ns
Forelimb length	31.2 ± 0.5 (30.2-33.2)	33.6 ± 0.6 (31.8-36.4)	35.5 ± 1.5 (32.5-37.2)	33.4	32.7 ± 0.6 (28.4-36.5)	3.192	3.29	0.038	ns	0.032	ns	ns	ns
Hindlimb length	57.2 ± 1.1 (54.0-60.5)	57.4 ± 1.0 (54.0-61.4)	64.3 ± 2.2 (60.9-68.5)	60.2	53.7 ± 1.6 (43.1-62.8)	4.071	3.29	0.016	ns	ns	ns	ns	0.013
4^{th} toe length	19.4 ± 0.5 (17.9-21.2)	19.9 ± 0.3 (18.8-21.2)	21.3 ± 1.6 (18.7-24.2)	18.3	18.5 ± 0.4 (15.4-21.0)	3.100	3.29	0.042	ns	ns	ns	ns	0.052
Toe index	33.9 ± 0.7 (31.4-35.8)	34.7 ± 0.7 (31.5-37.2)	33.0 ± 1.4 (30.7-35.4)	30.4	34.6 ± 0.6 (30.4-38.2)	0.646	3.29	0.59	ns	ns	ns	ns	ns
Tail length	184 ± 6 (174-200)	180 ± 5 (164-191)	92 (-) 230 (-)	(-)	197 ± 6 (149-214)	1.629	3.9	0.25	ns	ns	ns	ns	ns
Lamellae percSVL	0.94 ± 0.02 (0.83-1.10)	0.93 ± 0.02 (0.8-1.27)	1.03 ± 0.06 (0.97-1.14)	0.8	0.86 ± 0.02 (0.75-1.08)	4.825	3.29	0.0076	ns	ns	ns	ns	0.011

TABLE 4. Comparison of pholidotic characters (means ± SE; min. and max, between brackets) among male *Mesalina austroarabica* **sp. nov.** (n = 6), *M.* sp. (n = 1), *M. arnoldi* **sp. nov.** (n = 26), *M. guttulata* (n = 11) and syntypes of *M. guttulata* (n = 3*;* after Segoli *et al.* 2002), *M. bahaeldini* (n = 5). *Maus/Mg, Maus/Mb, Ma/Mg, Ma/Mb, Maus/Ma* = significance of the difference between species pairs. *Maus = M. austroarabica* **sp. nov.**, *Ma = M. arnoldi* **sp. nov.**, *Mg = M. guttulata, Mb = M. bahaeldini*.

Character	*M. bahaeldini* (lineage 1)	*M. guttulata* (lineage 2)	*M. austroarabica* sp. nov. (lineage 3)	*M.* sp. (lineage 4)	*M. arnoldi* sp. nov. (lineage 5)	F	df	P	*Maus/ Mg*	*Maus/ Mb*	*Ma/ Mg*	*Ma/ Mb*	*Maus/ Ma*
Supralabials	8.8 ± 0.4 (8-10)	9.0 ± 0.1 (8-10)	8.7 ± 0.3 (8-10)	8	9.0 ± 0.1 (8-10)	0.955	3.43	0.42	ns	ns	ns	ns	ns
Suboculars	5.2 ± 0.2 (5-6)	5 ± 0 (5-5)	5.2 ± 0.2 (5-6)	5	5.1 ± 0.1 (5-6)	0.742	3.43	0.53	ns	ns	ns	ns	ns
Gulars	22.6 ±0 .9 (20-25)	23.3 ± 0.5 (20-27)	24.7 ± 0.2 (24-25)	27	26.5 ± 0.5 (20-31)	9.521	3.44	<0.001	ns	ns	<0.001	0.002	ns
Plates in the collar	10.7 ± 0.4 (10-12)	9.8 ± 0.4 (7-12)	9.0 ± 0.4 (8-10)	10	10.6 ± 0.2 (9-14)	3.742	3.41	0.018	ns	ns	ns	ns	0.023
Dorsals	48 ± 1.7 (45-54)	42.3 ±1.0 (37-48)	41.2 ± 1.3 (39-47)	44	46.6 ± 0.8 (40-57)	6.415	3.44	0.0012	ns	0.026	0.015	ns	0.015
Ventrals across belly	8 ± 0 (8-8)	8.4 ± 0.2 (8-10)	8 ± 0 (8-8)	8	8.0 ± 0 (8-8)	2.739	3.42	0.055	ns	ns	ns	ns	ns
Transvers rows of ventrals	28.2 ± 0.2 (28-29)	29.1 ± 0.4 (27-31)	27.2 ± 0.48 (25-28)	26	29.7 ± 0.4 (26-34)	4.580	3.41	0.0074	ns	ns	ns	ns	0.0065
Femoral pores	26.6 ± 0.9 (24-29)	25.7 ± 0.8 (23-32)	26.8 ± 0.9 (23-30)	24	30.0 ± 0.4 (25-34)	10.614	3.42	<0.001	ns	ns	<0.001	0.021	0.020
Subdigital lamellae	21.2 ± 0.7 (20-22)	21.6 ± 0.4 (19-23)	20.8 ± 0.4 (20-22)	19	21.7 ± 0.2 (19-26)	0.978	3.44	0.41	ns	ns	ns	ns	ns

TABLE 5. Comparison of pholidotic characters (means ± SE; min. and max. between brackets) among female *Mesalina austroarabica* **sp. nov.** (n = 3), *M.* sp. (n = 1), *M. arnoldi* **sp. nov.** (n = 17), *M. guttulata* (n = 7) and syntypes of *M. guttulata* (n = 2; after Segoli *et al.* 2002), *M. bahaeldini* (n = 6). *Maus/Mg, Maus/Mb, Ma/Mg, Ma/Mb, Maus/Ma* = significance of the difference between species pairs. *Maus* = *M. austroarabica* **sp. nov.**, *Ma* = *M. arnoldi* **sp. nov.**, *Mg* = *M. guttulata, Mb* = *M. bahaeldini*.

Character	*M. bahaeldini* (lineage 1)	*M. guttulata* (lineage 2)	*M. austroarabica* sp. nov. (lineage 3)	*M.* sp. (lineage 4)	*M. arnoldi* sp. nov. (lineage 5)	F	df	P	*Maus/ Mg*	*Maus/ Mb*	*Ma/ Mg*	*Ma/ Mb*	*Maus/ Ma*
Supralabials	8.3 ± 0.2 (8-9)	8.7 ± 0.2 (8-9)	8.3 ± 0.3 (8-9)	9	8.9 ± 0.1 (8-10)	3.037	3.27	0.046	ns	ns	ns	0.064	ns
Suboculars	5 ± 0 (5-5)	5 ± 0 (5-5)	5 ± 0 (5-5)	5	5.1 ± 0.1 (5-6)	0.622	3.27	0.61	ns	ns	ns	ns	ns
Gulars	21.8 ± 0.6 (19-23)	23.3 ± 0.5 (22-25)	24.3 ± 0.3 (24-25)	23	25.6 ± 0.6 (21-30)	5.249	3.28	0.0053	ns	ns	ns	0.004	ns
Plates in the collar	10.3 ± 0.5 (8-11)	10 ± 0.2 (9-11)	8.7 ± 0.3 (8-9)	10	9.9 ± 0.3 (8-12)	1.795	3.27	0.17	ns	ns	ns	ns	ns
Dorsals	47.7 ± 1.6 (44-55)	44.9 ± 1.3 (40-51)	39.3 ± 0.3 (39-40)	44	44.6 ± 1.1 (36-52)	2.690	3.29	0.065	ns	0.039	ns	ns	ns
Ventrals across belly	8 ± 0 (8-8)	8 ± 0 (8-8)	8 ± 0 (8-8)	8	8.4 ± 0.2 (8-10)	0.933	3.26	0.44	ns	ns	ns	ns	ns
Transvers rows of ventrals	31.0 ± 0.5 (29-32)	30.8 ± 0.6 (29-33)	29 ± 0 (29-29)	29	31.9 ± 0.6 (29-37)	2.139	3.28	0.12	ns	ns	ns	ns	ns
Femoral pores	24.8 ± 0.5 (23-26)	21.1 ± 1.1 (18-26)	25.0 ± 1.2 (23-27)	27	26.8 ± 0.8 (21-31)	6.924	3.29	0.0012	ns	ns	<0.001	ns	ns
Subdigital lamellae	20.5 ± 0.4 (19-22)	21.4 ± 0.2 (21-22)	20.7 ± 0.3 (20-21)	23	21.5 ± 0.2 (20-23)	2.594	3.29	0.072	ns	ns	ns	0.089	ns

Multivariate analyses. The non-parametric MANOVA performed on mensural and meristic characters combined confirmed that the morphology of males and females significantly differed among lineages (males: $F = 3.931$, $P < 0.001$; females: $F = 3.157$, $P < 0.001$). Those models explained 24.2% and 29.2% of morphological variance for males and females, respectively. The CCA carried out on the male sub-sample showed that males of lineages 3 and 5 were clearly separated from each other, and from both lineages 1 and 2 (Fig. 4A). The first CCA best separated lineage 5 from all other species, and is mainly associated with measurements related to body morphology. Lower values associated to smaller body size with relatively longer, wider and deeper head, longer forelimb and hindlimb, longer 4th toe with denser lamellae. The second CCA best separated lineages 3 and 5 from lineages 1 and 2, and is mainly associated to pholidotic characters including SVL. Lower values of this second CCA associated to larger individuals with augmented pholidosis. The CCA performed on the female data set gave similar results, and clearly separated all lineages (Fig. 4B). Indeed, the first CCA clearly separated lineage 3 from all other lineages, and mainly linked measurements and body size. As for males, lower values of the first axis corresponded to smaller individuals with relatively longer and wider head, longer forelimb and hindlimb, and also longer 4th toe with more lamellae. The second CCA linked most pholidotic characters and some measurements including SVL, and best separated lineage 1 females from all other lineages. Lower values of this second axis corresponded to larger individuals with relatively larger and wider head, with all pholidotic characters but gulars augmented.

General comments on the two specimens of lineage 4 analyzed. Since only two genetically identified specimens of lineage 4 (a male and a female) were available for morphological examination, they were not included in the statistical analyses pending further studies. However, as a result of the relatively high genetic differentiation of lineage 4 (even from its sister taxon, lineage 3), some comments on the morphology of the two available specimens are provided. The two adult specimens of lineage 4 have the general appearance of specimens from lineage 3. However, in a detailed comparison to specimens from lineage 3, the only male of lineage 4 (BEV.10054; Kuwait) analyzed is larger, the head is shorter, as is the forelimb length, the hindlimb length, the 4th toe length, and the Lamellae percSVL (in percent of SVL). The number of gular scales is higher in this specimen of lineage 4, and the number of subdigital lamellae is lower. Measurements of the female from lineage 4 (BEV.10915; Jordan) fall within the variability of lineage 3, with the exception of Lamellae percSVL. Counts of gular scales are slightly higher in lineage 3 than in lineage 4, in turn, the number of plates in collar is lower in lineage 3, as well the number of dorsals and subdigital lamellae. In the two specimens from lineage 4, the lower eyelid has a window formed by two transparent scales, with margins bordered with dark (like in *M. guttulata, M. bahaeldini* and specimens belonging to lineage 3). The dorsal pattern is similar to the holotype of the new species of lineage 3 described herein. In the female from Azraq (a place located in the black basalt desert of Jordan) the background color is dark, while it is pale in the female from Kuwait, so there is a color polymorphism across the rather large distribution range of lineage 4 (Fig. 1).

Taxonomic account

According to our study and Kapli *et al*. (2008, 2015) and contrary to what was suggested by Segoli *et al.* (2002), *Mesalina guttulata* (lineage 2) is confined to North Africa and does not occur in the Sinai or in the Middle East, where other species are present. As presently delimited, *M. guttulata* is monophyletic, although the tree from Fig. 2 shows a high level of genetic variability in this species across North Africa. The phylogeography and evolution of North African populations of *Mesalina guttulata* will require further analysis that is beyond the scope of the present study. The specimens of *M. bahaeldini* from the southern Sinai Mountains are genetically very similar both in the mitochondrial and nuclear genes (there is allele sharing in the *MC1R* nuclear gene, see Fig. 3 and Appendix I) to populations previously classified as "*M. guttulata*" from other areas east of the Suez Canal in the Sinai, Israel, the West Bank, Jordan and northern Saudi Arabia. The compelling molecular evidence (see Fig. 2 and also Kapli *et al.* 2008, 2015) including specimens from the vicinity of the type locality of *M. bahaeldini* indicates that the "*M. guttulata*" populations from east of the Suez Canal and *M. bahaeldini* are the same species, to which the name *M. bahaeldini* should apply. Segoli *et al*. (2002) applied the name *M. bahaeldini* to *Mesalina* populations from the mountains of southern Sinai based mainly on their striped dorsal pattern. However, as pointed out by Baha El Din 2006, several other populations inhabiting high mountain regions in Egypt, Sudan and Arabia, show a stripped

pattern similar to the *M. bahaeldini* populations from the mountains of southern Sinai, suggesting that a stripped dorsal pattern has appeared several times independently during the evolution of the *M. guttulata* species complex, rendering this character not useful for revising the taxonomy of this group. As a result of the uncertainty of the type locality of the subspecies of *M. b. curatorum* (in an area between the distribution range of *M. guttulata* and *M. bahaeldin*i), the lack of clear morphological characters to sort out the taxonomy of this species complex, and the impossibility of including the holotype or paratypes in our molecular analyses, the taxonomy of this subspecies remains uncertain until more data is available. For the sake of taxonomic stability, in the mean time we propose to keep it as a subspecies of *M. bahaeldini*.

The molecular and morphological data indicate that the populations from southern Arabia belonging to lineage 3 in Fig. 2 (*M.* sp. 1 in Carranza *et al*. 2018) are a new species and, as a result of that, it is described below. Although the molecular data suggest that the geographically widespread populations belonging to lineage 4 in Fig. 2 are genetically very well differentiated and most probably represent a new species independent from lineage 3, the lack of enough material to carry out a proper morphological analysis (only one male and one female are available) prevent any taxonomic conclusions. Therefore, this lineage is provisionally left unnamed (*M.* sp.) until more material is available. The molecular and morphological data (Figs. 2–4) support Arnold's (1986a) hypothesis that the populations from the highlands of southwestern Arabia are a new species (*Mesalina* sp. A in Arnold 1986a) and, as a result of that, it is also described below.

***Mesalina austroarabica* sp. nov.**
(Figs. 1–5; Tables 1–5, Appendices I and III)

Mesalina adramitana Arnold 1980: 307 (part.); Arnold 1986a: 426 (part.); Sindaco & Jeremcenko 2008: 261 (part.); Gardner 2013: 292 (part). *Mesalina ayunensis* van der Kooij 2001: 20 (part.); *Mesalina spec*. van der Kooij 2001: 21. *Mesalina guttulata* Kapli *et al.* 2015: 6. *Mesalina* sp. 1 Carranza *et al.* 2018.

Holotype. Adult male MCCI-R1611, Oman, Dhofar Governorate, Jebel Samhan at 17.1161°N, 54.7131°E WGS84 (about 16 km E of Tawi Atair), 1,321 m a.s.l., 4 January 2010, R. Sindaco, C. Grieco, A. Venchi leg.

Paratypes. Two adult males and an adult female MCCI-R1624/1-3, same locality as the holotype, 19 November 2010, R. Sindaco, C. Grieco, A. Venchi leg.; a female (ONHM4331), same locality as the holotype, 30 April 2011, S. Carranza, E. Gómez-Díaz, F. Amat leg.; a male MCCI-R1810, Jebel Samhan at 17.1597°N, 54.8069°E WGS84, 1,594 m a.s.l., 14 October 2013, S. Carranza, M. Metallinou, R. Sindaco, J. Šmíd, R. Vasconcelos leg.; a male NMP6V-74966/1 and a young NMP6V-74966/2 Jebel Samhan at 17.1494°N, 54.9757°E WGS84, 233 m a.s.l., same date and collectors as MCCI-R1810.

Other specimens examined. Adult female NMP6V-74951, Oman, Dhofar, Jebel al Qamar at 16.8014°N, 53.2783°E, 1,076 m a.s.l., 27 December 2012, J. Šmíd, A. Chudárková leg., plus nine specimens used only for genetic analyses (no vouchers available, juvenile or damaged specimens); all listed in Appendix I.

Etymology. The species epithet "*austroarabica*" is an adjective that refers to the geographic range of its populations, distributed across southern Arabia.

Diagnosis. A small-sized *Mesalina* characterized by the following combination of morphological characters: (1) well-developed occipital scale in contact with the interparietal (Fig. 5E); (2) lower eyelid with a window made up of two large scales edged with black (Fig. 5D); (3) curved collar (Fig. 5F); (4) four upper labials in front of the subocular (Fig. 5D); (5) ventral plates in 8 straight longitudinal rows, the outermost much smaller (almost indistinct in MCCI-R1624) (Fig. 5B); (6) scales on the upper surface of the tibia keeled (Fig. 5A); (7) lamellae under 4th toe, 20-21; (8) dorsal coloration of adult, brown-greyish, with incomplete black-and-white ocelli (the white dots are not completely surrounded by black, but only flanked by specks on one or either sides), ordered in irregular longitudinal and transverse rows (Fig. 5A); (9) bluish tail in juvenile specimens.

There are no obvious diagnostic characters separating *M. austroarabica* **sp. nov.** from *M. guttulata*, *M. bahaeldini* and from the populations from the highlands of southwestern Arabia (*M.* sp. A in Arnold 1986a) described below. Statistical analyses (see Results above) show significant differences from *M. guttulata* in having smaller SVL (males), larger %HL (males and females) and larger %HW (females). *Mesalina austroarabica* **sp. nov.** shows significant differences from *M. bahaeldini* in having smaller SVL (males), less dorsals at midbody (males and females), and larger %HL and %forelimb length (females). *Mesalina austroarabica* **sp. nov.** shows

significant differences with the populations from the highlands of southwestern Arabia (*M.* sp. A in Arnold 1986a) that is described herein, in having smaller SVL (males), less enlarged plates in the collar (males), less dorsals at midbody (males), less transverse rows of ventrals (males), less femoral pores (males), larger %HW (males and females), larger %forelimb length (males), larger value of Lamellae percSVL (males and females), larger %HL (females), larger %hindlimb length (females), larger %4th toe length (females).

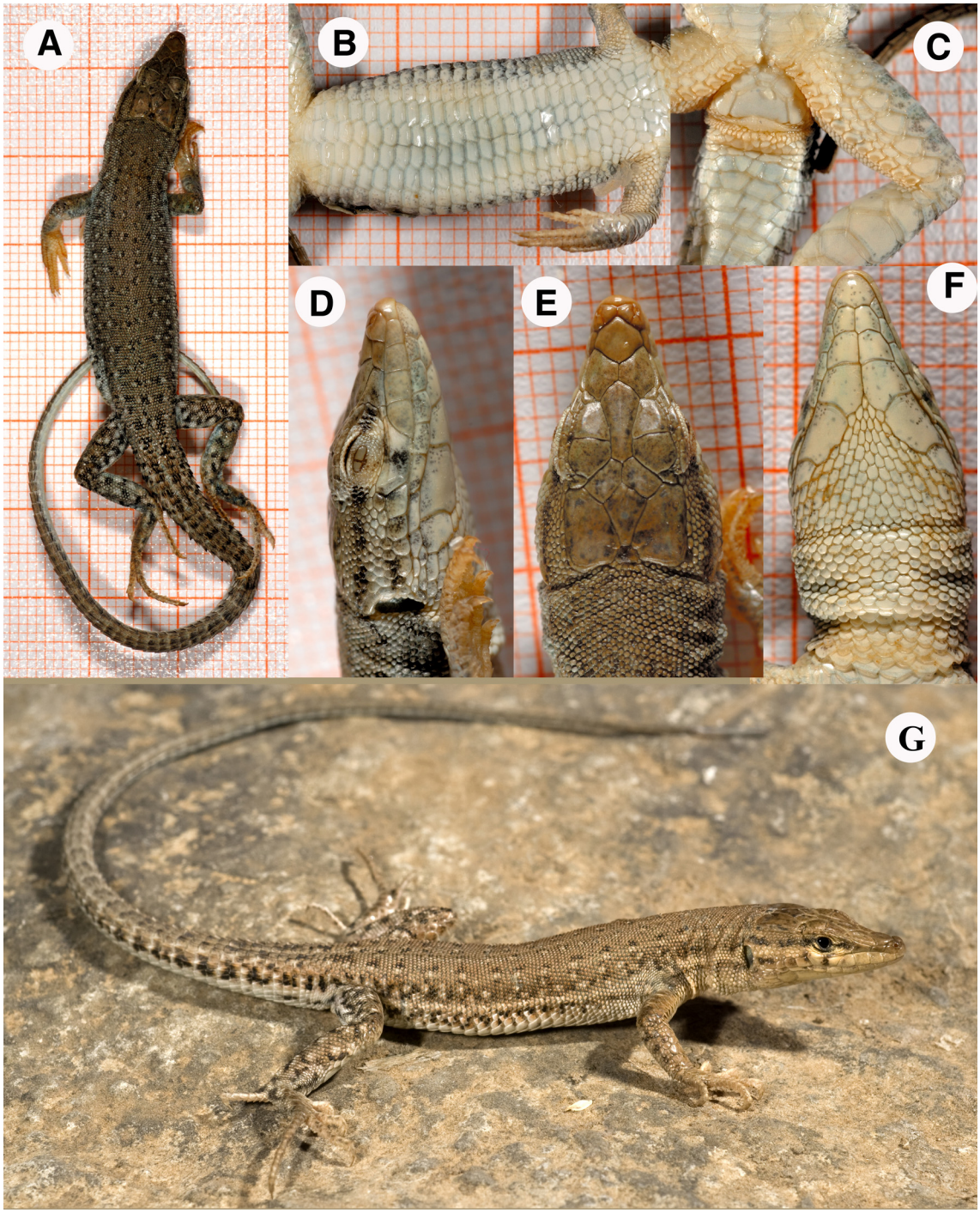


FIGURE 5. Pictures of the holotype of *Mesalina austroarabica* sp. nov. (MCCI-R1611). A) dorsal view of the body and tail; B) ventral view, C) detail of the femoral pores; D) right side of the head; E) upper (dorsal) part of the head; F) ventral (gular) side of the head; G) live specimen.

Genetic and phylogenetic remarks. The phylogenetic analyses by Kapli *et al*. (2015) and the phylogenetic and nuclear network analyses performed in this study (Fig. 2; Table 1) support the hypothesis that *M. austroarabica* **sp. nov.** is a different species. The level of genetic differentiation (*p*-distance) between the new species *versus* the

other members of the *Mesalina guttulata* species complex ranges between 3.6–6.6% in the *12S*, 4.3–6.4% in the *16S* and 11.7–15.7% in the *cytb* genes (Table 1). A network analysis of the nuclear gene *MC1R* indicates that, despite the large number of samples of the *M. guttulata* species complex included in the analysis (36 specimens; 72 alleles), all five haplotypes (22 alleles) of *M. austroarabica* **sp. nov.** are private (Fig. 3; Appendix I).

Description of the holotype. An adult male, with well-developed femoral pores, and original tail. Measurements, meristic characters and indexes: SVL = 41.5 mm, HL1 = 12.8 mm (31% of SVL), HL2 = 5.6 mm (13% of SVL), HL3 = 5.1 mm (12% of SVL), Head width = 7.0 mm (17% of SVL), Head depth = 5.0 mm (12% of SVL), pileus = 11.6 mm (28% of SVL), Forelimb length = 16.4 mm (40% of SVL), Hindlimb length = 31.4 mm (76% of SVL), 4th toe length = 9.9 mm (24% of SVL), Tail length = 93.0 mm, supralabials 8/9, subocular = 5/5, gulars = 25, enlarged plates in collar = 8, midbody scales = 39, longitudinal rows of ventrals = 8+2 (smaller), transversal rows of ventrals = 28, femoral pores = 13+13, lamellae under the 4th toe = 21. Head index = 183, Toe index = 32, Lamellae percSVL = 1.14. The two translucent scales forming the window in the lower eyelid are completely bordered by black.

Coloration in alcohol: numerous small incomplete ocelli, each one formed by 3 or 4 whitish scales forming a dot and surrounded left and/or right by a few black colored scales. These ocelli form 6-8 irregular longitudinal series and about 13 very irregular transverse series, between the fore- and hindlimbs; they further extend to the base of the tail and to the hindlimbs. These ocelli become small black and white dots on the neck and on small scales of the head. The pileus is creamy-grey with irregular blackish specks. On the sides of the head a discontinuous dark stripe is present from the upper border of the ear opening, across the eye, to the loreal scale. Another ill-defined dark stripe (that consists of a few blackish irregular spots) extends between the mid-ear opening and the subocular scale. Flanks with a more or less distinct latero-ventral whitish stripe and a usually indistinct dorso-lateral light stripe. The ventral side is creamy-white, immaculate, with the exception of the infralabial scales, which are irregularly dotted with small gray spots, as well as the outer ventrals and the anterior margin of thighs.

Variation. Quantitative variation (mensural and meristic) in the type series (n = 9) is summarized in Tables 2–5. In one paratype (MCC-R1624/1), an additional scale separates the supranasals, and the naso-frontal scale is fragmented on the left side. The latter anomaly is present in the paratype (MCC-R1624/2) too.

Coloration in life. Ground color brownish with more or less intense shades of gray (Fig. 5G). In October-November, the lateral parts of the belly and sides of the head have a pink-orange hue. Tail grayish with cyan shades in young specimens; the young depicted by van der Kooij (2001: 21) has the distal half of the tail distinctly cyan.

Distribution and habitat. The species is widely distributed across more than 1,200 km in southern Arabia; from the Jebel Samhan in Dhofar to the Yemen Mountains (Fig. 1). It is unknown if the distribution is continuous or discontinuous and restricted to mountains. The type locality is a flat area (possibly a filled sinkhole) close to an escarpment, very scarcely vegetated, surrounded by low rocky hills covered by shrubs. Specimens were active among stones at the base of hills' slopes. Other syntopic reptiles are the newly described species of *Tropiocolotes* (Machado *et al*. 2018), *Pristurus* sp. 1, *Pristurus carteri*, *Pseudotrapelus dhofarensis, Psammophis schokari* (a possible predator).

Notes. Sexual maturity is probably reached with SVL ≥ 30 mm, as a male with SVL= 31 mm collected in October had femoral pores that produce secretions.

Mesalina arnoldi **sp. nov.**

(Figs. 1–4, 6; Tables 1–5, Appendices I and III)

Mesalina sp. A Arnold 1986a: 427, Schätti & Gasperetti 1994: 371; *Mesalina guttulata* Sindaco & Jeremcenko 2008: 262 (part.).

Holotype. Adult female MCCI-R890, Yemen, Amran Governatorate, plateau between Zakatin village (Hababah) to Kawkaban (Haraz Mt.) (about 15.51°N, 43.86°E WGS84), 2,600-2,800 m a.s.l., R. Sindaco and C. Sindaco leg., 7 February 1998.

Paratype. Adult male MZUF-28670, Yemen, Al Mahwit Governatorate, Kawkaban (about 15.50°N, 43.90°E WGS84), M. Poggesi, M. Borri, M. Manetti and M. Sammicheli leg., 31 January 1984.

Other specimens examined. Forty-four specimens in the collections of the Natural History Museum in

London and in the Museum "La Specola" in Florence (see Appendix I) plus four specimens used only for genetic analyses (no vouchers available, juvenile or damaged specimens); all listed in Appendix I.

Etymology. The species epithet "*arnoldi*" is a genitive Latin noun to honor the British herpetologist Dr E. Nicholas Arnold for his life-long dedication and contribution to Arabian herpetology, including the recognition of this taxon as a distinct species that he provisionally referred to as *Mesalina* sp. A in Arnold (1986a).

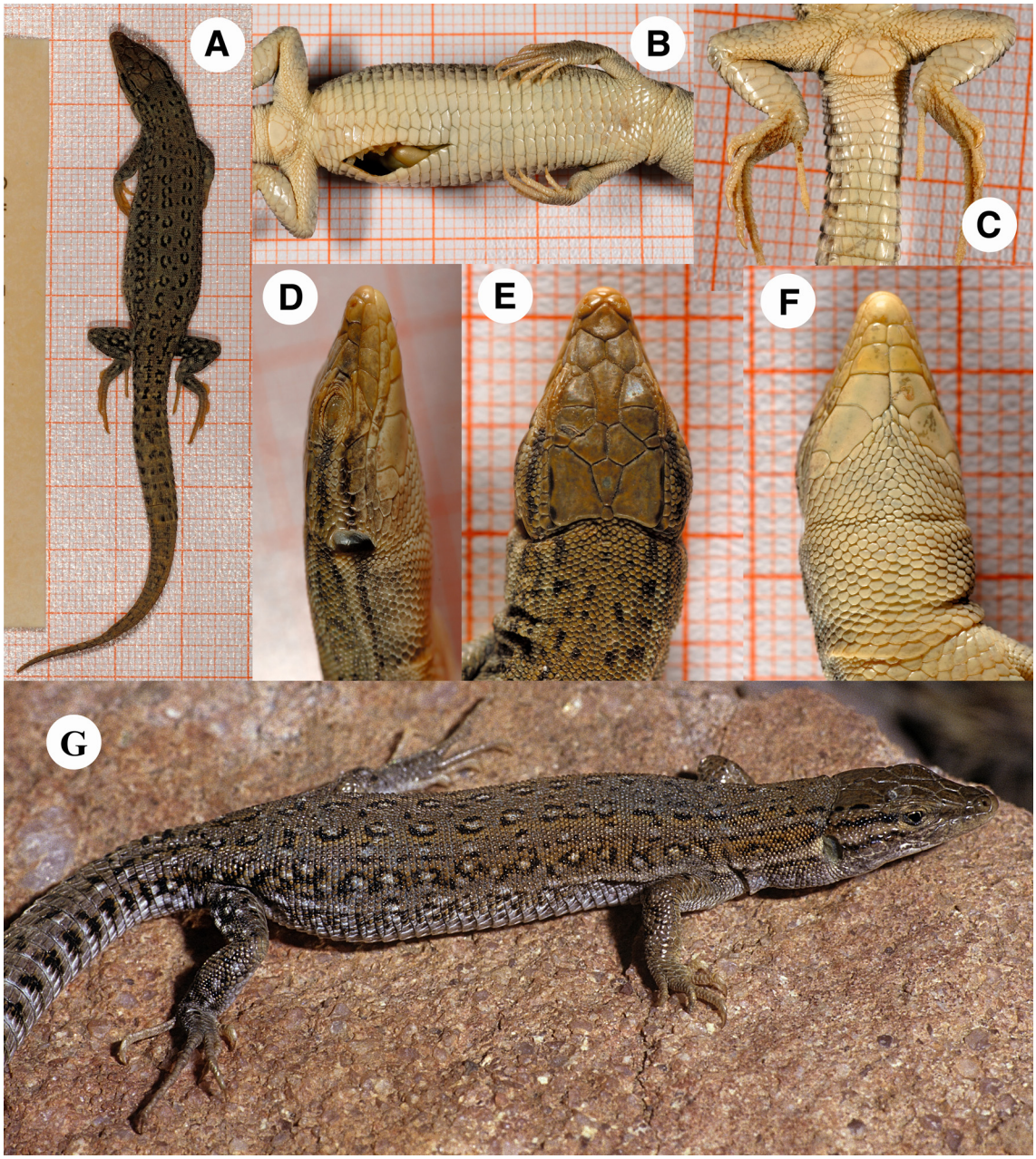


FIGURE 6. Pictures of the holotype of *Mesalina arnoldi* sp. nov. (MCCI-R890). A) dorsal view of the body and tail; B) ventral view, C) detail of the femoral pores; D) right side of the head; E) upper (dorsal) part of the head; F) ventral (gular) side of the head; G) live specimen.

Diagnosis. A relatively large-sized *Mesalina* characterized by the following combination of morphological characters: (1) well-developed occipital scale in contact with the interparietal (with rare exceptions) (Fig. 6E); (2) lower eyelid with a window made of up two large scales (in 57% of examined specimens) or fragmented into smaller scales (43%) (Fig. 6D), often without black edges (67%); (3) curved collar (Fig. 6F); (4) four upper labials in front of the subocular in 89% of the samples and five in 11% of the samples (Fig. 6D); (5) ventral plates in 10 (very rarely 8) straight longitudinal rows, the outermost much smaller (Fig. 6B); (6) scales on the upper surface of the tibia keeled (Fig. 6A); (7) lamellae under 4th toe, 19–26 (median = 22); (8) dorsal pattern usually very marked,

background color brown-greyish, with many complete ocelli (i.e. a white spot completely surrounded by a black ring) or near so, ordered in irregular longitudinal and transverse rows. Dorsolateral and light stripes are usually evident, often interrupted; some specimens are clearly striped, while in others these lines are inconspicuous, only rarely absent (Fig. 6A)

There are no obvious morphological characters separating *M. arnoldi* **sp. nov.** from *M. guttulata*, *M. bahaeldini* and *M. austroarabica* **sp. nov.** The statistical analyses (see Results above) show significant differences, with *M. arnoldi* **sp. nov.** having more gulars (males), more dorsals at midbody (males), more femoral pores (males and females) than *M. guttulata*. Moreover, *M. arnoldi* **sp. nov.** has smaller %HD (males), smaller %4th toe length (males), smaller toe-index (males), lesser value of Lamellae percSVL (males). *Mesalina arnoldi* **sp. nov.** shows significant differences from *M. bahaeldini* in having more gulars (males and females), more femoral pores (males) and more supralabials (females). Differences between *M. arnoldi* **sp. nov.** and *M. austroarabica* **sp. nov.** are discussed in the description of the latter species (see above).

Genetic and phylogenetic remarks. This species had not been included in any previous phylogenetic analyses, not even the comprehensive study by Kapli *et al*. (2015). The phylogenetic analyses performed in this study (Fig. 2; Table 1) support the hypothesis that *M. arnoldi* **sp. nov.** is an independent species. The level of genetic differentiation (*p*-distance) between the new species and the other members of the *Mesalina guttulata* species complex ranges between 5.2–6.6% in the *12S,* 6.1–7.1% in the *16S* and 11.9–15.7% in the *cytb* genes (Table 1). A network analysis of the nuclear gene *MC1R* indicates that, despite the large number of samples of the *M. guttulata* species complex included in the analysis (36 specimens; 72 alleles), all four haplotypes (10 alleles) of *M. arnoldi* **sp. nov.** are private (Fig. 3; Appendix I).

Description of the holotype. An adult female with partly regenerated tail. Measurements, meristic characters and indexes: SVL = 53.0 mm, HL-1 = 11.7 mm (22% of SVL), HL-2 = 5.0 mm (9% of SVL), HL-3 = 4.3 mm (8% of SVL), Head width = 7.3 mm (14% of SVL), Head depth = 4.9 mm (9% of SVL), pileus = 10.4 mm (20% of SVL), Forelimb length = 16.3 mm (31% of SVL), Hindlimb length = 26.6 mm (50% of SVL), 4th toe length = 8.6 mm (16% of SVL), Tail length = 62.0 mm (partly regenerated), supralabials 9/9, subocular = 5/5, gulars = 23, enlarged plates in collar = 9, midbody scales = 48, longitudinal rows of ventrals = 8+2 (smaller), transversal rows of ventrals = 36, femoral pores = 14+14, lamellae under the 4th toe = 21. Head index = 160, Toe index = 32, Lamellae percSVL = 0.77.

Coloration in alcohol: numerous ocelli, each one formed by several whitish scales forming a dot and surrounded by an almost complete ring of black colored scales (ocelli are reduced to black dots on the neck). These ocelli form 4-6 rather regular longitudinal series (the paravertebral and lateral ones more marked) and about 13 very irregular transverse series, between fore- and hindlimbs; black and white dots are present on the tail and hindlimbs. The pileus is grey without specks (only the outer margin of the parietals is bordered with black). On the sides of the head a continuous dark stripe is present from near the upper border of the ear opening, across the eye, to the loreal scale. Another well-defined dark stripe lies between the mid- ear opening and the subocular scale. Flanks with two series of ocelli, without evident stripes. The ventral side is creamy-white, immaculate, with the exception of infralabial scales, irregularly sprinkled with gray, as well as outer ventrals and the anterior margin of thighs.

Variation. In specimens MZUF-28132 the occipital scale is almost absent. The two lateral rows of ventrals are usually much smaller than the inner ventrals, sometimes subequal in size, and absent in specimen MZUF-28132. The dorsal pattern is very variable; specimens with the pattern similar to the holotype are frequent, but in several specimens the white dots of outer dorsal ocelli tend to form a whitish, more or less interrupted, supraciliar stripe along the sides of the back. In several specimens, instead of small ocelli, there are dark blotches on the back, parallel to the light supraciliar stripes, forming a distinct striped pattern (BM1938.8.1.27, BM1977.423). In specimens BM1977.425 and MZUF-28673 there are four uninterrupted white stripes: two supraciliar stripes and two subocular stripes along the sides of the body.

Coloration in life. Ground color brownish with more or less intense shades of gray. Ocelli whitish surrounded by dark brown incomplete rings (Fig. 6G).

Distribution and habitat. Specimens referable to *Mesalina arnoldi* **sp. nov.** are widespread in the highlands of southwestern Saudi Arabia and Western Yemen. The holotype was collected in a stony plateau with basaltic rocks and scarce vegetation, at an altitude of 2,600-2,800 m a.s.l. The paratype was collected in the same area, between 1,950 and 2,300 m a.s.l. According to Schätti & Gasperetti (1994) this species is found as low as 1,300 m a.s.l.

Discussion

The systematic revision of the *Mesalina guttulata* species complex using an integrative approach including both molecular and morphological data has solved the taxonomic problem of paraphyly of *M. guttulata* by delimiting the species *M. guttulata* and *M. bahaeldini* to the west and east of the Suez Canal, respectively, and has resulted in the description of two new species endemic to Arabia: *M. austroarabica* **sp. nov.** and *M. arnoldi* **sp. nov.** Once more, the use of the combination of molecular and morphological data has proven very informative to solve the taxonomy of an Arabian reptile group, to confirm from a molecular point of view the existence of previously undescribed diversity (Arnold 1986a) and to discover some new deep lineages. This integrative approach to taxonomy has recently uncovered considerable levels of undescribed diversity in Arabia (Carranza *et al.* 2016; Carranza & Arnold 2012; Metallinou & Carranza 2013; Šmíd *et al.* 2015, 2017a; Vasconcelos & Carranza 2014) including several remarkable examples of cryptic diversity (Badiane *et al.* 2014; Garcia-Porta *et al*., 2017; Simó-Riudalbas *et al.* 2017, 2018; Machado *et al.* 2018). Thanks to these studies, our knowledge of the reptile diversity in Arabia has increased considerably in recent years and will likely continue to do so in the next few years. As an example, a recent study by Carranza *et al.* (2018) showed that, only in Oman, the number of species has increased by 17.8% in the last 10 years.

Unfortunately, the lack of enough morphological and nuclear data for one of the five deep phylogenetic lineages of the *M. guttulata* species complex (lineage 4 in Fig. 2) prevented its detailed study. As a result of that, it has been left undescribed (*Mesalina* sp.) pending the collection of enough morphological and molecular evidence to check if it represents a new species or a highly divergent lineage of *M. austroarabica* **sp. nov.** (work in progress). *Mesalina* sp. was included in the mitochondrial DNA phylogeny by Kapli *et al*. (2015) and, like in our work, it branched in both ML and BI analyses with relatively high support as sister taxon to the only two samples of *M. austroarabica* **sp. nov.** included in their study. The level of genetic differentiation (*p*-distance) between *M.* sp. and the other members of the *Mesalina guttulata* species complex ranges between 3.6–5.3% in the *12S,* 4.3–6.4% in the *16S* and 11.7–13.2% in the *cytb* genes (Table 1), values that fall within the genetic differentiation between the species of *Mesalina* included in our study. The network analysis of the nuclear gene *MC1R* indicates that all three haplotypes (8 alleles) of *M.* sp. are private and are at a minimum of 5 mutational steps from the haplotypes of the sister taxon *M. austroarabica* **sp. nov.** (Fig. 3; Appendix I). In summary, like with the other four deep lineages of the *M. guttulata* species complex, the molecular data and especially the results of the network analysis suggest that *Mesalina* sp. is an independently evolving lineage genetically isolated from the other species of the complex.

Geographically, it seems that the sister taxa *Mesalina* sp. and *M. austroarabica* **sp. nov.** are allopatric, separated by a minimum gap of 1,000 km (Fig. 1; Appendix I). While *Mesalina* sp. is distributed across the dry lowland areas of Arabia, *M. austroarabica* **sp. nov.** is adapted to live in the areas of influence of the monsoon belt of southern and southwestern Arabia, where most rain falls in July and August, resulting in the unique green vegetation on the south-facing (sea) side of the mountain ranges (Carranza *et al*. 2018). The geographical gap between *Mesalina* sp. and *M. austroarabica* **sp. nov.** is mainly covered by the Rub al Khali Desert, the largest continuous sand desert in the world and a clear geographical barrier for *Mesalina* populations. The effect of sand barriers in promoting isolation and allopatric speciation in Arabian reptiles is very well known and has been suggested for the snakes of the genus *Echis* (Arnold *et al.* 2009) and the geckos of the genera *Ptyodactylus* (Metallinou *et al.* 2015), *Pristurus* (Badiane *et al.* 2014), *Trachydactylus* (de Pous *et al.* 2016) and *Hemidactylus* (Carranza & Arnold 2012; Šmíd *et al.* 2013) among other groups. This suggests that, most probably, the sister taxa *Mesalina* sp. and *M. austroarabica* **sp. nov.** split as a result of the formation of the Rub al Khali Desert. Moreover, at least in Oman, the gravel plains that separate the coastal areas where *M. austroarabica* **sp. nov.** lives and the southern edges of the Rub al Khali Desert are occupied by another species, *M. adramitana*, an Arabian arid adapted species specialized in living on flat hard surfaces (sometimes also more sandy areas) with sparse vegetation and small stones which it uses as refuges (Arnold 1980; Carranza *et al*. 2018). Interestingly, even though there are several species of *Mesalina* living in southern Arabia, they essentially replace geographically one another and, when present in the same general area, they tend to occupy different habitats and to accentuate their morphological differentiation (Arnold 1980). According to the results, both *M. austroarabica* **sp. nov.** and *M. arnoldi* **sp. nov.** occur in the mountains of southwestern Arabia, one of the top biodiversity hotspots of Arabia (Arnold 1986a; Schätti & Desvoignes 1999; Schätti & Gasperetti 1994; Šmíd *et al.* 2015, 2017b). Although no data is available on

the ecology of these two species in this area, the collection records indicate that both species occur geographically very close to each other and at very high altitudes. The only two specimens of *M. austroarabica* **sp. nov.** from the highlands of Western Yemen included in our study are from Kapli *et al*. (2015) and had been found at 1,900 and 2,000 m a.s.l. Kapli *et al*. (2015) did not include *M. arnoldi* **sp. nov.** but the specimens analyzed here range between 1,000 and 3,500 m a.s.l. At present, *M. austroarabica* **sp. nov.** has not been found in Saudi Arabia, but the geographic continuity of the southwestern Arabian Mountains suggest that it may also be found in this country in the near future.

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APPENDIX I: Information on the specimens used in the phylogenetic (Sample code) and morphological (Morph. = yes) analyses, with corresponding locality data and sequence accession numbers. Locality numbers (Loc.) are presented in Figures 1 and 2. The column "Hap." indicates to which haplotype of the network analysis belongs each one of the two alleles of the phased *MC1R* nuclear gene (Figure 3). Voucher codes of specimens available refer to the following collections; [BEV] Biogéographie et Écologie des Vertébrés, Centre d'Écologie Fonctionnelle et Évolutive, Montpellier, France; [BM]: Natural History Museum, London, UK; [HUJR] The Hebrew University of Jerusalem, Israel; [IBE]: Institute of Evolutionary Biology (CSIC-UPF), Barcelona, Spain; [MCCI] Museo Civico di Storia Naturale, Carmagnola, Turin, Italy; [MZUF] Università di Firenze, Museo Zoologico "La Specola", Firenze, Italy; [ONHM] Oman Natural History Museum; [TAU] The Steinhardt Museum of Natural History, Tel Aviv, Israel; [ZFMK] Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; [NMP] National Museum Prague, Czech Republic; The holotype (*) and paratypes are underlined. The "Lineage number" refers to the five lineages recognized within the *M. guttulata* complex, while taxon names (Species name) correspond to changes proposed in this study.

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
1	*M. bahaeldini*	NHMC80.3.72.22			Egypt	38	29,97	33,16	511		EF555242	EF555284		
1	*M. bahaeldini*		TAU-R.10871	yes	Egypt	39	29,25	33,50	843					
1	*M. bahaeldini*	S2835	MCCI-R.1562		Egypt	40	28,79	33,73	1099	MH039938	MH039978	MH040031	MH040072	h2/h3
1	*M. bahaeldini*	NHMC80.3.108.5			Egypt	41	28,71	33,75	844		EF555241	EF555283		
1	*M. bahaeldini*		TAU-R.7733	yes	Egypt	42	31,10	33,83	27					
1	*M. bahaeldini*		TAU-R.7718	yes	Egypt	42	31,10	33,83	27					
1	*M. bahaeldini*		TAU-R.7736	yes	Egypt	42	31,10	33,83	27					
1	*M. bahaeldini*	S2496	MCCI-R.1559(3)		Egypt	43	28,55	33,95	1612	MH039937	MH039979	MH040030	MH040071	h3/h3
1	*M. bahaeldini*	NHMC80.3.108.1			Egypt	44	28,54	33,98	1951		EF555243	EF555285		
1	*M. bahaeldini*	NHMC80.3.108.2			Egypt	44	28,54	33,98	1951		EF555244	EF555286		
1	*M. bahaeldini*	NHMC80.3.108.3			Egypt	44	28,54	33,98	1951		EF555245	EF555287		
1	*M. bahaeldini*	NHMC80.3.108.4			Egypt	44	28,54	33,98	1951		EF555246	EF555288		
1	*M. bahaeldini*		TAU-R.16133	yes	Israel	45	30,89	34,42	229					
1	*M. bahaeldini*	TAU16293	TAU-R.16293		Israel	46	30,86	34,44	259	MH039941	MH039980	MH040034	MH040074	h4/h9
1	*M. bahaeldini*	TAU16294	TAU-R.16294		Israel	47	30,85	34,45	272	MH039942	MH039981	MH040035	MH040075	h11/h11
1	*M. bahaeldini*		TAU-R.541	yes	Israel	48	30,50	34,63	930					
1	*M. bahaeldini*		TAU-R.951	yes	Israel	49	30,59	34,73	866					
1	*M. bahaeldini*	HUJR-TAIL-27			Israel	50	31,21	34,77	290	MH039931	MH039982	MH040024	MH040066	h3/h8
1	*M. bahaeldini*		TAU-R.554	yes	Israel	51	31,24	34,79	269					
1	*M. bahaeldini*	HUJR-TAIL-28			Israel	52	31,20	34,79	325	MH039932	MH039983	MH040025	MH040067	h3/h5
1	*M. bahaeldini*	TAU16256	TAU-R.16256		Israel	53	31,19	34,81	313	KY967177	KY967117	KY967145	KY967100	h3/h4

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APPENDIX 1. (Continued)

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
1	*M. bahaeldini*		TAU-R.948	yes	Israel	54	30,79	34,77	548					
1	*M. bahaeldini*	NHMC80.3.72.93	BEV.8799		Israel	55	30,71	34,78	690		KM410941	KM411093		
1	*M. bahaeldini*	NHMC80.3.72.94	BEV.8800		Israel	55	30,71	34,78	690		KM410942	KM411094		
1	*M. bahaeldini*	NHMC80.3.72.88	BEV.T1616		Israel	56	30,62	34,82	573		KM410948	KM411100		
1	*M. bahaeldini*	NHMC80.3.72.95	BEV.8831		Israel	57	31,06	34,84	372		KM410943	KM411095		
1	*M. bahaeldini*	NHMC80.3.72.96	BEV.8832		Israel	57	31,06	34,84	372		KM410944	KM411096		
1	*M. bahaeldini*		TAU-R.548	yes	Israel	58	30,89	35,14	19					
1	*M. bahaeldini*	HUJR-19066	HUJR-19066		Israel	59	31,25	35,16	516	MH039929	MH039984	MH040022	MH040065	h1/h1
1	*M. bahaeldini*	TAU16263	TAU-R.16263		Israel	60	31,26	35,17	526	MH039940	MH039985	MH040033	MH040073	h3/h6
1	*M. bahaeldini*	HUJR-TAIL-29			Israel	61	31,33	35,23	380	MH039933	MH039986	MH040026	MH040068	h7/h10
1	*M. bahaeldini*	HUJR-TAIL-30			Israel	61	31,33	35,23	380	MH039934	MH039987	MH040027		
1	*M. bahaeldini*	NHMC80.3.72.24			Jordan	62	29,57	35,41	971		EF555279	EF555321		
1	*M. bahaeldini*		TAU-R.14169	yes	Jordan	63	29,57	35,42	945					
1	*M. bahaeldini*	NHMC80.3.72.98	BEV.T3753		Jordan	64	29,69	35,43	788		KM411028	KM411180		
1	*M. bahaeldini*	NHMC80.3.72.99	BEV.T3765		Jordan	65	29,65	35,43	825		KM411029	KM411181		
1	*M. bahaeldini*	NHMC80.3.72.111	ZFMK63501		Jordan	66	30,33	35,44	911		KM411049	KM411201		
1	*M. bahaeldini*	HUJR-TAIL-26			West Bank	67	31,99	35,44	11	MH039930	MH039988	MH040023		
1	*M. bahaeldini*	NHMC80.3.72.13			Jordan	68	30,70	35,58	1410		EF555253	EF555295		
1	*M. bahaeldini*	NHMC80.3.72.10			Jordan	69	31,25	35,61	297		EF555251	EF555293		
1	*M. bahaeldini*	NHMC80.3.72.11			Jordan	69	31,25	35,61	297		EF555252	EF555294		
1	*M. bahaeldini*	NHMC80.3.72.20			Jordan	69	31,25	35,61	297		EF555250	EF555292		
1	*M. bahaeldini*	S3746			Jordan	70	30,17	35,67	1211	MH039939		MH040032		
1	*M. bahaeldini*	NHMC80.3.72.50	BEV.10891		Jordan	71	31,88	35,68	18		KM411025	KM411177		
1	*M. bahaeldini*	NHMC80.3.72.100			Jordan	72	31,56	35,78	574		KM411030	KM411182		
1	*M. bahaeldini*	NHMC80.3.72.47			Jordan	73	31,21	35,97	851		KM411022	KM411174		
1	*M. bahaeldini*	NHMC80.3.72.48			Jordan	73	31,21	35,97	851		KM411023	KM411175		
1	*M. bahaeldini*	NHMC80.3.72.49			Jordan	74	31,60	35,99	750		KM411024	KM411176		

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APPENDIX 1. (Continued)

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
1	*M. bahaeldini*	NHMC80.3.72.14			Jordan	75	31,91	36,62	635		EF555275	EF555317		
1	*M. bahaeldini*	NHMC80.3.72.15			Jordan	75	31,91	36,62	635		EF555276	EF555318		
1	*M. bahaeldini*	NHMC80.3.72.16			Jordan	75	31,91	36,62	635		EF555277	EF555319		
1	*M. bahaeldini*	NHMC80.3.72.17			Jordan	75	31,91	36,62	635		EF555278	EF555320		
1	*M. bahaeldini*	J66/04			Jordan	76	30,76	36,68	886	MH039935	MH039989	MH040028	MH040069	h14/h15
1	*M. bahaeldini*	S10345	IBE-S10345		Saudi Arabia	79	27,32	41,43	1147	MH039936	MH039990	MH040029	MH040070	h12/h13
2	*M. guttulata*	SPM003430			Western Sahara	1	27,14	-13,18	70	MH039950	MH039992	MH040043	MH040082	h21/h21
2	*M. guttulata*	NHMC80.3.72.53			Morocco	2	29,37	-8,20	494		KM411059	KM411210		
2	*M. guttulata*	NHMC80.3.72.55			Morocco	3	29,45	-8,06	466		KM411061	KM411212		
2	*M. guttulata*	NHMC80.3.72.54			Morocco	4	30,39	-6,88	923		KM411060	KM411211		
2	*M. guttulata*	NHMC80.3.72.18			Morocco	5	31,09	-6,47	1289		EF555257	EF555299		
2	*M. guttulata*	NHMC80.3.72.97	BEV.8162		Morocco	6	30,08	-6,24	1041		KM410945	KM411097		
2	*M. guttulata*	NHMC80.3.72.9			Morocco	7	31,40	-5,73	1408		EF555256	EF555298		
2	*M. guttulata*	NHMC80.3.72.21			Morocco	8	31,71	-4,92	1125		EF555258	EF555300		
2	*M. guttulata*	NHMC80.3.72.5			Morocco	9	32,05	-4,41	1303		EF555255	EF555297		
2	*M. guttulata*	NHMC80.3.72.82	BEV.10021		Morocco	10	33,29	-3,84	879		KM410936	KM411092		
2	*M. guttulata*	NHMC80.3.72.83	BEV.10022		Morocco	10	33,29	-3,84	879		KM410937	KM411088		
2	*M. guttulata*	NHMC80.3.72.51	BEV.10456		Morocco	11	32,59	-3,76	1793		KM411026	KM411178		
2	*M. guttulata*	NHMC80.3.72.84	BEV.975		Morocco	12	32,12	-1,58	1262		KM410938	KM411089		
2	*M. guttulata*	NHMC80.3.72.85	BEV.976		Morocco	12	32,12	-1,58	1262		KM410939	KM411090		
2	*M. guttulata*	NHMC80.3.72.87			Algeria	13	34,68	3,25	1140		KM410947	KM411099		
2	*M. guttulata*	NHMC80.3.72.45			Algeria	14	34,42	3,48	940			KM411167		
2	*M. guttulata*	NHMC80.3.72.44	BEV.10189		Algeria	15	25,35	8,38	1444		KM411014	KM411165		
2	*M. guttulata*	NHMC80.3.72.46	BEV.10188		Algeria	15	25,35	8,39	1438		KM411021	KM411173		
2	*M. guttulata*	NHMC80.3.72.90			Algeria	16	25,50	9,00	1142		KM410950	KM411102		
2	*M. guttulata*	NHMC80.3.72.89			Algeria	17	24,44	9,41	1052		KM410949	KM411101		
2	*M. guttulata*	NHMC80.3.72.91			Algeria	18	23,31	9,43	819		KM410951	KM411103		

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APPENDIX 1. (Continued)

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
2	*M. guttulata*	NHMC80.3.72.1			Tunisia	19	33,52	9,99	485		EF555268	EF555310		
2	*M. guttulata*	NHMC80.3.72.2			Tunisia	19	33,52	9,99	485		EF555269	EF555311		
2	*M. guttulata*	NHMC80.3.72.7			Tunisia	20	33,15	10,29	400		EF555270	EF555312		
2	*M. guttulata*	S3612			Libya	21	30,31	10,45	475	MH039944	MH039993	MH040037	MH040077	h21/h22
2	*M. guttulata*	S3907			Libya	21	30,31	10,45	475	MH039945	MH039994	MH040038		
2	*M. guttulata*	NHMC80.3.72.28			Libya	22	31,98	12,67	711		KM410982	KM411131		
2	*M. guttulata*	NHMC80.3.72.31			Libya	23	32,06	12,72	492		KM410984	KM411133		
2	*M. guttulata*	NHMC80.3.72.25			Libya	24	32,12	12,81	318			KM411130		
2	*M. guttulata*	NHMC80.3.72.26			Libya	24	32,12	12,81	318		KM410981	KM411129		
2	*M. guttulata*	NHMC80.3.72.35			Libya	24	32,12	12,81	318		KM410987	KM411135		
2	*M. guttulata*	NHMC80.3.72.57			Libya	25	28,44	12,78	572		KM411071	KM411222		
2	*M. guttulata*	NHMC80.3.72.8			Libya	26	30,47	24,54	154		EF555254	EF555296		
2	*M. guttulata*		BM1924.12.8.20	yes	Egypt	27	31,35	27,24	6					
2	*M. guttulata*		BM1938.8.40.28(1)	yes	Egypt	28	25,52	29,20	129					
2	*M. guttulata*		BM1938.8.40.28(2)	yes	Egypt	28	25,52	29,20	129					
2	*M. guttulata*		BM1938.8.40.28(3)	yes	Egypt	28	25,52	29,20	129					
2	*M. guttulata*	SPM002382(8)			Egypt	29	30,83	29,20	10	MH039949	MH039995	MH040042	MH040081	h18/h18
2	*M. guttulata*	SUD12/2010-68	NMP74773		Sudan	30	21,07	30,69	181	MH039951	MH039996	MH040044	MH040083	h17/h19
2	*M. guttulata*		BM97.10.28.382	yes	Egypt	31	30,90	31,68	4					
2	*M. guttulata*		BM97.10.28.396	yes	Egypt	32	25,72	32,60	78					
2	*M. guttulata*		BM97.10.88.397	yes	Egypt	32	25,72	32,60	78					
2	*M. guttulata*		BM97.10.28.384-87	yes	Egypt	33	25,69	32,64	84					
2	*M. guttulata*		BM97.10.28.384-7(1)	yes	Egypt	33	25,69	32,64	84					
2	*M. guttulata*		BM97.10.28.384-7(2)	yes	Egypt	33	25,69	32,64	84					
2	*M. guttulata*		BM97.10.28.384-7(3)	yes	Egypt	33	25,69	32,64	84					
2	*M. guttulata*		BM97.10.28.388	yes	Egypt	34	25,71	32,65	82					

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APPENDIX 1. (Continued)

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
2	*M. guttulata*		BM97.10.28.389	yes	Egypt	34	25,71	32,65	82					
2	*M. guttulata*		BM97.10.28.390	yes	Egypt	34	25,71	32,65	82					
2	*M. guttulata*		BM97.10.28.391	yes	Egypt	34	25,71	32,65	82					
2	*M. guttulata*		BM97.10.28.392	yes	Egypt	34	25,71	32,65	82					
2	*M. guttulata*		BM99.5.12.4	yes	Egypt	35	25,66	33,95	584					
2	*M. guttulata*		BM1900.5.12.5	yes	Egypt	35	25,66	33,95	584					
2	*M. guttulata*	NHMC80.3.72.92	BEV.7207		Egypt	36	23,11	35,59	17		KM410940	KM411091		
2	*M. guttulata*	SPM002367(7)			Egypt	37	22,18	36,67	33	MH039947	MH039997	MH040040	MH040079	h20/h20
2	*M. guttulata*	SPM002368(93)			Egypt	37	22,18	36,67	33	MH039948	MH039998	MH040041	MH040080	h16/h17
2	*M. guttulata*	SPM001477U			Morocco	n/a	n/a	n/a	n/a	MH039946	MH039999	MH040039	MH040078	h23/h23
3	*M. austroarabica* **sp. nov.**	NHMC80.3.72.108	ZFMK43535		Yemen	102	16,23	43,97	1916		KM410997	KM411144		
3	*M. austroarabica* **sp. nov.**	NHMC80.3.72.109	ZFMK43533		Yemen	109	14,65	45,05	2040		KM410998	KM411145		
3	*M. austroarabica* **sp. nov.**	JEM109			Yemen	110	14,90	49,03	1064	MH039921	MH039968	MH040014	MH040057	h25/h25
3	*M. austroarabica* **sp. nov.**	JIR70			Oman	112	16,80	53,28	1101	MH039922	MH039969	MH040015	MH040058	h27/h27
3	*M. austroarabica* **sp. nov.**	S2421			Oman	114	17,11	54,71	1307	MH039923	MH039970	MH040016	MH040059	h25/h25
3	*M. austroarabica* **sp. nov.**	S2599			Oman	114	17,11	54,71	1307	MH039924	MH039971	MH040017	MH040060	h25/h25
3	*M. austroarabica* **sp. nov.**	S2701			Oman	114	17,11	54,71	1307	MH039925	MH039972	MH040018	MH040061	h25/h26
3	*M. austroarabica* **sp. nov.**	S2725			Oman	114	17,11	54,71	1307	MH039926		MH040019	MH040062	h25/h25
3	*M. austroarabica* **sp. nov.**	S2838			Oman	114	17,11	54,71	1307	MH039927	MH039973	MH040020	MH040063	h25/h25
3	*M. austroarabica* **sp. nov.**	S7324	ONHM4331	yes	Oman	115	17,12	54,71	1308	MH039928	MH039974	MH040021	MH040064	h25/h28
3	*M. austroarabica* **sp. nov.**	CN7638	MCCI-R1810	yes	Oman	116	17,16	54,81	1594	MH039919	MH039975	MH040012	MH040055	h24/h25
3	*M. austroarabica* **sp. nov.**	CN7392	NMP6V-74966/2	yes	Oman	117	17,15	54,98	671	MH039918	MH039976	MH040011	MH040054	h25/h25
3	*M. austroarabica* **sp. nov.**	CN7641	NMP6V-74966/1	yes	Oman	117	17,15	54,98	671	MH039920	MH039977	MH040013	MH040056	h25/h28

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APPENDIX 1. (Continued)

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
3	*M. austroarabica* **sp. nov.**		NMP6V-74951	yes	Oman	111	17,00	53,00	848					
3	*M. austroarabica* **sp. nov.**		MCCI-R1611*	yes	Oman	113	17,12	54,71	1307					
3	*M. austroarabica* **sp. nov.**		MCCI-R1624(1)	yes	Oman	113	17,12	54,71	1307					
3	*M. austroarabica* **sp. nov.**		MCCI-R1624(2)	yes	Oman	113	17,12	54,71	1307					
3	*M. austroarabica* **sp. nov.**		MCCI-R1624(3)	yes	Oman	113	17,12	54,71	1307					
4	*M.* sp.	NHMC80.3.72.52	BEV.10915	yes	Jordan	77	31,88	36,91	517	MH039956	KM411027	KM411179	MH040088	h30/h31
4	*M.* sp.	J16/04			Jordan	78	32,17	37,01	795	MH039955	MH040002	MH040047	MH040087	h31/h31
4	*M.* sp.	NHMC80.3.72.39			Saudi Arabia	80	23,28	46,35	815		KM411035	KM411187		
4	*M.* sp.	NHMC80.3.72.40			Saudi Arabia	81	23,19	46,42	618		KM411036	KM411188		
4	*M.* sp.	NHMC80.3.72.41			Saudi Arabia	82	23,24	46,45	637		KM411037	KM411189		
4	*M.* sp.	S10332	IBE-S10332		Saudi Arabia	83	25,27	46,62	635	MH039958	MH040003	MH040048	MH040090	h29/h31
4	*M.* sp.	NHMC80.3.72.36			Saudi Arabia	84	26,43	47,38	429		KM411032	KM411184		
4	*M.* sp.	NHMC80.3.72.38			Saudi Arabia	85	26,42	47,47	398		KM411034	KM411186		
4	*M.* sp.	NHMC80.3.72.37			Saudi Arabia	86	26,41	47,71	354		KM411033	KM411185		
4	*M.* sp.	NHMC80.3.72.59	BEV.10054	yes	Kuwait	87	29,46	47,64	109	MH039957	KM411087	KM411238	MH040089	h31/h31
5	*M. arnoldi* **sp. nov.**		BM1979.971	yes	Saudi Arabia	88	18,27	42,37	2946					
5	*M. arnoldi* **sp. nov.**		BM1978.1354	yes	Saudi Arabia	89	18,22	42,51	2229					
5	*M. arnoldi* **sp. nov.**		BM1978.1355	yes	Saudi Arabia	89	18,22	42,51	2229					
5	*M. arnoldi* **sp. nov.**		BM1980.190	yes	Saudi Arabia	89	18,22	42,51	2229					
5	*M. arnoldi* **sp. nov.**		MZUF-28112	yes	Yemen	90	17,28	43,28	959					
5	*M. arnoldi* **sp. nov.**		MZUF-27874	yes	Yemen	91	17,01	43,53	2384					
5	*M. arnoldi* **sp. nov.**		MZUF-28115	yes	Yemen	92	17,08	43,53	2187					
5	*M. arnoldi* **sp. nov.**		MZUF-28113	yes	Yemen	93	17,02	43,55	2469					
5	*M. arnoldi* **sp. nov.**		MZUF-28111	yes	Yemen	93	17,02	43,55	2469					
5	*M. arnoldi* **sp. nov.**		MZUF-28089	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28128	yes	Yemen	94	17,02	43,56	2422					

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APPENDIX 1. (Continued)

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
5	*M. arnoldi* **sp. nov.**		MZUF-28127	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28132	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28134	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28137	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28131	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28133	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28138	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-28136	yes	Yemen	94	17,02	43,56	2422					
5	*M. arnoldi* **sp. nov.**		MZUF-27889	yes	Yemen	95	17,12	43,57	1997					
5	*M. arnoldi* **sp. nov.**		MZUF-28126	yes	Yemen	95	17,12	43,57	1997					
5	*M. arnoldi* **sp. nov.**		MZUF-28123	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28120	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28121	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28118	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28117	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28123	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28125	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28119	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28124	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28122	yes	Yemen	96	17,20	43,62	1971					
5	*M. arnoldi* **sp. nov.**		MZUF-28114	yes	Yemen	97	17,80	43,55	2169					
5	*M. arnoldi* **sp. nov.**		MZUF-28116	yes	Yemen	98	17,80	43,62	2065					
5	*M. arnoldi* **sp. nov.**		MZUF-28805	yes	Yemen	99	15,37	43,75	1435					
5	*M. arnoldi* **sp. nov.**		MZUF-28670	yes	Yemen	100	15,48	43,88	2606					
5	*M. arnoldi* **sp. nov.**	MCCI-R890	MCCI-R890*	yes	Yemen	101	15,51	43,88	2927	MH039915	MH039963	MH040008		
5	*M. arnoldi* **sp. nov.**		BM1986.660	yes	Yemen	103	15,28	43,98	3534					
5	*M. arnoldi* **sp. nov.**		BM1986.662	yes	Yemen	103	15,28	43,98	3534					

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APPENDIX 1. (Continued)

Lineage number	Species name	Sample code	Voucher code	Morph.	Country	Loc.	Lat.	Lon.	Alt. (m)	GenBank Accession Numbers				Hap.
										12S	*16S*	*cytb*	*MC1R*	
5	*M. arnoldi* **sp. nov.**		BM1938.8.1.27	yes	Saudi Arabia	104	17,45	44,08	1351					
5	*M. arnoldi* **sp. nov.**	S3615			Yemen	105	14,78	44,28	2340	MH039916	MH039964	MH040009	MH040052	h34/h35
5	*M. arnoldi* **sp. nov.**	S4049			Yemen	105	14,78	44,28	2340	MH039917	MH039965	MH040010	MH040053	h33/h34
5	*M. arnoldi* **sp. nov.**		MZUF-28674	yes	Yemen	106	15,05	44,37	2663					
5	*M. arnoldi* **sp. nov.**		MZUF-28672	yes	Yemen	106	15,05	44,37	2663					
5	*M. arnoldi* **sp. nov.**		MZUF-28673	yes	Yemen	106	15,05	44,37	2663					
5	*M. arnoldi* **sp. nov.**		MZUF-28671	yes	Yemen	106	15,05	44,37	2663					
5	*M. arnoldi* **sp. nov.**	JEM4			Yemen	107	15,38	44,45	2689	MH039914	MH039966	MH040007	MH040051	h32/h32
5	*M. arnoldi* **sp. nov.**	JEM015			Yemen	108	15,36	44,47	2782	MH039913	MH039967	MH040006		
	M. adramitana	CN8005	IBE-CN8005		Oman					MH039912	MH039962	MH040005	MH040050	
	M. balfouri	S2500			Yemen					MH039943	MH039991	MH040036	MH040076	
	M. brevirostris	SPM001455U			UAE					KY967187	KY967187	KY967153	KY967109	
	M. kuri	S5368			Yemen					KY967179	KY967119	KY967147	KY967102	
	M. martini	NHMC80.3.166.2	BEV.9006		Egypt					MH039952	KM410953	KM411105	MH040084	
	M. olivieri	S5404			Egypt					MH039953	MH040000	MH040045	MH040085	
	M. rubropunctata	SUD12/2010-57	NMP74765/1		Sudan					MH039954	MH040001	MH040046	MH040086	
	M. watsonana	VAZ10			Iran					MH039959	MH040004	MH040049	MH040091	
	A. longipes (outgroup)	RIM099			Mauritania					KX296853	MH039960	KX297100	KX297256	
	A. scutellatus (outgroup)	SPM002360(36)			Egypt					KX296836	MH039961	KX297085	KX297227	

APPENDIX II. Amplification conditions and information on markers used in this study. The PCR conditions were as follows: 94 °C for 5 min, 35 cycles of denaturation at 94 °C for 30 sec, annealing temperature (*) for 45 sec, and extension at 72 °C for 1 min, and a final extension step at 72 °C for 5 min.

Gene	Sequence (5'-3')	Order	Temp (*)	Reference
12S	12Sa AAACTGGGATTAGATACCCCACTAT	F	48 °C	Kocher *et al.* 1989
	12Sb GAGGGTGACGGGCGGTGTGT	R		
16S	16Sa CGCCTGTTTATCAAAAACAT	F	48 °C	Carranza *et al.* 2004
	16Sb CCGGTCTGAACTCAGATCACGT	R		
cytb	GludG TGACTTGAARAACCAYCGTTG	F	49 °C	Palumbi *et al.* 1991
	Cytb2 CCCTCAGAATGATATTTGTCCTCA	R		
MC1R	MC1R-F AGGCNGCCATYGTCAAGAACCGGAACC	F	56 °C	Pinho *et al.* 2010
	MC1R-R ACTCCGRAAGGCRTAAATGATGGGGTCCAC	R		

APPENDIX III. ML phylogenetic analyses of the nuclear gene *MC1R*. The dataset used was phased in order to show the two alleles of each specimen. All the haplotypes are private for the all *Mesalina* species.