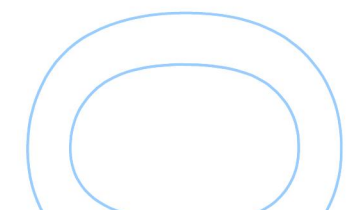
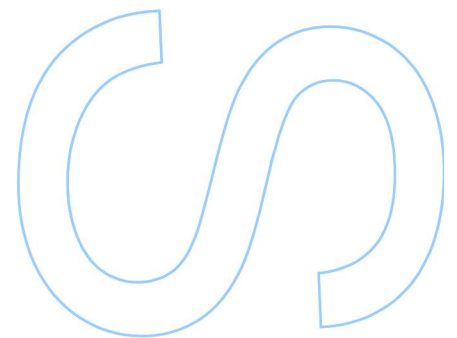
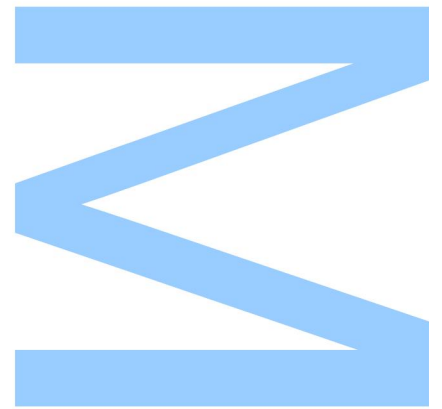


Phylogeography and systematics of the *Mesalina olivieri* species complex (Squamata: Lacertidae) from North-West Africa



Cristian Pizzigalli

Master in Biodiversity, Genetics and Evolution
Department of Biology of the Faculty of Sciences of the University of Porto
2019

Orientador

José Carlos Alcobia Rogado de Brito,
Principal Researcher, CIBIO- InBIO/FCUP

Co-orientador

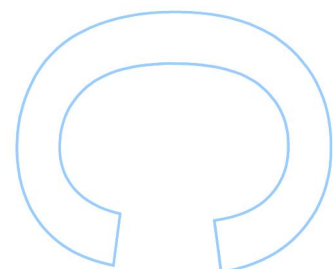
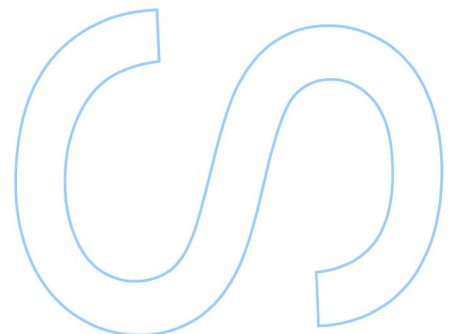
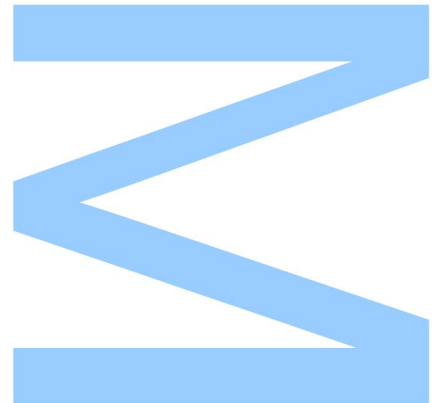
Guillermo Velo-Antón,
Auxiliary Researcher, CIBIO-InBIO

Fernando Martínez-Freiría
Post-Doctoral Researcher, CIBIO-InBIO



Todas as correções determinadas
pelo júri, e só essas, foram efetuadas.
O Presidente do Júri,

Porto, ____ / ____ / ____



To my parents

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92 Abstract

93 *Mesalina* is a genus of small xeric lizards currently comprising 19 species distributed from
94 West Africa throughout the Saharo-Sindian deserts to the Indo-Iranian plateau. Previous
95 phylogenetic studies highlighted the presence of cryptic diversity within the genus and
96 described new *Mesalina* species from its eastern lineages. In this study, we investigated
97 the taxonomy and systematics within the *Mesalina olivieri* species complex, focusing on
98 the Atlantic Sahara (from Morocco to Mauritania). The species complex is currently
99 represented by three recognised species, all of them present in this region: *M. olivieri*, *M.*
100 *pasteuri* and *M. simoni*. Using an integrative taxonomy approach based on morphological
101 (pholidotic, coloration and pattern) and molecular (one mtDNA and four nuDNA markers)
102 datasets, we provide robust evidences for the existence of additional taxa within the *M.*
103 *olivieri* complex is provided, including an undescribed species in Mauritania. *Mesalina* sp.
104 nov. . All *M. olivieri* that cluster together with *M. simoni* were proposed to be included as
105 subspecies of the latter (*M. simoni* ssp. nov.). The clade including *Mesalina* sp. nov. and
106 *M. simoni* diverged from *M. olivieri* and *M. pasteuri* around 9.5 Mya whereas these two-
107 latter species separated 1 or 2 Mya later in the end of the Miocene. The combined
108 analyses supported a new classification of the *Mesalina olivieri* species complex into four
109 extant species. The new species is sympatric with *M. pasteuri* in Mauritania but it is
110 phylogenetically and morphologically divergent from it. Species distribution modelling
111 suggests that the new taxon occurs exclusively in the rocky areas of the Adrar Atar plateau
112 and neighbouring regions. The relatively wide but fragmented distribution of *Mesalina* sp.
113 nov. suggests that its conservation status is Least Concern (LC).

114

115 Keywords

116 Adrar Atar, Atlantic Sahara, cytonuclear discordance, Ecological model, Integrative
117 Taxonomy

118

120 Resumo

121 *Mesalina* é um género de pequenos lagartos xéricos, actualmente constituídos por 19
122 espécies distribuídas desde a África Ocidental pelos desertos Saara-indianos até ao
123 planalto Indo-Iraniano. Estudos filogenéticos anteriores destacaram a presença de
124 diversidade críptica dentro do género e novas espécies de *Mesalina* foram descritas das
125 linhagens orientais. Neste estudo, investigou-se a taxonomia e a sistemática no complexo
126 de espécies *Mesalina olivieri*, com foco no Saara Atlântico (de Marrocos à Mauritânia).
127 Actualmente, o complexo de espécies é representado por três espécies reconhecidas,
128 todas presentes nesta região: *M. olivieri*, *M. pasteuri* e *M. simoni*. Utilizando uma
129 abordagem de taxonomia integrativa baseada em conjuntos de dados morfológicos
130 (folidose, coloração e padrão) e moleculares (um marcador mtDNA e quatro marcadores
131 nuDNA), são fornecidas evidências robustas da existência de taxa adicionais no complexo
132 *M. olivieri*, incluindo uma espécie não descrita na Mauritânia. *Mesalina* sp. nov. Além
133 disso, a parafilia taxonómica em *M. olivieri* foi resolvida. Todos os indivíduos de *M. olivieri*
134 que agrupam com *M. simoni* foram propostos para serem incluídos como subespécies
135 deste último táxon (*M. simoni* ssp. Nov.). O clado incluindo *Mesalina* sp. nov. e *M. simoni*
136 divergiu de *M. olivieri* e *M. pasteuri* há cerca de 9,5 Ma, enquanto as duas últimas
137 espécies separaram-se cerca de 1 ou 2 Ma depois, no final do Mioceno. As análises
138 combinadas sustentaram uma nova classificação do complexo *Mesalina olivieri* em quatro
139 espécies. A nova espécie é simpática com *M. pasteuri* na Mauritânia mas é filogenética e
140 morfológicamente divergente. A modelação da distribuição sugere que o novo táxon
141 ocorre exclusivamente nas áreas rochosas do planalto de Adrar Atar e nas regiões
142 vizinhas. A distribuição relativamente ampla, porém fragmentada, de *Mesalina* sp. nov.
143 sugere que o estatuto de conservação seja Pouco Preocupante (LC).

144

145 Palavras-chave

146 Adrar Atar, discordância citonuclear, Modelo ecológico, Saara Atlântico, Taxonomia
147 Integrativa

148

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List of Abbreviations

BSP	Bayesian Skyline plots
B-fib7	beta fibrinogen intron 7 gene
CCS	Confirmed Candidate Species
Cyt-b	Cytochrome b gene
DCL	Deep Conspecific Lineage
ENM	Ecological Niche-based Model
ESU	Evolutionary Significant Units
HPD	High posterior density
Indel	Insertion-Deletion
MC1R	Melanocortin receptor 1 gene
Mya	Million years ago
mtDNA	Mitochondrial DNA
MU	Management Unit
nDNA	Nuclear DNA
OD	ornithine decarboxylase gene
OXPHOS	Oxidative Phosphorylation
PCA	Principal Component Analysis
PCR	Polymerase chain reaction
PgD7	Phosphogluconase dehydrogenase intron 7 gene
PP	Posterior Probability
scnDNA	Single-copy nuclear DNA
sp. nov.	specie nova
ssp. nov.	subspecies nova
s.s.	Sensu stricto
UCS	Unconfirmed Candidate Species
WSS	West Sahara-Sahel

160

162 1. INTRODUCTION

163

164 1.1 GLOBAL BIODIVERSITY DECLINE

165

166 Biodiversity is defined as the diversity among living organisms based on the hereditarily variation
167 at all levels of organization, from the genes within a single local population or species, to the
168 species composing all or part of a local community, and to the communities themselves that
169 compose the living parts of Earth's ecosystems (Wilson, 1997). Biodiversity is fundamental to
170 ecosystem functioning since it regulates its stability, its fertility, the vulnerability to possible invasive
171 species, and ensures the supplying of all its ecosystem services. There are numerous examples of
172 ecosystem services provided by environments with high biodiversity levels at multiple scales, from
173 the support of the hydrological cycles in the Amazonian forest that are fundamental for water
174 supply and temperature control for most of South America (i.e. with providing pure water,
175 hydroelectric power, and diminish temperature increases; Nobre *et al.*, 1991), to the Mexican
176 Long-Tongued Bat (*Choeronycteris mexicana*) that pollinate agave plants from which tequila is
177 produced (Flores-Abreu *et al.*, 2019).

178 Biodiversity is facing a decline that aggravated in the last decades (Butchard *et al.*, 2010). While
179 previous mass extinctions were caused by catastrophic geological events and consequent climate
180 changes distributed over a vast geological time scale (Hallam & Hallam, 2005), human footprint is
181 currently leading the sixth massive extinction process that will be the faster in the history of this
182 planet (Singh, 2002; UN General Assembly, 2019). Long is the list of the anthropogenic activities
183 that affect biodiversity, such as invasive species introduction, overfishing, bush-meat overhunting,
184 warfare, pollution and greenhouse gasses (Stork, 1997; Hoffmann *et al.*, 2010; Barnosky *et al.*,
185 2011; Tittensor *et al.*, 2014; Brito *et al.*, 2018). However, the most important causes of biodiversity
186 decline are habitat loss and fragmentation together with global warming and climate change (Stork,
187 1997; Pimm, 2008).

188 According to the *Catalogue of Life* (2018) around 8.7 million of species are now living on our planet
189 and just 20% of them have been described, of which the highest concentration is recorded in the
190 tropical biomes (Mace, 2005). Biodiversity hotspots are high priority conservation areas (Reid,
191 1998) selected based on their species richness and percentage of rare species concentration
192 (Myers *et al.*, 2000). At both local and global scales, quantifying species richness, their distribution
193 and extinction rate is therefore a priority measure to safeguard the biodiversity of an ecosystem
194 and of the services provided by it. Species identification is especially important for conservations
195 purposes given that it allows the identification of Conservation Units that will help to preserve the
196 species themselves, the ecological role that it carry out, and the ecosystem to which they belong

197 (Mace, 2005). To this respect, the International Union for Conservation of Nature's guidelines for
198 the Red List of Threatened Species (IUCN Red List) allows to track the health of global biodiversity
199 by providing information about the range, population size, habitat and ecology, use and/or trade,
200 threats, and conservation actions that will help inform necessary conservation decisions and policy
201 options that are critical to protect the natural resources we need to survive (IUCN, 2019).

202

203 1.2 INTEGRATIVE TAXONOMY

204

205 The definition of a species is one of the most intriguing and unresolved biological questions. Most
206 of the scientific community agrees on the fact that species derive from separate evolving lineages
207 of populations or meta-populations (Wiley, 1978). Given that speciation is a continuum process,
208 discordances arise about which is the threshold after which divergence between separate
209 lineages should allow recognizing them as distinct species (Hey, 2006; Mallet, 2008). Nowadays,
210 we realized that what matters for the study of speciation and to decide the threshold that defines a
211 species from another, is to know what caused the origin of these species and what determined
212 their evolutionary trajectories. This knowledge requires inferences about origin, genetic structure,
213 degree of ecological interchangeability of divergent lineages and, most of the times, the
214 reconstruction of the population history, phylogenetic relationships and biogeographic background
215 of the lineages (Bond *et al.*, 2008; Dávalos *et al.*, 2009; Padial *et al.*, 2010). Therefore, an
216 integrative approach to taxonomy is necessary because it allows studying species boundaries from
217 multiple, complementary perspectives that will address in the most complete way possible the
218 complexity of the biology of a species (Dayrat *et al.*, 2005).

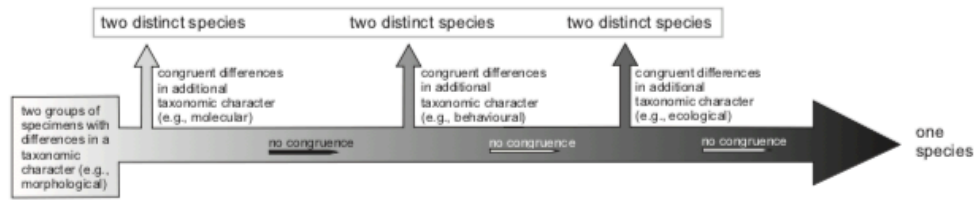
219 Integrative taxonomy is the science that aims to delimit the units of life's diversity in a
220 multidisciplinary perspective, integrating the objectives of taxonomy (description, identification and
221 classification) with the study of phylogeography, comparative morphology, population genetics,
222 ecology, development, and behaviour (Fig. 1.1; Dayrat *et al.*, 2005; Padial *et al.*, 2010). The need
223 of an integrative taxonomy approach starts from the fact that the traditional "Linnaean taxonomy"
224 (based on the identification, description and classification of species using morphological
225 dichotomous characters) just allows the description of what Cain (1953) defined as "morpho-
226 species". Nowadays, we know that this approach is incomplete (Dayrat *et al.*, 2005) to corroborate
227 a species status. Indeed a "morpho-species" should be analysed via different approaches and with
228 different kinds of data, such as DNA variation, which provides strong evidences in evolutionary
229 studies (Ballard & Whitlock, 2004). Mitochondrial (mtDNA) and nuclear (nDNA) DNA differ strongly
230 in the way they evolve and in the modes of inheritance. The mtDNA is a haploid molecule inherited
231 just from the egg cell that accumulates nucleotide substitutions several times faster than a single-
232 copy nuclear DNA (scnDNA) not only because of its effective population size but also because it is

233 subject to damage from reactive oxygen molecules released as a product during OXPHOS
234 (Oxidative Phosphorylation), and it lacks the repair mechanisms found in the nucleus. Because of
235 its fast-evolutionary rate, mtDNA is particularly useful and accurate to resolve relationships among
236 recently diverged species/populations (Wan *et al.*, 2004). On the contrary, nDNA is inherited from
237 both parents and has much slower evolution rate than mtDNA, and thus give less sharp resolving
238 power for recent divergences (Wan *et al.*, 2004). Given these structural differences between
239 mitochondrial and nuclear markers, the use of both markers is required to obtain a complete
240 picture of the evolutionary history of organisms and accurate delimitation of lineages (e.g, Godinho
241 *et al.*, 2008).

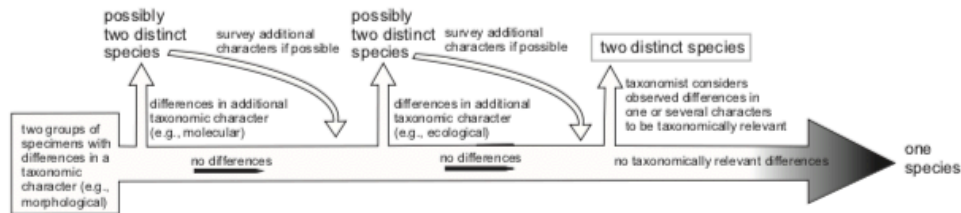
242 Currently, species described through DNA barcoding approaches are rising in number thanks to
243 the developmental advances in analysing molecular markers and computational methods, such as
244 employing the coalescent theory to produce phylogenetic trees (Jennings *et al.*, 2005). These
245 advances are contributing to the increased use of genetic methods to delimit species and to study
246 intraspecific diversity and phylogeography (Templeton *et al.*, 2001; Hickerson *et al.*, 2010), which
247 brought light to both the “morpho” and “cryptic” (species that differ only at genetic level) species
248 (Malhotra & Thorpe, 2004; Gvoždík *et al.*, 2010; Ghielmi *et al.*, 2016). However, knowing that a
249 species differs from another by a certain amount of molecular or morphological level does not
250 allow studying the life’s diversity *per se*, but just how the organisms differ between each other’s
251 from a genetic or morphological point of view. More information are needed about the ecological
252 role, the effective and potential distribution, and the dispersal rate. To cope with these issues, the
253 use of ecological niche-based models (ENMs) and topographic, environmental and land-cover
254 georeferenced data provide complementary approaches to describe the biology and the ecology of
255 a species (Kozak *et al.*, 2008; Elith, 2009). The use of ENMs allows correlating species
256 observational data (usually presence/absence data) with environmental variables to determine and
257 map the realized niche of a species, predict possible suitable areas outside its range, and
258 projected these predictions into different times (past or future) to forecast putative areas of climatic
259 refugia or ecological corridors (Waltari *et al.*, 2007; Franklin, 2010).

260 After archived the scientific porpoise of Integrative Taxonomy (delineate and classifying species), it
261 is important to proceed with the naming of species and identifying characters that allow to
262 recognise them in the easiest and fastest way possible (Dyar *et al.*, 2005). Evolutionary Significant
263 Units (ESU) and Management Units (MU) are used now in conservation to characterise
264 populations. ESUs are classified based on the historical population structure and mitochondrial
265 phylogeny, and they are helpful to plan long term conservation needs. On the other hands MUs,
266 are defined based on allele frequencies between populations and then on current population
267 structure and are used for short-term management issues. To integrate the identification of both in
268 an integrative taxonomy workflow is pivotal to define taxa with a more critical conservation status
269 according to the IUCN guidelines.

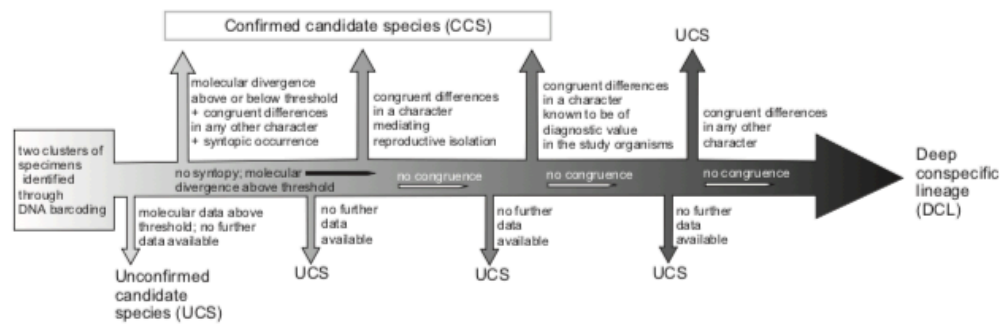
a Integrative taxonomy by congruence



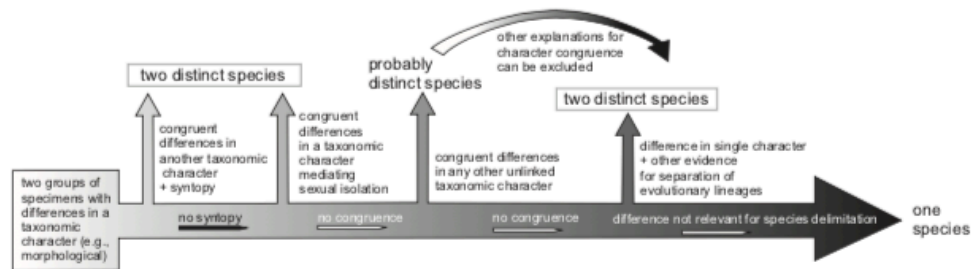
b Integrative taxonomy by cumulation



c Candidate species approach



d Consensus protocol for integrative taxonomy



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Fig 1.1. Schematic representation of work protocols in taxonomy (adapted from Padial *et al.*, 2010). Workflow in (a) integrative taxonomy by congruence and (b) by cumulation; (c) work protocol to define Unconfirmed Candidate Species (UCS), Confirmed Candidate Species (CCS) and Deep Conspecific Lineages (DCL) in an automated approach that starts with DNA barcoding and (d) a general work protocol for integrative taxonomy proposed here that combines advantages of cumulative and congruence approaches. Increasing black colour intensity in a-d represents increasing uncertainty about species status and the need of a more thorough evaluation of data.

281 1.3 BIOGEOGRAPHY OF NORTH AFRICA

282

283 Biogeographic realms are large spatial regions within which ecosystems share a broadly similar
284 biological evolutionary history. The realms delineate the large areas of the Earth's surface within
285 which organisms have been evolving in relative isolation over long periods of time, separated from
286 one another by geographic features, such as oceans, broad deserts, or high mountain ranges, that
287 constitute barriers to migration. As such, biogeographic realm designations are used to indicate
288 general groupings of organisms based on their shared biogeography. At the global level, eight
289 terrestrial biogeographic realms are typically recognized, corresponding roughly to the continents.
290 North Africa is situated at the turn of the Palaearctic and the Afro-tropic biogeographical realms.
291 Although is one of the most arid areas on Earth, North Africa is an emblematic biogeographic
292 region inasmuch including nine out of sixteen biomes present in the whole continent (Olson *et al.*,
293 2001): (i) Coniferous forests, (ii) Mountain grasslands and shrublands, (iii) Mediterranean Forests,
294 Woodlands and Shrublands, (iv) Flooded grasslands and Savannas, (v) Desert and Xeric
295 Shrublands, (vi) Grasslands, Savannas, and Shrublands, (vii) Moist Broadleaf Forests, (viii) Lakes
296 and (ix) Mangroves. Among these regions, the Sahara Desert and the xeric shrublands of the
297 Sahel ecoregions constitute the largest warm desert in the world, covering about 11,230,000 km²
298 (Dinerstein *et al.*, 2017). The West Sahara-Sahel (WSS), covering Mauritania and southern
299 Morocco, exhibits high diversity of topographic features, from salt pans below sea level to
300 mountain plateaux, and heterogeneous climates due to the substantial variability in temperature
301 and precipitation (Brito *et al.*, 2014).

302 The desiccation of the Sahara began in the Miocene (7 or 6 Mya) in Chad (Schuster *et al.*, 2006;
303 Kröpelin *et al.*, 2008; Holmes, 2008) or later in the western region (Schuster *et al.*, 2006) when the
304 area was prone to drastic climatic oscillations with a consequent gradual decrease of precipitations
305 and an increase of the dust flow that consequently lead to a vegetation collapse (Waller *et al.*,
306 2007; Wang *et al.*, 2008; Claussen *et al.*, 2009). Thereby, multiple dry-wet cycles have
307 characterised the Sahara-Sahel ecoregions since the Pleistocene (5.3 to 2.5 Mya) (Le Houérou,
308 1997). The succession of these dry and humid periods was hypothesized as the main cause of
309 speciation in the Sahara-Sahel, in the absence of adaptation processes (Brito *et al.*, 2014). The
310 population fragmentation due to the contraction and expansion of both dry and humid areas
311 caused long-term isolation and a consequent interruption of gene flow within species which turned
312 out into a series of vicariant events. This allopatric effect led to evolutionarily independent lineages
313 or new species according to the isolation time and their habitat requirements. Xeric species had
314 diversification processes probably during humid periods. On the contrary, mesic species (adapted
315 to arid conditions but still requiring some moisture) had population contraction and diversification
316 events under hyper-arid, and water-dependent species were abundant during wet periods along

317 permanent or temporary rivers but become extinct or isolated in small wetlands (oases and
 318 mountain rock pools) during dry periods (Fig. 1.2 adapted from Brito *et al.*, 2014). Mountains and
 319 coastal areas likely played a key role in diversification patterns across the Sahara-Sahel by acting
 320 as refugia and/or corridors for many species and facilitating gene flow during favourable climatic
 321 conditions (Geniez *et al.*, 2011; Vale *et al.*, 2015; Gonçalves *et al.*, 2012, 2018). Several studies
 322 have assessed the strong climatic variations of the Sahara-Sahel and how those variations shaped
 323 the biodiversity dynamics (e.g. Wang *et al.*, 2008; Claussen, 2009; Trape *et al.*, 2012; Brito *et al.*,
 324 2014).
 325 Knowledge on biodiversity distribution across the Sahara-Sahel is still scarce if compared to
 326 neighbouring areas. Large portions of northern-eastern Mauritania, northern Mali, western Algeria,
 327 southern Libya, and almost all mountain regions are under-sampled due to the harsh conditions
 328 and the current political instability that characterise these countries (Ewi *et al.*, 2010; Brito *et al.*,
 329 2014, 2018). In the cases of the Adrar des Ifoghas, Tibesti, Ennedi, and Marra mountains there is
 330 scarce or non-existent sampling effort and the current knowledge on local species richness and
 331 distribution is particularly low.

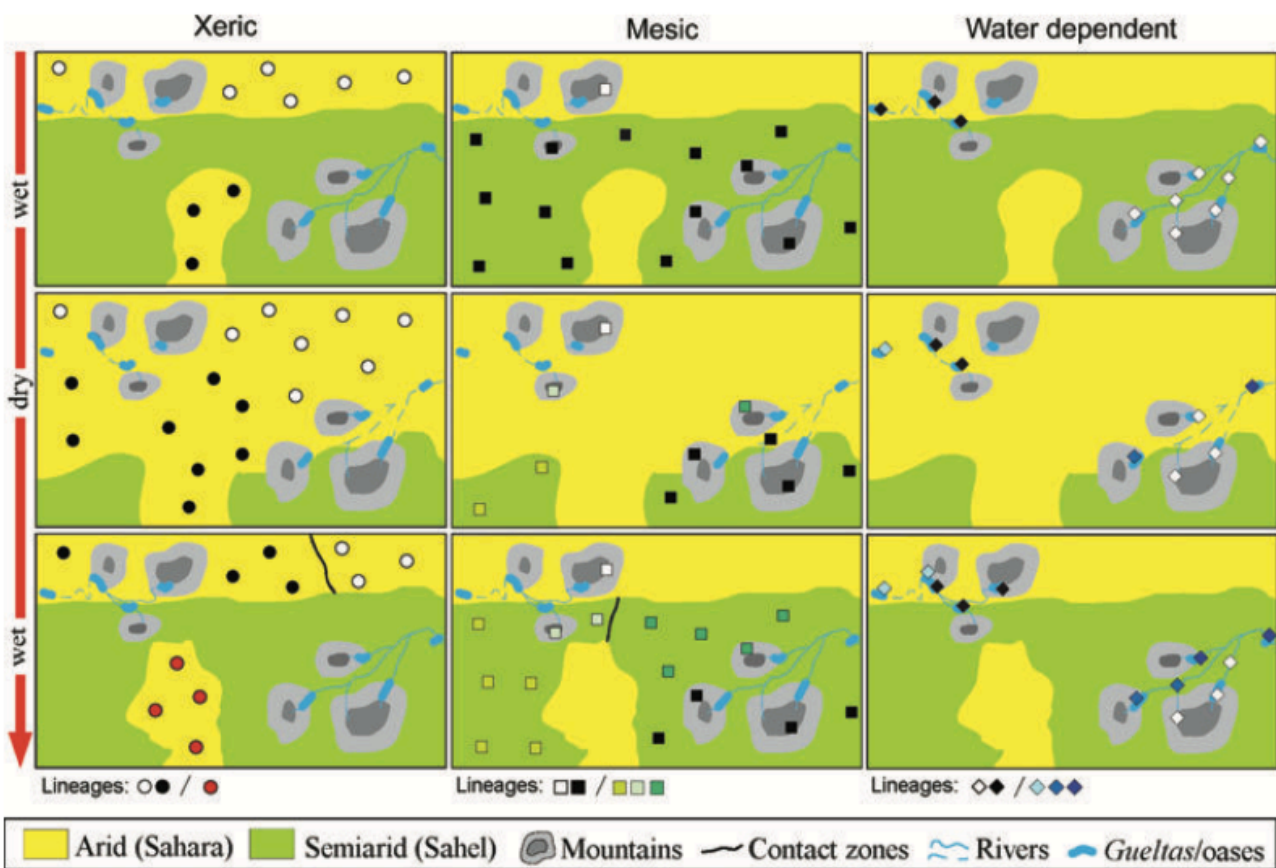


Fig 1.2. Summary of hypothetical diversification mechanisms through allopatric processes expected for three types of Sahara- adapted species (adapted from Brito *et al.*, 2014): xeric (circles), mesic (squares) and water-dependent species (diamonds). A time series of climatic cycles is shown from top to bottom. Wet periods associated with a cooler climate lead to expansion of semi-arid environments (Sahel) while dry periods, associated with a warmer climate, lead to wider arid environments (Sahara). Cycles of range expansion-contraction lead to the formation of new lineages (colours) and subsequent contact zones between lineages (black lines).

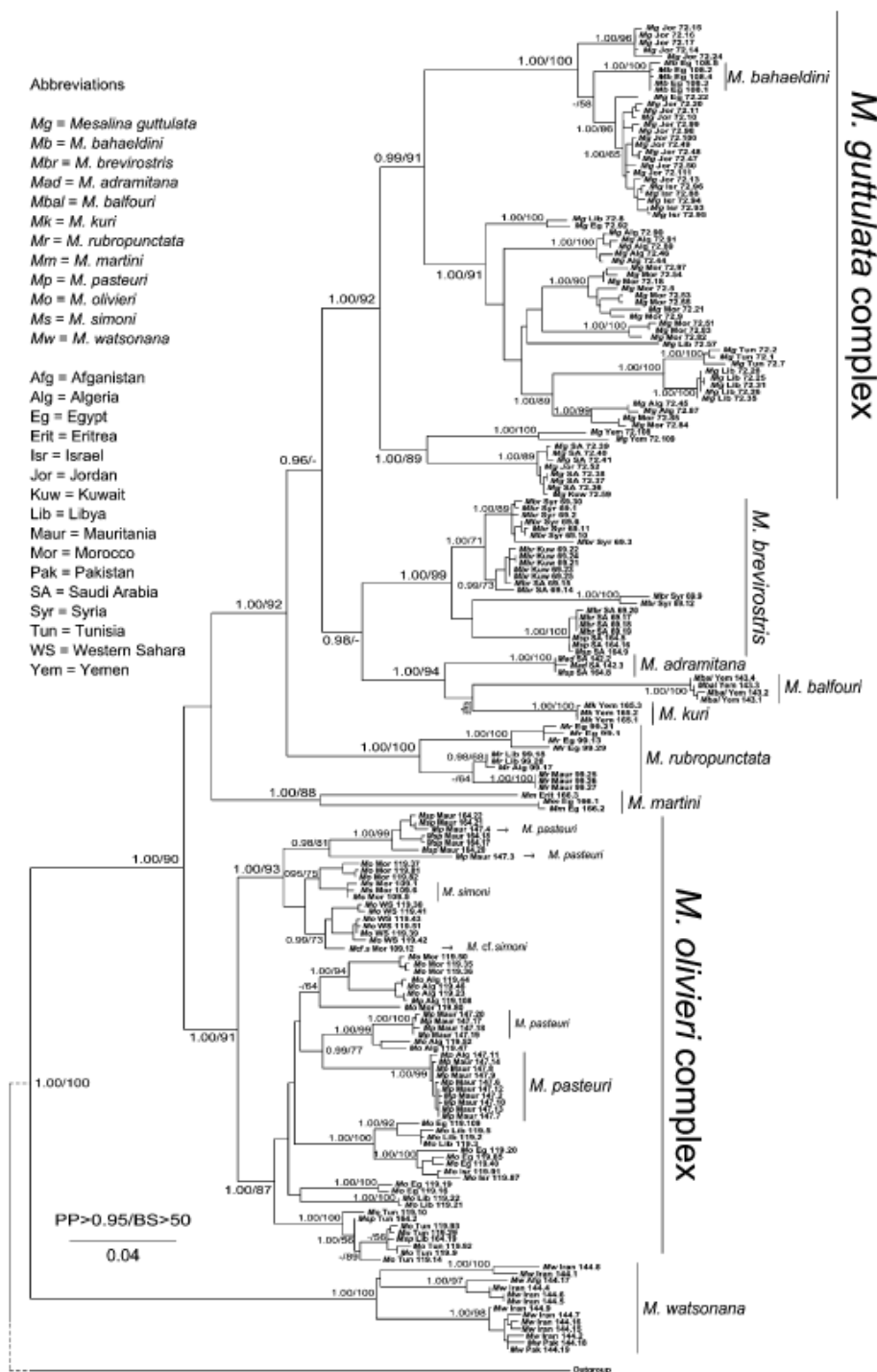
338 1.4 THE LIZARDS OF GENUS *MESALINA*

339

340 The genus *Mesalina* (subfamily: *Lacertinae*, family: *Lacertidae*, tribe: *Eremiadini*) has been
341 presented for the first time to the scientific community by Grey, 1838 together with the inclusion in
342 the genus of the first *Mesalina*: *Mesalina lichtensteini* (now *Mesalina rubropunctata* Gray 1845)
343 named after the zoologist Hinrich Lichtenstein (1780-1857), who initially described the species in
344 1823 (as *Lacerta rubropunctata*). The genus comprises diurnal xeric-adapted small lizards that can
345 be found from the Atlantic Sahara all the way through North Africa, Middle East, and Arabian
346 Peninsula to Pakistan (Sindaco & Jeremcenko, 2008). These fast-moving lizards differ in habitat
347 selection patterns, inhabiting rocky and mountain areas (i.e. *M. guttulata*), sand dunes (i.e. *M.*
348 *pasteuri*), xeric shrublands and mesic areas along the Mediterranean and Atlantic coasts (i.e. *M.*
349 *olivieri* and *M. simoni*) (Trape *et al.*, 2012). The genus currently comprises 19 species (Arnold *et*
350 *al.*, 2007; Uetz *et al.*, 2019), which makes it the third most species-richness genus within the tribe
351 *Eremiadini* (Mayer & Pavlicev, 2007).

352 Genus *Mesalina* is divided into seven species complexes (Fig. 1.3): (i) *M. watsonana*, (ii) *M.*
353 *martini*, (iii) *M. olivieri*, (iv) *M. rubropunctata*, (v) *M. adramitana* group, (vi) *M. brevirostris* and (vii)
354 the *M. guttulata* group. Since its restoration at generic status, the taxon, has been largely
355 investigated from a phylogenetic, systematic (Kapli *et al.*, 2008; Šmíd & Frynta, 2012; Šmíd *et al.*,
356 2017a; Sindaco *et al.*, 2018; Simó-Riudalbas *et al.*, 2019) and biogeographical point of view, using
357 both molecular and morphological approaches (Arnold, 1986; Moravec, 2004; Kapli *et al.*, 2015;
358 Hosseinian, 2015; Simó-Riudalbas *et al.*, 2019). The genus provides a case-study to address the
359 influence of geological events and past climatic oscillations in diversification events across the
360 Sahara-Sahel, and other drylands of the Palaeartic. The recent studies of Kapli *et al.* (2015) and
361 Simó-Riudalbas *et al.* (2019) agreed about the evolutionary history of the genus: after diversifying
362 from the genus *Adolfus* (Arnold *et al.*, 2007) in south-west Asia, it was subjected to a first intra-
363 generic split during the early Miocene (c.22 Ma) when a temporary connection between the current
364 Arabian Peninsula with the Eurasian continent allowed the dispersal of one lineage into Arabia. A
365 series of tectonic events (described in detail in Popov *et al.*, 2004; Agard *et al.*, 2011) contributed
366 then to the geographical isolation of the Eurasian lineage that diversified in what is currently
367 recognised as *M. watsonana*. Then, a second major divergence occurred at c. 17 Mya between the
368 ancestral forms of *M. martini* and the rest of the *Mesalina*, which successively split again during a
369 third major diversification event into the *M. olivieri* species complex and the ancestral form of the
370 *M. guttulata*, *M. rubropunctata* *M. brevirostris*, and *M. adramitana* groups, with the dispersal
371 throughout North Africa of the former species complex while the other four taxa remained in
372 Arabia. Progressively, these four taxa diversified into *M. rubropunctata* and *M. guttulata* (which
373 also dispersed into North Africa during the Late Miocene), *M. brevirostris*, *M. microlepis*, *M.*

374 *bernoullii*, *M. saudiarabica*, *M. austroarabica*, *M. arnoldi*, *M. adrarmitana*, *M. ayunensis*, *M. kuri*,
 375 and *M. balfouri* (that colonized the Socotra Archipelago at the Miocene-Pliocene boundary).
 376 Recent dispersal into Asia took place in the *M. brevirostris* group when *M. bernoullii* and *M.*
 377 *brevirostris* colonized Iran in the Pleistocene (reviewed by Simó-Riudalbas *et al.*, 2019).



378
 379 **Fig 1.3.** Phylogenetic relationships of *Mesalina* from North Africa and the Middle East, according to the maximum likelihood (ML)
 380 method adapted from Kapli *et al.* (2015). The numbers on the branches indicate the posterior probabilities (PP) of the Bayesian
 381 inference (only values above 0.95 are shown) followed by the bootstrap supports (BS) of the ML method (only values above 50 are
 382 shown). Seven samples of the genus *Gallotia* and two of the genus *Eremias* were used as outgroup taxa.

383

384 After the successful colonisation of North Africa, *M. olivieri* species complex diversified at about 8
385 Mya into two well-supported lineages (Kapli *et al.*, 2015), one ranging from Morocco and
386 Mauritania through the north-eastern part of the African continent and the second one restricted to
387 Morocco, Mauritania and Atlantic Sahara that diversified into *M. simoni* and *M. pasteuri*. This
388 distribution pattern could be explained by the fact that the species retracted to the mountain of
389 Morocco and Mauritania, which worked as refugia during the humid and arid cycles that
390 characterised the history of Sahara-Sahel (reviewed in Brito *et al.*, 2014). From Kapli *et al.* (2015),
391 the estimation for the isolation of the Tunisian lineage from the “Eastern clade” of the *M. olivieri*
392 species complex was due to a series of orogenetic events that occurred during the Messinian
393 period, which caused vicariance between the Tunisian populations from other North African
394 populations. This hypothesis is corroborated by the occurrence of distinct Tunisian lineages in
395 other North African species (Beddek *et al.*, 2018), such as in genus *Podarcis* and *Hyla* (Recuero *et al.*,
396 2007; Kaliontzopoulou *et al.*, 2011). Then, less than 2.5 Mya, a final colonisation of the Middle
397 East by populations of *M. olivieri* started, likely due to the desiccation of the Nile, which occurred in
398 the Pleistocene and lasted about a million years (Baha El Din, 2006). There are currently five
399 recognised species in North West Africa (Fig. 1.4): *M. guttulata*, *M. rubropunctata* (these two not
400 part of the *M. olivieri* species complex), *M. olivieri*, *M. pasteuri* and *M. simoni*. Previous studies
401 about the systematics (Arnold *et al.* 2007), phylogeny (Kapli *et al.*, 2008), phylogeography, and
402 biogeography of *Mesalina* (Kapli *et al.*, 2015; Simó-Riudalbas *et al.*, 2019), stressed the huge
403 intraspecific variation that characterise the *M. olivieri* species complex, including the possible
404 presence of at least two new species, one from Mauritania (Fig. 1.4) and another from Tunisia, not
405 yet studied.

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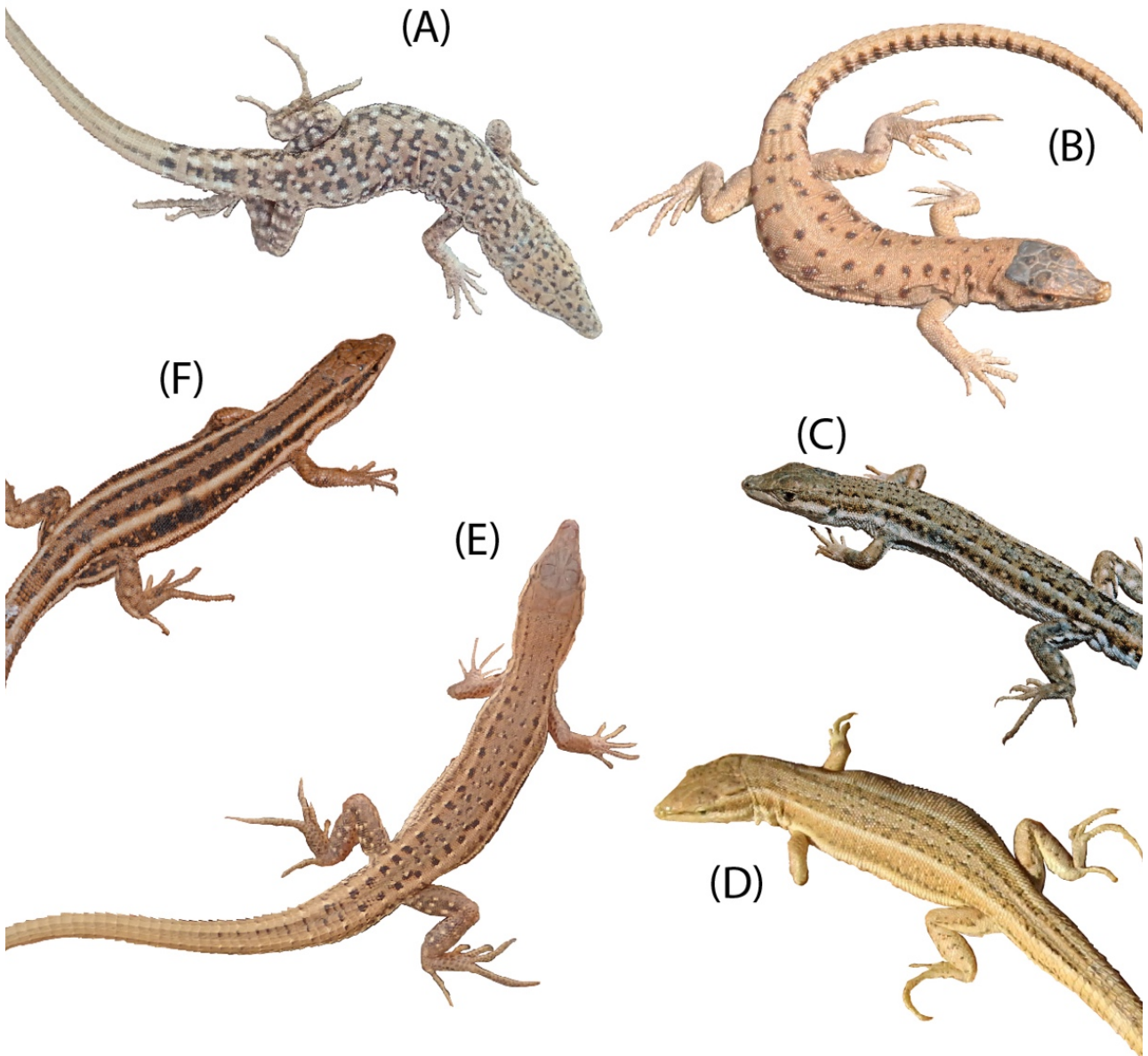
407 1.5 OBJECTIVES

408

409 The aims of this study are to: (i) investigate the genetic and morphological diversity within the
410 *Mesalina olivieri* species complex; (ii) understand if the genetic and phenotypic variation is spatially
411 structured; (iii) determine how many lineages can be identified; (iv) understand if identified lineages
412 correspond to true species; (v) map their potential distribution; (vi) determine which is their
413 extinction risk. Overall, it is aimed to solve the systematics of *Mesalina* lineages distributed in the
414 Atlantic Sahara addressing the taxonomy of the species complex through an integrative approach.

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Fig 1.4. Examples of *Mesalina* lizards from the *M. olivieri* species complex in North Africa. In a clockwise direction: (A) *M. guttulata*, (B) *M. rubropunctata*, (C) *M. simoni*, (D) *M. pasteuri*, (E) *Mesalina* sp. (Kapli et al., 2015) (F) *M. olivieri*. Pictures from José Carlos Brito and Philippe Geniez

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749 2. PHYLOGEOGRAPHY AND SYSTEMATICS OF
750 THE *MESALINA OLIVIERI* SPECIES COMPLEX
751 (SQUAMATA: LACERTIDAE) FROM NORTH-WEST
752 AFRICA WITH THE DESCRIPTION OF A NEW
753 SPECIES AND SUBSPECIES

754

755 This work is under preparation to be submitted as manuscript to a scientific journal:

756 Pizzigalli, C., Crochet, P.-A., Geniez, P., Martínez-Freiría, F., Velo-Antón, G., Brito, J.C. Phylogeography and
757 systematics of the *Mesalina olivieri* species complex (Squamata: Lacertidae) from North-West Africa with the
758 description of a new species and subspecies.

759

760 2.1. INTRODUCTION

761

762 In Africa, the Sahara Desert and the neighbouring Sahel are ecoregions where past climatic
763 oscillations have left strong imprints on current biodiversity patterns. The origin of the current
764 Sahara is set approximately 7 to 6 million years ago (Mya) in Chad (Schuster et al., 2006; Kröpelin
765 et al., 2008; Holmes, 2008) or even more recently further west (Schuster et al., 2006), when a
766 gradual decrease in precipitation and increase of the dust flow led to vegetation collapse (Waller et
767 al., 2007; Wang et al., 2008; Claussen et al., 2009). After the Pleistocene (5.3 to 2.5 Mya), multiple
768 dry-wet cycles impacted the region and induced a succession of dry-humid periods. Population
769 fragmentation and connectivity were induced by episodes of contraction and expansion of both dry
770 and humid areas. These episodes likely caused long term isolation and interruption of gene flow
771 within ancestral forms, which promoted diversification of evolutionarily independent lineages and
772 speciation, depending on isolation time and habitat requirements (Brito et al., 2014). For instance,
773 mountains and coastal areas have played a key role in diversification patterns across the Sahara-
774 Sahel by acting as refugia and/or corridors for many species and facilitating gene flow during
775 favourable climatic conditions (e.g. Gonçalves et al., 2018a,b; Velo-Antón et al., 2018). Several
776 studies assessed the effects of past climatic variation in the Sahara-Sahel and how such climatic
777 shifts shaped current biodiversity patterns (reviewed in Brito et al., 2014). However, large portions
778 of northern-eastern Mauritania, northern Mali, western Algeria or southern Libya, and almost all
779 mountain regions, are under-sampled due to their remote character and long-term regional
780 instability (Brito et al., 2014, 2018). Consequently, in comparison to other biomes, knowledge

781 about biodiversity distribution across the Sahara-Sahel is still relatively scarce (Brito and
782 Pleguezuelos, 2019).

783 The lizards of the genus *Mesalina* (Lacertidae, Lacertinae, Eremiadini) provide a case-study to
784 address the influence of geological events and past climatic oscillations on diversification events
785 across the Sahara-Sahel and other drylands of the Palaeartic. The genus comprises diurnal xeric-
786 adapted small lizards that can be found from the Atlantic Sahara all the way through North Africa,
787 the Middle East, and the Arabian Peninsula to Pakistan (Sindaco & Jeremcenko, 2008). These
788 fast-moving lizards differ in habitat selection, inhabiting rocky and mountain areas (i.e. the *M.*
789 *guttulata* group), sand dunes (*M. pasteuri*) or xeric shrublands and mesic areas along the transition
790 between the Sahara and the Mediterranean and Atlantic coasts (i.e. the *M. olivieri* group, Trape et
791 al., 2012). The genus currently comprises 19 species (Uetz et al., 2019), subdivided into seven
792 species complexes: (i) *M. watsonana*, (ii) *M. martini*, (iii) *M. olivieri*, (iv) *M. rubropunctata*, (v) *M.*
793 *adramitana* group, (vi) *M. brevisrostris* and (vii) *M. guttulata* group (see also Kapli et al., 2008, 2015;
794 Simó-Riudalbas et al., 2019). Previous studies have addressed the phylogeny, systematics and
795 biogeography of the genus (Arnold, 1986; Moravec, 2004; Kapli et al., 2008; Hosseinian and
796 Pouyani, 2015; Kapli et al., 2015; Šmíd and Frynta, 2008; Šmíd et al., 2017; Sindaco et al., 2018;
797 Simó-Riudalbas et al., 2019) using both molecular and morphological approaches. The studies of
798 Kapli et al. (2015) and Simó-Riudalbas et al. (2019) agreed about the evolutionary history of the
799 genus *Mesalina*: it diverged from the sister genus *Adolfus* (Arnold et al., 2007) in south-west Asia
800 and started to diversify during the early Miocene (c.22 Mya) when a temporary connection between
801 the current Arabian Peninsula with the Eurasian continent allowed the dispersal of one lineage into
802 Arabia. A series of tectonic events (described in detail in Popov et al., 2004; Agard et al., 2011)
803 contributed then to the geographical isolation of the Eurasian lineage that diversified into what is
804 currently recognised as *M. watsonana*. Then, a second major divergence occurred at c. 17 Mya
805 between the ancestral form of *M. martini* and the rest of the *Mesalina*. A subsequent split occurred
806 during a third major diversification event into the *M. olivieri* species complex and the ancestral form
807 of the *M. guttulata*, *M. rubropunctata*, *M. brevisrostris*, and *M. adramitana* groups, with the dispersal
808 throughout North Africa of the former species complex while the later four taxa remained in Arabia.
809 Progressively, these four taxa diversified into: *M. rubropunctata* and *M. guttulata* (which both also
810 dispersed into North Africa during the Late Miocene); *M. brevisrostris*, *M. microlepis*, *M. bernoullii*,
811 *M. saudiarabica*, *M. austroarabica*, *M. arnoldi*, *M. adramitana*, *M. ayunensis*, *M. kuri*, and *M.*
812 *balfouri* (the last two colonised the Socotra Archipelago at the Miocene-Pliocene boundary).
813 Recent dispersal into Asia took place in the *M. brevisrostris* group when *M. bernoullii* and *M.*
814 *brevisrostris* colonized Iran in the Pleistocene (reviewed in Simó-Riudalbas et al., 2019). After the
815 successful colonisation of North Africa, *M. olivieri* species complex diversified at about c. 8 Mya
816 (Kapli et al., 2015) into two well-supported lineages, one restricted to Morocco through Atlantic
817 Sahara to Mauritania and one ranging from Israel to Mauritania, Atlantic Sahara and southern

818 Morocco (Fig. 2.1). This distribution pattern could be explained by a retraction of the distribution to
819 the refugia present in the area (as the Atlantic coast or the mountain areas of Morocco and
820 Mauritania) during the humid and arid cycles that characterised the history of Sahara-Sahel
821 (reviewed in Brito et al., 2014). Arnold et al. (2007), Kapli et al. (2008; 2015) or Simó-Riudalbas et
822 al. (2019) all stressed the wide distribution and huge intraspecific variation of the *M. olivieri* species
823 complex, suggesting the presence of several undescribed species. In addition, numerous
824 paraphyletic clades have been found within *M. olivieri* and *M. pasteuri*, including: i) one *olivieri*
825 lineage from Algeria clustering with one lineage of *M. pasteuri* from Mauritania; ii) one *olivieri*
826 lineage from the Atlantic Sahara and iii) one *olivieri* lineage from the Atlas Mountains in Morocco,
827 clustering with the Moroccan endemic *M. simoni* and iv) a *pasteuri* specimen from the Tagant
828 region in Mauritania embedded in the *olivieri*-like specimens of the same region. Last, the *olivieri*-
829 like specimens from Mauritania constitutes a divergent lineage restricted to this country and sister
830 to *M. simoni*; it has been suggested to constitute a new species by Kapli et al. (2015).

831 The aim of this study is to investigate the genetic and morphological variation within the *Mesalina*
832 *olivieri* species group, aiming to clarify the paraphyletic situation within the complex by revising its
833 systematics. This required formally describing the new species suggested by Kapli et al. (2015)
834 and revising the status of the *M. olivieri* populations from the Atlas Mountains, Atlantic Sahara and
835 south-west Morocco.

836

837 2.2. MATERIALS AND METHODS

838

839 2.2.1 Sampling and study area

840 In this study, we were mainly interested on the population status of the *M. olivieri* complex from
841 Mauritania and south-western Morocco (including Atlantic Sahara = Western Sahara). For
842 specimens outside our study area, we only selected samples from each major lineage identified by
843 Kapli et al. (2015). A total of 128 samples were sequenced for this work from *M. olivieri*, 57 from *M.*
844 *pasteuri*, 23 from *M. simoni*, and 28 from the undescribed *Mesalina* lineage from Mauritania (Fig.
845 2.1). The complete list of all the new specimens sequenced for this work plus those sequences
846 derived from GENE BANK (a total of 450 for the genetic analysis and 104 for the morphological
847 analysis) with their collecting localities are given in Tables S2 and S4.

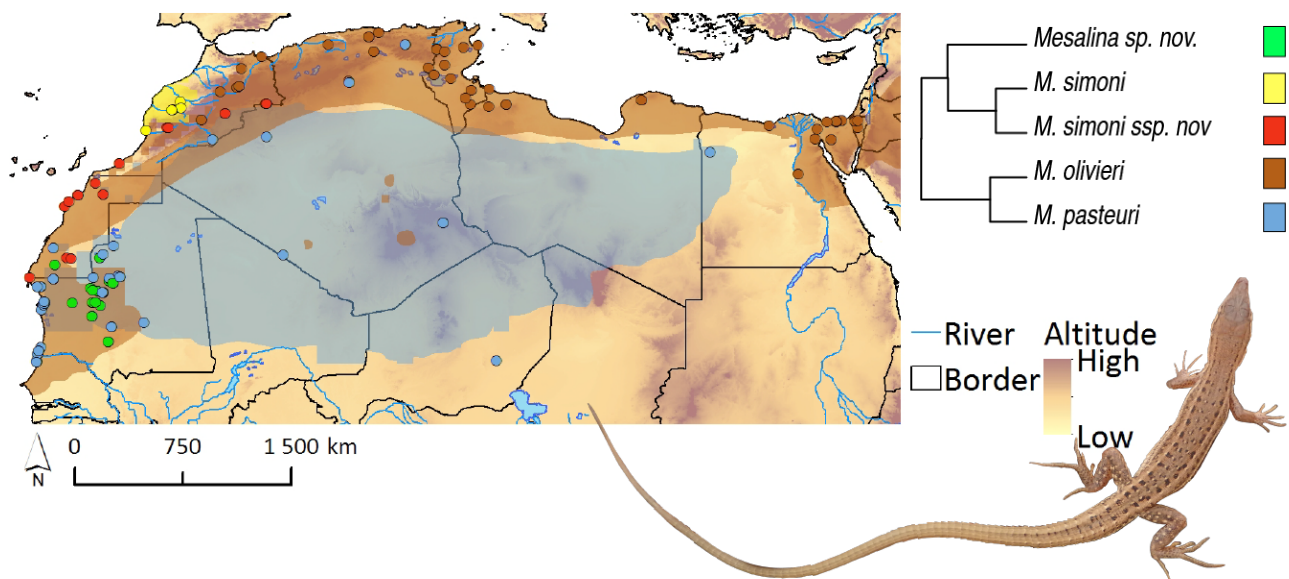
848 2.2.2. GENETIC ANALYSES

849 2.2.2.1 DNA extraction and amplification

850 DNA was extracted from ethanol-preserved tissue using a proteinase K (10 mg/ml) digestion
851 followed by a standard salt-extraction protocol (Bruford et al., 1992). Amplifications were
852 performed in 5 µL of 2× MyTaq Mix and 0.4 µM of each primer. The PCR conditions adopted for

853 every primer are specified in Table S1. Some samples required minor adjustments on the
 854 temperature and time of annealing to the reported conditions. We amplified one fragments from the
 855 mitochondrial (mtDNA) cytochrome b gene (cyt-b, 400 bp; appositely designed for the *Mesalina*
 856 genus by Kapli et al., 2015), and four nuclear DNA (nDNA) gene fragments from the beta
 857 fibrinogen intron 7 (B-fib7, 600 bp), ornithine decarboxylase gene (OD, 396 bp),
 858 phosphogluconase dehydrogenase intron 7 (PgD7, 420 bp) and melanocortin receptor 1 gene
 859 (MC1R, 630 bp, Table S2). PCR products were cleaned using ExoSAP, and the purification and
 860 sequencing was outsourced to GENEWIZ Leipzig, Germany.

861



862

863 **Fig. 2.1.** Localities of the *Mesalina olivieri* species complex samples included in this study, polygons correspond to the
 864 relative species distribution from Roll *et al.* (2017) (left) and species tree (upper right). All the branches of the tree display
 865 PP >95%. Inset picture shows a specimen of the new species from Mauritania.

866

867 2.2.2 Genetic analyses

868 Amplified fragments were sequenced for the forward strand only. Obtained DNA sequences were
 869 edited and checked for errors manually using Codon-Code Aligner (v. 2.0.6, Codon Code
 870 Corporation). Heterozygote positions of nuclear sequences were coded using IUPAC ambiguity
 871 codes. MEGA7 was used to check for stop codons. DNA sequences were aligned using MAFFT
 872 v.7 (Kato and Standley, 2013) applying parameters by default (Auto strategy, Gap opening
 873 penalty: 1.53, Offset value: 0.0). Homozygous indels were coded with dashes to maintain the
 874 overall alignment. As there is no IUPAC ambiguity code for heterozygous indels, they were
 875 encoded with dashes. In all analyses were kept just the number if dashes necessary to maintain
 876 the alignment in the portions with missing data (indels), the rest were discarded. All newly
 877 determined sequences in the present study were deposited in GenBank (access codes XXX-XXX;
 878 Table S2).

879

880 2.2.2.2 Phylogenetic analyses and haplotype networks

881 A mitochondrial (cyt-b) dataset was first created by adding sequences produced in this study and
882 sequences from Kapli et al. (2015) for a preliminary analysis to assess the morphological
883 identification of the samples as recorded in the field. The tree was rooted with four different
884 outgroups sequences from Kapli et al. (2015): *Podarcis peloponnesiacus* (AY896116),
885 *Psammotromus algirus* (DQ150365) *Eremias brenchleyi* (EF490071) *Gallotia atlantica*
886 (KF003365).

887 Different approaches were then used to infer phylogenetic relationships. First, cyt-b and nuclear
888 (four concatenated loci: B-fib7, MC1R, PgD7, and OD) datasets were analysed separately, then
889 the two datasets were merged in a single concatenated alignment. For all datasets, Bayesian
890 inferences (BI) were performed with BEAST 1.10.4 (Drummond et al., 2012). The best-fitting model
891 of nucleotide substitutions for each gene was determined with PartitionFinder v.1.1.1 (Lanfear et
892 al., 2012). The program was set as follows: branch lengths unlinked, only models available in
893 BEAST were evaluated, initial partitions by gene, BIC model selection criterion applied and all
894 partition schemes analysed. The partition scheme and models of sequence evolution selected
895 were B-fib7: HKY+G; MC1R: HKY+I; OD: HKY; PgD7: K80+G; and Cyt-b: HKY+G+I. No partition
896 by codon position was selected for any of the genes.

897 To test whether the genes studied evolve in a clock-like manner (strict clock) a preliminary run was
898 done using a strict-clock for all the markers. The results were then analysed in TRACER 1.6.
899 (<http://tree.bio.ed.ac.uk/software/tracer>). The strict-clock model was rejected when the ucl.d.mean
900 parameter was different from zero. Then a Speciation Yule Process model was selected assuming
901 a constant lineage birth rate for each branch in the tree. Three independent MCMC runs of 100
902 million generations were implemented for each analysis for each dataset, sampling every 10,000
903 generations, and 10% of the trees were discarded as burn-in. The convergence of chains and
904 effective sample sizes (ESSs) for all parameters was verified using TRACER 1.6.
905 (<http://tree.bio.ed.ac.uk/software/tracer>; ESSs higher than 400 for all parameters). Log and tree
906 files of the three independent runs were combined using LOGCOMBINER. The subsequent
907 maximum clade credibility summary tree with posterior probabilities for each node, using the
908 median values, was obtained in TREEANOTATOR (both available in the BEAST package). The
909 resulting tree was visualized and edited with FIGTREE 1.4.1
910 (<http://tree.bio.ed.ac.uk/software/figtree>). Nodes were considered as strongly supported if they
911 received a posterior probability (PP) ≥ 0.95 . Independent haplotype networks were constructed in
912 TCS (Clement et al., 2000) with a 95% parsimony threshold for the nuclear genes: B-fib7 (186
913 sequences), MC1R (152 sequences), OD (120 sequences), and PgD7 (124 sequences). The
914 PHASE algorithm, implemented in DNASP 5.10.01 (Librado and Rozas, 2009), was used to
915 reconstruct the haplotypes of nuclear data. The algorithm was run five times, for 10,000 iterations,
916 with a burn-in of 1,000. The most probable reconstructed haplotypes were used to create the

917 haplotype network. For this analysis, the aim was to highlight differences between the *M. olivieri*
918 lineage from Mauritania and all the other lineages without addressing the diversity within the
919 species *M. olivieri* and *M. pasteuri*. The Cyt-b sequences produced for this study were previously
920 aligned with those from by Kapli *et al.* (2015) available in GENE BANK. This dataset (Dataset 0)
921 has been used to ensure the quality of the sequences produced for this study. Three additional
922 datasets were then produced: i) Dataset 1: a single-locus (Cyt-b) mitochondrial dataset including
923 all sequences available from the most recent publications from Kapli *et al.* (2015), Šmíd *et al.*
924 (2017), Sindaco *et al.* (2018) and Simó-Riudalbas *et al.* (2019) for a total of 402 sequences; ii)
925 Dataset 2: a concatenated multilocus nuclear dataset with a total of 78 sequences with (1700 bp),
926 and iii) Dataset 3: a concatenated cytonuclear Dataset with a total of 87 concatenated sequences
927 (1986 bp). The dataset including only samples with at least three genes out of five and has been
928 used to calculate the phylogeny of the species complex and the time of divergence adding *Gallotia*
929 *atlantica*, *Psammotromus algirus*, *Podarcis pityusensis* and *Podarcis lilfordi* as outgroup for this
930 last analysis. For the specific of the analysis where the datasets have been used see Table S3.

931

932 2.2.2.3. *Species-tree*

933 The phylogeny of the complex was also investigated using a coalescent-based species-tree
934 estimation in *BEAST (Bouckaert *et al.*, 2019). The data set for this analysis contained only
935 specimens with as many gene sequences as possible. A total of 83 samples were used in the
936 analysis (Table S2). The preliminary species subdivision was based on the results of the separate
937 analysis on the mitochondrial and nuclear datasets. The four-putative species were: *M. olivieri*, *M.*
938 *pasteuri*, *M. simoni* (subdivided into two lineages, *M. simoni* s.s. and the other *M. olivieri* from the
939 Atlantic Sahara and Atlas Mountains), and the new potential species from Mauritania. The
940 subdivision in two lineages for *M. simoni* is due to the genetic divergence between the lineage from
941 the Atlas Mountain and Atlantic Sahara and the formal *M. simoni* (Table 1). Substitution, clock and
942 tree models were unlinked across all partitions. Since the genes and the samples used for this
943 analysis were the same as in the previous ones, the substitution models and partitions used have
944 been kept the same. The strict-clock model was used for the four nuclear markers, meanwhile an
945 uncorrelated relaxed clock was used for the mitochondrial marker. Speciation Yule Process model
946 were used as tree priors. Three independent MCMC runs of 100 million generations were
947 implemented for each analysis for each dataset, sampling every 10,000 generations, and 10% of
948 the trees were discarded as burn-in. The convergence of the chains and effective sample sizes
949 (ESSs) for all parameters were verified using TRACER 1.6. Log and tree files of the three
950 independent runs were combined using LOGCOMBINER. The subsequent maximum clade
951 credibility summary tree with posterior probabilities for each node, using the median values, was
952 obtained in TREEANNOTATOR (both available in the BEAST package). The resulting tree was

953 visualized and edited with FIGTREE 1.4.1 (<http://tree.bio.ed.ac.uk/software/figtree>). Nodes were
954 considered strongly supported if they received a posterior probability (PP) ≥ 0.95 .

955

956 2.2.2.4. Time of divergence

957 To infer the time of divergence between the new potential species and *M. simoni* a concatenated
958 cytonuclear dated tree has been produced in BEAST 1.10.4. To root and calibrate the tree four
959 outgroups were used: *Gallotia atlantica*, *Psammodromus algirus*, *Podarcis pityusensis* and
960 *Podarcis lilfordi*. Inferred models of sequence evolution are described in Table S3. The calibration
961 points and priors applied to the divergence time analysis are the same as Kapli et al. (2015) and
962 Simó-Riudalbas et al. (2019) and are: i) the split between *Gallotia atlantica* and *Psammodromus*
963 *algirus* (age of the of the Canary Islands Fuerteventura and Lanzarote; normal distribution, mean
964 18, stdev 2); and ii) the split between *Podarcis pityusensis* and *Podarcis lilfordi* (endemic to the
965 Balearic Islands) at the end of the Messinian Salinity Crisis (normal distribution, mean 5.32, stdev
966 0.05). A Speciation Yule Process model was used as tree priors. Three independent runs of 100
967 million generations were implemented, sampling every 10000 generations and 10% of the trees
968 discarded as burn-in (1000 trees). TRACER v.1.6 (Rambaut and Drummond, 2007) was used to
969 verify that the sampling achieved stationarity (ESSs higher than 300 for all parameters). Samples
970 from each run were combined using the software LogCombiner v.1.7.5. (available in the BEAST
971 package), and a consensus chronogram with node height distribution was generated and
972 visualized using TreeAnnotator v.1.7.5. (available in the BEAST package) and FigTree v.1.3.1.

973

974 2.2.2.5. Genetic distances

975 Computation of sequence divergence (uncorrected *p*-distances, distance is the proportion
976 “*p*” of nucleotide sites at which two sequences being compared are different) for the Cyt-b
977 fragment was performed in MEGA 10 (Kumar et al., 2013) to provide an overview of the
978 genetic divergence among taxa. The grouping referred to the topology of the Cyt-b tree
979 built using a database containing the sequences from this study and those published by
980 Kapli et al. (2015).

981

982 2.2.2.6. Historical demography

983 Mitochondrial DNA (Cyt-b) was used to recover the historical demography of the species complex.
984 Clades were selected based on the preliminary phylogenetic analysis conducted with the same
985 dataset and the results of the haplotype networks. A coalescent-based Bayesian skyline plot (BSP)
986 approach implemented in BEAST 1.10.4 was used to provide a temporal perspective on the
987 historical changes in population size for the *M. olivieri* species complex. The Coalescent Bayesian
988 Skyline divides the time between the present and the root of the tree (the tMRCA) into segments,

989 and estimates a different effective population size for each segment. The endpoints of segments
990 are tied to the branching times (also called coalescent events) in the tree, and the size of
991 segments is measured in the number of coalescent events included in each segment. The
992 Coalescent Bayesian Skyline groups coalescent events into segments and jointly estimates
993 the population size and the size of each segment. No outgroups were included in the analysis for
994 each and all clades combined, as BEAST estimates the root of the individual gene trees (Heled
995 and Drummond, 2010). The best-fitting model of nucleotide substitutions was determined with
996 PartitionFinder v.1.1.1 (Lanfear et al., 2012). The program was set as follows: branch lengths
997 unlinked, only models available in BEAST were evaluated, initial partitions by gene, BIC model
998 selection criterion applied and all partition schemes analysed. The partition scheme and models of
999 sequence evolution selected was HKY+G+I. The strict clock and a Coalescent Bayesian Skyline
1000 model were used as tree priors. The final MCMC simulation ran for 100 000 000 generations,
1001 sampling every 10 000 generations and a 10% burn-in was used. TRACER v.1.6 was used to
1002 check for convergence and stationarity of the effective population sizes.

1003

1004 2.2.3 MORPHOLOGICAL ANALYSES

1005 2.2.3.1. Morphological dataset

1006 A total of 32 morphological variables were measured in 252 specimens, 19 for the lineage of the
1007 potential new species from Mauritania, 109 of *M. olivieri*, 36 of *M. pasteuri*, 21 of *M. simoni*, 17 of
1008 *M. rubropunctata*, and 50 of *M. guttulata* (the latter two species not used in the analysis, see
1009 Tables S4, S5 and S6). Variables were selected according to their relevance as diagnostic
1010 characters in the genus *Mesalina* (Trape et al., 2012) or based on our own examination of
1011 specimens of the various lineages. We scored each individual for (i) five quantitative biometric
1012 variables, *SVL* = snout-vent length (mm), *TL* = tail length (mm), *HL* = head length (mm), *HW* =
1013 head width (mm), *HH* = head height (mm); (ii) eleven quantitative pholidotic variables, *D* = number
1014 of longitudinal rows of dorsal scales counted around mid-body, *V* = number of transverse rows of
1015 ventral plates, *G* = number of gular scales in one straight line from the collar to the infralabials
1016 (collar included), *Pf* = number of femoral pores on the right and left sides (*Dx* and *Sx*); *Lam* =
1017 number of lamellae beneath the fourth toe; *NTS* = number of rows of temporal granulae (average
1018 of left and right side); *TR* = number of scales around the tail at the 10th scale ring; *SL* = number of
1019 supralabials in contact with the subocular on the right and left sides (*Dx* and *Sx*); *IL* = number of
1020 infralabials on the right and left sides (*Dx* and *Sx*); *Col* = number of enlarged scales forming a
1021 collar; *EL* = number of enlarged scales on the lower eyelid (forming the palpebral disks, average of
1022 left and right side); (iii) ten semi-quantitative (ordinal) chromatic variables: *EBL* = black line
1023 surrounding the eyelids scales (0 = absent; 1 = present); *DBF* = dark bands along the flanks (0 =

024 absent; 1 = fragmented; 2 = continuous); *PSDBF*= pale spots inside the dark bands along the
025 flanks (0 = absent; 1 = small pale spots 2 = ocelli); *PDLL* = pale dorso-lateral line (0 = absent; 1 =
026 fragmented; 2 = continuous); *SPDLL* = number of scales included into the width of the pale dorso-
027 lateral line; *DDSL* = Dark supra-dorsolateral line (0 = absent; 1 = fragmented; 2 = continuous);
028 *SDDL* = number of scales included into the width of the dark supra-dorsolateral line; *PSDDL* =
029 Pale spots within the dark supra-dorsolateral line (0 = absent; 1 = small pale spots 2 = ocellus);
030 *DSO* = small ocelli arranged in rows along the mid dorsum 0 = absent; 1 = small pale spots 2 =
031 ocelli); *TC* = under tail coloration (0 = white; 1 = yellowish; 2 = yellow) and (iii) four semi-
032 quantitative (ordinal) variables describing morphological states: *TE* = tail enlargement (from 0 to 2);
033 *RN* = raised nostrils (from 0 to 2); *PS* = pointed snout (from 0 to 2), *DS* = shape of the dorsal
034 scales (0=flat; 1 = pointed; 2 = weakly crenated (tectiform); 3 = well crenated). Scale
035 nomenclature, scale counts, and measurements follow Bons and Geniez (1995). All morphological
036 data were obtained by the same observer (C.P.).

037

038 2.3.2 Morphological variation

039 The main objective was to identify diagnostic characters and to quantify the amount of
040 morphological differentiation between the potential new species from Mauritania and the other
041 species within the *olivieri* complex. Analyses were restricted to adult specimens to avoid errors due
042 to the strong ontogenetic modifications in colour patterns in genus *Mesalina*. Both sexes were
043 treated separately, as preliminary analyses revealed significant sexual dimorphism for many
044 variables in every clade (results not shown). Due to the reduced sample size, statistical tests were
045 not conducted. Three datasets were created to analyse separately biometric (Table S4), pholidotic
046 (Table S5) and coloration (Table S6). An exploratory investigation was first performed with Excel
047 using a heating map to facilitate an immediate visualization of the most relevant interspecific
048 differences. Then, PCAs were run on each database for a pairwise comparison of the potential
049 new species with the other species of the complex. The data on pholidosis and colorations were
050 normalised (to zero mean and unit variance) prior to PCAs. All analyses were run on PAST 3.24
051 Software (Hammer *et al.*, 2001).

052 2.2.4 HABITAT COMPARISON AND DISTRIBUTION MODELLING OF THE POTENTIAL NEW SPECIES

053 The percentage of presences of each lineages of the *M. olivieri* species complex in each land
054 cover unit was taken as a measure of the biogeographic affinities of each group (Brito *et al.*, 2009).
055 Selection among land cover units was quantified from the percentages of training observations
056 using the Standardized Levin's B measure of niche breadth: $B_s \frac{1}{n} B_{-1/n-1}$, where B is the Levin's
057 index and n the total number of land cover units. B is given by $1/P(p^2)$, where p is the proportion of
058 observations in each land cover unit. The standardized index was used because of unbalanced

.059 sample size among groups. Eleven land cover units were selected: yellow dunes (14.6%), white
.060 dunes (8.2%), orange dunes (20.3%), compact sand (8%), compact soil (6.1%), rocky plateaus
.061 (16.8%), bare rocks (6.3%), gravel and sand floodplains (1.9%), grasslands (9.1%), savannah
.062 (2.9%), croplands (5.7%).

.063 An ecological niche model (ENM) was used to assess the potential distribution and characterise
.064 the realized ecological niche of the new species from Mauritania. The study area encompasses an
.065 area of approximately 1,979,127km², varying between 28°N, 14°N, 17°W and 4°W, comprising
.066 southern Morocco, south-western Algeria, full extent of Mauritania, south-western Mali and north-
.067 eastern Senegal. Models were based on the 28 presence records available based on genetic or
.068 morphological assignment. Morphological identifications of specimens not sequenced were based
.069 on pictures of live unvouchered animals or from the direct examination of specimens deposited in
.070 museum collections. Only records based on adult specimens exhibiting distinctive characteristics
.071 of the new species were treated as valid. To remove duplicated observations from the same
.072 geographic locations, data were thinned reducing to 20 the number of observations to build
.073 models. Models were built using a spatial resolution of 1km.

.074 Variables used for the modelling were: i) Terrain Roughness Index (TRI) calculated by upscaling a
.075 digital elevation model (USGS, 2006) from 90 meters to 1 km; ii) 18 land cover categories (Table
.076 S7) for the West Sahara-Sahel, adapted from Campos and Brito (2018) and up-scaled from 30m to
.077 1km; iii) four uncorrelated bioclimatic variables, maximum temperature of warmest month (BIO5),
.078 minimum temperature of coldest month (BIO6), temperature annual range (BIO7), and annual total
.079 precipitation (BIO12) from Hijmans et al. (2005).

.080 The models were developed using the Maximum Entropy approach implemented in Maxent v.3.3
.081 (Phillips et al., 2006) with the following settings: 5,000 maximum number of iterations;
.082 regularization multiplier equal to 1; 10,000 maximum number of background points; 20 replicates
.083 selected by bootstrap. The area under the receiver-operating curve (AUC) of each replicate run
.084 was taken as a measure of model accuracy and ensemble models were generated by averaging
.085 the 20 model replicates. Response curves and jackknife analyses were performed to assess the
.086 importance of each variable in each model replicate (e.g. Vale et al., 2014). Finally, the minimum
.087 training presence threshold was applied to the ensemble model given that less restrictive
.088 thresholds should be applied for conservation purposes (Liu et al., 2005). The resulting binary map
.089 (depicting presence/absence areas) was used to calculate the extent of occurrence and area of
.090 occupancy following IUCN guidelines for assessing Red List categories (IUCN, 2017).

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.093

1094 2.2.5. TAXONOMIC RANKING

1095 This study adhered to the principles of the Biological Species Concept (de Queiroz, 2007) and
1096 regard the evolution of reproductive isolation as the prime criterion for recognizing independent
1097 lineages as valid species. We thus treated sympatric or parapatric lineages which do not exchange
1098 genes when they are not isolated by geographic barriers as species. For allopatric lineages, we
1099 used level of genetic divergence as a proxy for taxonomic ranking and treated independent
1100 evolutionary lineages that are as divergent as related valid species as species. Moreover, this
1101 study adopts the framework of integrative taxonomy based on the assumption that divergences in
1102 any of the attributes can provide evidence for the species' existence (Dayrat, 2005; Padial et al.
1103 Vences, 2010). We have divided our dataset into five categories that can each be regarded as
1104 distinct lines of evidences. They can be combined and compared in order to assess the
1105 congruence of the putative species limits among the *M. olivieri* species complex: (i) the mtDNA
1106 data can be used to test the criteria of reciprocal monophyly and the presence/absence of
1107 barcoding gaps, (ii) the multilocus nDNA data can be used to test, independently from the mtDNA
1108 set, the criteria of reciprocal monophyly, notably in coalescence theory framework, (iii) the
1109 phenotypic data allows to test the criteria of morphological divergence, and (iv) habitat and (v)
1110 distribution range data-set can be used as a complementary approach to test the criteria of
1111 ecological divergence.

1112

1113 2.3. RESULTS

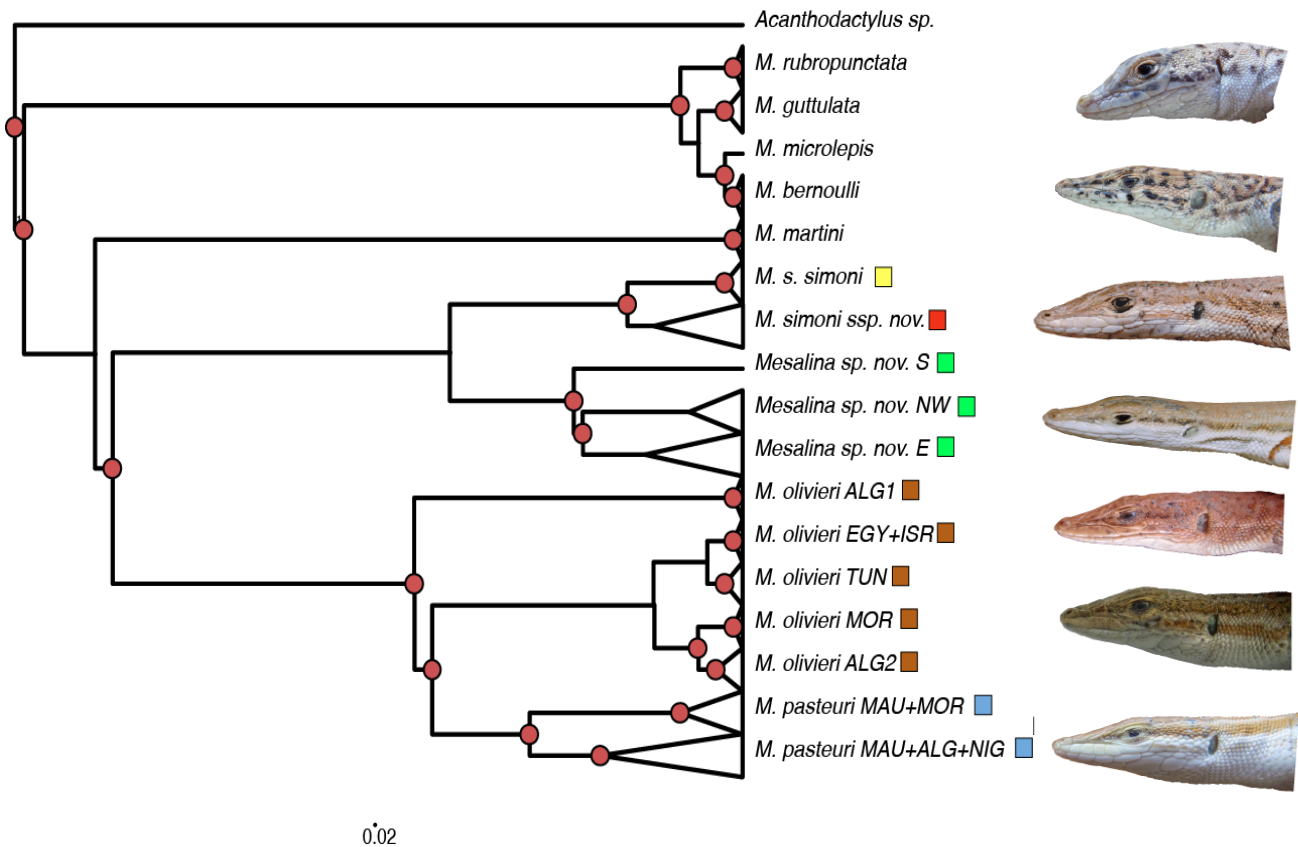
1114 2.3.1 PHYLOGENETIC ANALYSES

1115 A total of 79, 70, 85, 71 and 69 samples were successfully sequenced for Cyt-b (286 bp), B-fib7
1116 (384 bp), MC1R (582 bp), PgD7 (309 bp) and OD (425 bp).

1117 All three runs of BEAST for each dataset converged with ESS values >400 for all parameters
1118 indicating adequate mixing of the MCMC analyses. The Bayesian Inference results for Dataset 3
1119 are shown in Fig. 2.2, those for Datasets 0, 1 and 2 are showed in Figures S2 and S3. Since not all
1120 samples were successfully amplified for all genes and the data sets were pruned to contain only
1121 specimens with as many genes sequenced as possible, some samples were discarded in the
1122 concatenate analysis.

1123 All the trees produced displayed a similar topology although the number of samples included in the
1124 analysis differs between them (Figs. 2.1, 2.2, S2, S3 and S4). *Mesalina watsonana* branch (when
1125 present) was located as basal of all the other *Mesalina*. The other species of *Mesalina* used as
1126 outgroups always clustered outside the *M. olivieri* species complex, except for *M. martini*. This later
1127 species has been recorded to be basal of the *M. olivieri* species complex in the results for datasets
1128 1 and 3, and to all the *Mesalina* except *M. watsonana* for dataset 0, and sister taxa to the *M.*

129 *simoni* clade for dataset 2. *Mesalina olivieri* species complex is divided in two main deep well
130 supported clades, one including the potential new species from Mauritania and the *M. simoni*
131 group (including *M. simoni* plus the two lineages of *M. olivieri* from the Atlantic Sahara and Atlas
132 Mountains), and the other clade including the remaining *M. olivieri* and *M. pasteuri*.
133 *Mesalina olivieri* presents four paraphyletic clades: the potential new species from Mauritania; the
134 two lineages (above mentioned) from North West Africa recorded to be sister taxa of *M. simoni* (in
135 all results); one lineage from Algeria (samples BEV.9225 and BEV.T3038) that fall within the
136 continental lineage of *M. pasteuri* when mtDNA is analysed alone (datasets 0 and 1; Figs. S2 and
137 S3) and basal to the clade including *M. pasteuri* and the *M. olivieri* from the West Morocco until
138 Israel in the nuclear and cytonuclear trees (results for dataset 2 and dataset 3). The lineage of the
139 potential new species from Mauritania resulted to be paraphyletic to the remaining *M. olivieri* with
140 high support (posterior probability [PP] = 100%) in all trees produced. However, this lineage
141 represents another case of cytonuclear discrepancy: it is basal to the entire *M. olivieri* species
142 complex (that here include *M. martini*) in the results for dataset 2 and it was recovered as sister to
143 *M. simoni* and the Alas Mountain and Atlantic Sahara lineages of *M. olivieri* in all trees that
144 included mtDNA in the analysis (datasets 0, 1 and 3). The two individuals previously recognised as
145 *M. pasteuri* (Codes 147.4 and 147.3) in Kapli et al. (2015), grouped with the lineage of the potential
146 new species from Mauritania.



147 **Fig. 2.2.** Results of the Bayesian Inference analysis on the concatenate cytonuclear dataset (Dataset 3). Red dots on the
 148 notes indicate a PP>95%. Colours correspond to those in the maps and haplotype networks. Pictures on the side
 149 represent the phenotypic variability of the genus *Mesalina* in North West Africa. From the top, respectively: *M.*
 150 *rubropunctata*, *M. guttulata*, *M. simoni simoni*, *M. simoni ssp. nov.*, *Mesalina sp. nov.*, *M. olivieri*, and *M. pasteuri*.

151

152 **2.3.2 HAPLOTYPE NETWORKS AND GENETIC DIVERGENCE**

153 Allele network reconstructions (Fig. 2.3) for the four nDNA genes indicates that all haplotypes of
 154 the new species here described (marked in green in Fig. 2.3) are private and not connected with
 155 any other haplotype in genes β -fib7, OD and PgD7. A connection with the other lineages is
 156 observed in gene MC1R where the potential new species is separated from at least three mutation
 157 steps from the nearest haplotype (*M. olivieri* lineage from the Atlantic Sahara). *Mesalina simoni*
 158 and the two *M. olivieri* lineages from Atlas Mountains and Atlantic Sahara confirm to belong to the
 159 same cluster in agreement with the phylogenetic results. All haplotypes from this clade are private
 160 and show a complete separation from the other lineages in β -fib7 and PgD7 networks. A
 161 connection between this lineage and the others is recorded in MC1R and OD where they still
 162 diverge from *M. olivieri* by one and two mutational steps respectively. In the network analysis for

163 MC1R, *M. simoni* show isolation from *M. olivieri* from the Atlas and the Atlantic Sahara diverging
 164 by five mutational steps.

165 All lineages are seemingly parapatric or sympatric (Fig. 2.3). The new potential species has been
 166 observed only in the rocky highlands of the Adrar Atar in Mauritania and surrounding refugia being
 167 sympatric with *M. pasteuri* and parapatric with the Atlantic Sahara lineage of *M. olivieri*.

168

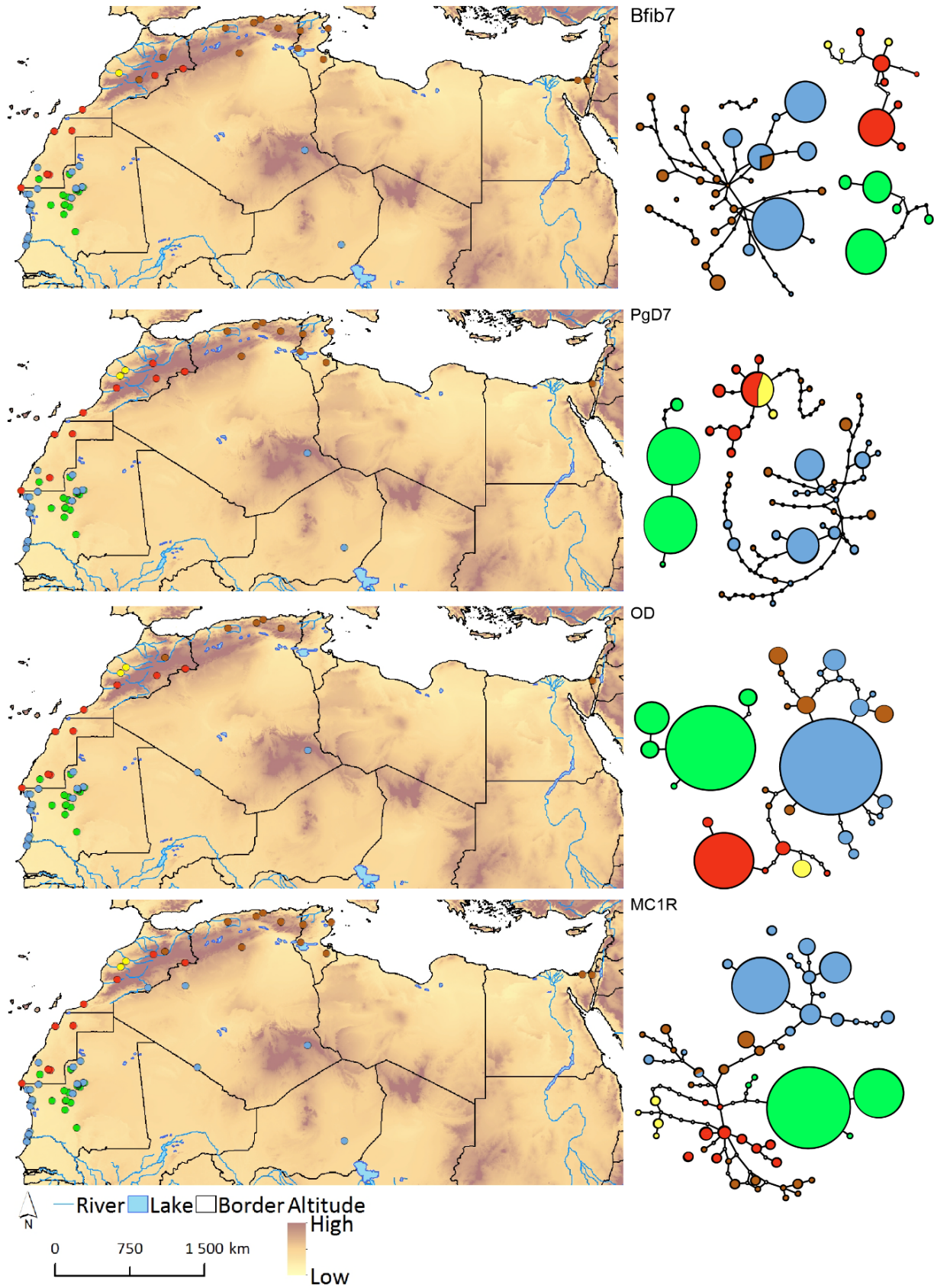
169 **Table 2.1** Estimates of evolutionary divergence over sequence pairs between *Mesalina* species present in NW Africa
 170 (above) and between the different lineages of *M. simoni* (below). The number of base substitutions per site from
 171 averaging over all sequence pairs between groups are shown. Analyses were conducted using the Maximum Composite
 172 Likelihood model [1]. This analysis involved 118 nucleotide sequences. Codon positions included were
 173 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option).
 174 There were a total of 286 positions in the final dataset. Evolutionary analyses were conducted in MEGA X [2]. Distances
 175 in *M. simoni* include the two subspecies.

	<i>Mesalina</i> sp. nov.	<i>M.</i> <i>olivieri</i>	<i>M.</i> <i>pasteuri</i>	<i>M. simoni</i>	<i>M. guttulata</i>
<i>M. olivieri</i>	0.14				
<i>M. pasteuri</i>	0.13	0.11			
<i>M. simoni</i>	0.08	0.11	0.11		
<i>M. guttulata</i>	0.20	0.19	0.22	0.18	
<i>M. rubropunctata</i>	0.21	0.19	0.18	0.21	0.16
	<i>M. s. simoni</i>			<i>M. simoni</i> ssp.nov. <i>AM</i>	
<i>M. simoni</i> ssp.nov. <i>AM</i>	0.03				
<i>M. simoni</i> ssp.nov. <i>AS</i>	0.04			0.05	

176

177 The level of genetic divergence (p-distance) between the potential new species and *M. pasteuri*
 178 estimated from the analysis on the mitochondrial (Cyt-b) genetic divergence is 13.7%, while it
 179 ranged from 8 to 14.7% between the potential new *Mesalina* and the other members of the *M.*
 180 *olivieri* species complex. The lowest intraspecific genetic divergence within the group was
 181 observed between the *M. olivieri* from the Atlas Mountain and Atlantic Sahara and *M. simoni*
 182 (Table 2.1).

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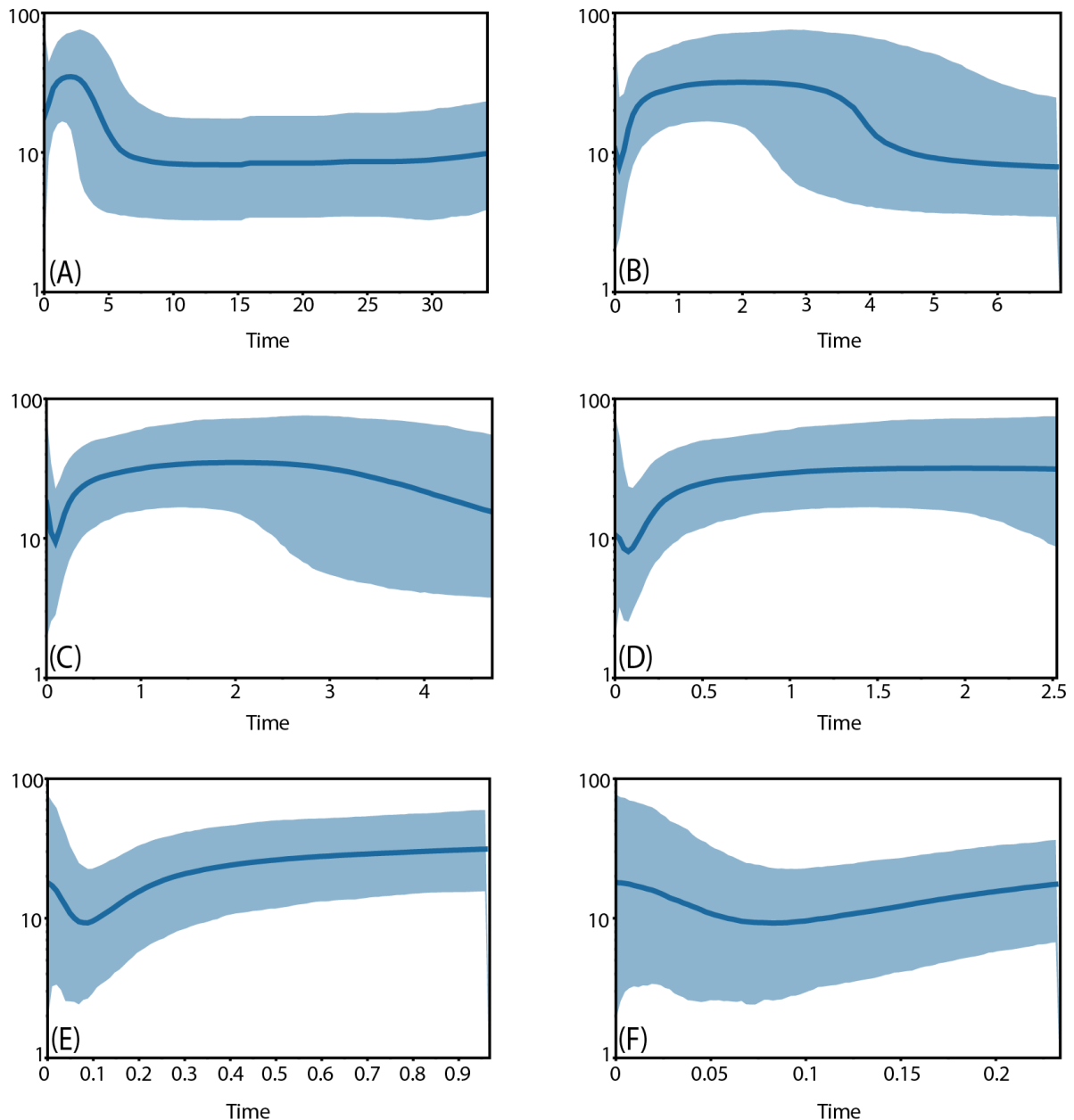
Fig. 2.3 Results geographical distribution of the *Mesalina olivieri* species complex and unrooted haplotype networks of the nuclear markers (B-fib7, PgD7, OD, MC1R) analysed for the *M. olivieri* species complex. Circle size is proportional to the number of alleles with colours corresponding to those shown in Fig. 2.1. Small circles show the number of mutational steps between two haplotypes.

189 2.3.3 TIME DIVERGENCE AND HISTORICAL DEMOGRAPHIC ANALYSIS

190 The divergence time estimation analysis using dataset 3 and including the outgroups (see 2.2.2.4)
191 indicates that the *M. olivieri* species complex started to diversify in the Late Miocene, c. 9.6 Mya
192 (6.92-12.87 Mya, 95% highest posterior densities [HPD]; Fig. S4). In this period, two main groups
193 of lineages were split. One group including *M. olivieri* and *M. pasteuri* and the other group including
194 the potential new species and *M. simoni*. The latter two species also diversified in the same period
195 (c. 8.94 Mya; 6.30-12.8 Mya 95% HPD). Most of the intraspecific diversification in the four species
196 of the complex occurred in the Plio-Pleistocene transition. For instance, the two lineages of *M.*
197 *olivieri* clustering together with *simoni* split at c. 3.5 Mya (2.05-4.37 Mya 95% HPD) and the
198 eastern/north-western and southern lineages of the potential new *species* c. 3.17 Mya (2.01-4.54
199 Mya 95%).

200 The Bayesian Skyline plots (BSP) showed the effective population size throughout time (Mya) and
201 detected signs of expansion and contractions for each of the analysed clades (Fig. 2.4). A general
202 expansion of the population size in the genus started around c. 6 or 7 Mya (Fig. 2.4 A) that later
203 shrink during a bottleneck event that lasted from 2.5 Mya to 500.000 years ago, and then
204 expanded again until today. The individual clade BSP showed the same trend for each different
205 lineage. The analysis regarding all clades merged revealed an expansion that started between 7.5
206 and 10 Mya. This expansion was preceded by population stabilization, during the last 22 Mya
207 years.

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Fig. 2.4 Bayesian skyline plots for mitochondrial DNA (Dataset 1) for the species included into the *M. olivieri* species complex. The median estimate (black line) and 95% highest posterior density limits (blue background) are indicated. The y-axis represents the scaled population size and the x-axis indicates measures time in substitutions per site per million years. (A) All *Mesalina*, (B) *M. olivieri*, (C) *M. pasteuri*, (D) *Mesalina* sp. nov., (E) *M. simoni simoni*, (F) *M. simoni* ssp. nov.

216

2.3.4 MORPHOLOGICAL ANALYSES

217

Measurements of all individuals examined as well as those obtained from the literature are given in Table S4, S5 and S6. Descriptive statistics of the morphological data are shown in Table 2.2. Morphological differences were found between the *M. olivieri* lineage from Mauritania and the remaining species of the complex inhabiting its distribution (Table 2.2, 2.3, 2.4 and 2.5; Fig. S5, S6

220

221 and S7). For instance, individuals of Mauritanian *M. olivieri* tend to have a narrower and pointed
222 snout, more dorsal and gular scales, more femoral pores, and higher number of lamellae beneath
223 the fourth toe than the other species of the complex (Table 2.2). The nostrils of Mauritanian *M.*
224 *olivieri* have been recorded to be more exposed than those of *M. simoni* and *M. pasteuri*. Principal
225 Component Analysis for the biometry also shows a clear separation on the PC1 axes between
226 males of the Mauritanian *M. olivieri*, *M. simoni* and *M. pasteuri* (Fig. S5). This result highlighted
227 that the Mauritanian *M. olivieri* have a more narrowed snout and raised nostrils than *M. simoni*, and
228 they are smaller than *M. pasteuri* (Fig. S5).

229 Females of the Mauritanian *M. olivieri* differ from the other *M. olivieri* from the number of scales
230 composing the tail ring, higher in the latter; from the females of *M. simoni* in number of ventral
231 scales, lower for the Mauritanian *M. olivieri*; from the females of *M. pasteuri* in head height, higher
232 in *M. pasteuri*.

233 Shape and disposition of scales that compose the eyelid in both sexes of the new species is
234 resemble *M. guttulata* and *M. simoni* (5-6 large scales composing the eyelids), but without dark line
235 separating the scales. Major differences were also found in the dorsal coloration. PCAs on these
236 characters between *M. olivieri* and the new species shows main differences in the presence of pale
237 dorsal spots on the dorsum (PSDDSL), i.e. more evident in both male and females of the
238 Mauritanian *M. olivieri*, and on the dark band on the dorsum (SDDL) and on the flanks (DBF), i.e.
239 thicker and better defined in the other *M. olivieri* than in the Mauritanian lineage. Similar results
240 were obtained in the comparison between *M. pasteuri* and the Mauritanian *M. olivieri* where the
241 former also presents a pattern composed mostly by defined and continuous lines in the dorso-
242 lateral part of the body when the latter presents fragmented dark supra-dorsolateral line and a
243 mostly shaded pale dorso-lateral line. Differences were recorded also in the background
244 colorations from pictures of live specimens: ochre-bronze brown in the Mauritanian *M. olivieri*,
245 orange fire for *M. simoni*, from orange to yellowish in *M. pasteuri*, and brownish in the other *M.*
246 *olivieri*.

247

248

Table 2.2 Minimum-maximum value, mean and standard deviation (n=sample size) for selected characters in the *Mesalina olivieri* species complex.

		<i>Mesalina</i> sp. nov.			<i>M. simoni</i> ssp. nov.			<i>M. simoni</i>		<i>M. olivieri</i>			<i>M. pasteuri</i>		
		M	F	J	M	F	J	M	F	M	F	J	M	F	J
SVL	min-max	33-38	41-53	25-25	36-43	42.46-45.75	-	43-51	43-51	33-50	36-47	20-42	48-48	40-42	28-28
	mean ± SD	34±2.3	42±5.54	25±0	42±3.03	44.10±2.32	-	45±2.81	45±2.61	41±4.39	42±3.3	34±7.01	45±2.9	41±1.01	28±0
	N	(4)	(3)	(1)	(4)	(45.75)	-	(4)	(6)	(24)	(21)	(8)	(7)	(2)	(1)
HL	min-max	9-11	9-10	7-7	8-10	8.47-9.45	-	10.29-11.32	8.77-10.3	8.07-12.17	8.27-11.04	5.86-10.42	9.95-12.01	8.94-10.09	7.19-7.19
	mean ± SD	10±1.07	9±0.62	7±0	9±0.7	9±0.69	-	11±0.39	10±0.48	10±1.03	9±0.64	8±1.22	11±0.72	10±0.81	7.19±0
	N	(4)	(3)	(1)	(4)	(9.45)	-	(8)	(8)	(25)	(21)	(15)	(7)	(2)	(1)
HW	min-max	5.57-6.65	4.92-6.13	4.41-4.41	5.28-6.26	4.86-6.75	-	6.61-7.44	5.62-6.67	4.45-8.84	4.78-6.92	3.29-6.69	5.57-7.74	5.56-5.59	4.54-4.54
	mean ± SD	6±0.47	5±0.54	4.41±0	5.77±0.69	5.9±0.73	-	7.05±0.26	6.28±0.3	6.28±1.09	5.98±0.53	4.88±0.96	6.71±0.84	5.58±0.02	4.54±0
	N	(4)	(4)	(1)	(2)	(5)	-	(8)	(8)	(25)	(21)	(15)	(7)	(2)	(1)
HH	min-max	3.09-3.62	3-4.26	3.9-3.9	3.17-4.89	3.6-4.36	-	3.76-4.6	4.52-5.43	2.88-5.49	3.31-5.08	2.21-4.29	3.9-5.63	4.16-4.25	2.99-2.99
	mean ± SD	3.28±0.23	3.73±0.57	3.9±0	4.21±0.63	3.98±0.53	-	4.28±0.3	4.82±0.29	4.13±0.85	4.16±0.45	3.65±0.55	4.55±0.71	4.21±0.06	2.99±0
	N	(4)	(4)	(1)	(5)	(2)	-	(8)	(8)	(20)	(21)	(15)	(7)	(2)	(1)
TE	min-max	2-3	1-2	-	1-3	1-2	1-2	2-3	1-2	1-3	1-2	1-2	1-3	1-2	2-2
	mean ± SD	3±1	1±1	-	2.28±0.75	2.28±0.70	1.5±0.70	3±0.48	1±0.46	2±0.55	1±0.47	2±0.51	2±0.55	1±0.51	2±0
	N	(4)	(4)	-	(5)	(2)	(2)	(10)	(8)	(32)	(22)	(15)	(17)	(8)	(3)
RN	min-max	1-2	1-2	1-2	1-2	1-2	1-3	1-2	1-2	1-2	1-2	1-1	1-2	1-2	1-2
	mean ± SD	2±0.5	2±0.54	2±0.57	1±0.53	2±0.57	2±1	1±0.51	1±0.48	2±0.43	1±0.4	1±0	1±0.51	2±0.5	2±0.57
	N	(11)	(5)	(3)	(7)	(3)	(3)	(10)	(10)	(34)	(25)	(3)	(21)	(9)	(3)
PS	min-max	1-3	3-3	1-3	1-3	1-1	2-3	1-3	1-3	1-3	1-3	1-3	1-3	1-3	2-3
	mean ± SD	3±0	3±0	2±1.15	2±0.81	1±0	3±0.57	2±0.7	1±0.58	2±0.7	1±0.58	2±0.67	2±0.65	3±0.72	2±0.53
	N	(10)	(5)	(3)	(7)	(2)	(3)	(10)	(25)	(35)	(25)	(15)	(21)	(9)	(3)
V	min-max	27-33	32-34	31-32	28-34	34-34	31-32	29-33	33-35	27-35	27-35	25-35	28-33	30-34	26-34

		<i>Mesalina</i> sp. nov.			<i>M. simoni</i> ssp. nov.			<i>M. simoni</i>			<i>M. olivieri</i>			<i>M. pasteuri</i>		
		M	F	J	M	F	J	M	F	M	F	J	M	F	J	
	mean ± SD	30.14±2.03	33.25±0.95	31.67±0.57	30.6±2.19	34±0	31.5±0.7	30.56±1.23	34±1.41	30.22±1.78	31.55±1.73	30±2.56	30.17±1.68	31.13±1.6	30.33±4.04	
	N	(7)	(4)	(3)	(5)	(2)	(2)	(8)	(5)	(22)	(21)	(16)	(18)	(6)	(3)	
<i>D</i>	min-max	45-56	44-52	52-52	34-54	39-46	-	42-49	36-50	40-64	37-60	36-50	39-43	38-39	42-42	
	mean ± SD	50.5±4.65	47±3.82	52±0	44.57±10.06	42.33±3.51	-	45.63±2.06	42.5±4.78	45.54±5.64	45.38±5.16	42.79±4.19	40.43±1.51	38.5±0.7	42±0	
	N	(4)	(4)	(1)	(3)	(3)	-	(8)	(8)	(24)	(21)	(13)	(7)	(2)	(1)	
<i>TR</i>	min-max	14-17	12-15	16-16	15-1	15-15	-	15-18	13-16	14-20	12-18	14-18	15-18	14-16	14-14	
	mean ± SD	15.75±1.25	14±1.41	16±0	15.2±0.44	15±0	-	15.88±0.99	14.38±0.91	16.63±1.66	16.22±1.84	15.31±1.6	16±1.15	15±1.41	14±0	
	N	(4)	(4)	(1)	(5)	(2)	-	(8)	(8)	(21)	(15)	(13)	(7)	(2)	(1)	
<i>SL (Sx)</i>	min-max	4-5	4-4	-	4-5	4-4	-	4-5	4-4	4-6	3-5	4-5	5-7	4-4	5-5	
	mean ± SD	4.2±0.44	4±0	±	4.29±0.48	4±0	-	4.09±0.3	4±0	4.35±0.56	4.09±0.42	4.24±0.43	5.33±0.7	4±0	5±0	
	N	(5)	(4)	()	(7)	(2)	-	(11)	(11)	(24)	(22)	(17)	(9)	(2)	(1)	
<i>SL (Dx)</i>	min-max	4-5	4-4	4-5	4-5	4-4	4-4	4-5	3-4	4-6	4-5	3-6	4-6	4-6	5-6	
	mean ± SD	4.27±0.46	4±0	4.33±0.57	4.25±0.5	4±0	4±0	4.13±0.35	3.88±0.35	4.31±0.53	4.29±0.46	4.06±0.55	4.91±0.42	5±0.5	5.33±0.57	
	N	(11)	(5)	(3)	(4)	(2)	(2)	(8)	(8)	(32)	(24)	(17)	(22)	(9)	(3)	
<i>IL(Sx)</i>	min-max	7-9	7-9	7-8	7-9	7-8	8-8	7-9	7-8	7-9	7-9	6-10	6-11	8-9	6-8	
	mean ± SD	7.8±1.09	7.5±1.41	7.5±0.7	7.83±0.75	7.5±0.7	8±0	7.7±0.67	7.2±0.42	7.93±0.79	7.86±0.57	7.41±0.93	7.73±1.48	8.33±0.57	7±1.41	
	N	(5)	(4)	(2)	(6)	(2)	(1)	(10)	(10)	(29)	(21)	(17)	(11)	(3)	(2)	
<i>IL(Dx)</i>	min-max	6-9	7-8	7-8	7-9	7-7	7-7	8-9	6-8	6-10	6-9	5-9	6-10	6-9	6-8	
	mean ± SD	7.11±0.92	7.6±0.54	7.33±0.57	7.8±0.83	7±0	7±0	8.25±0.46	7.38±0.74	7.91±1.05	7.68±0.69	7.41±0.93	7.32±0.99	7.22±0.97	7±1	
	N	(9)	(5)	(3)	(5)	(2)	(2)	(8)	(8)	(32)	(24)	(17)	(22)	(9)	(3)	
<i>G</i>	min-max	21-32	24-28	24-27	24-28	26-28	22-30	21-27	20-24	20-34	21-33	17-29	22-31	24-28	25-30	
	mean ± SD	27.63±2.82	25.75±2.06	25.33±1.52	25.4±1.67	27±1.41	26±5.65	23.43±2.12	22.86±1.6	25.73±3.29	24.77±2.8	23.41±2.98	26.46±2.56	26.5±1.73	29±2.64	
	N	(8)	(4)	(3)	(5)	(2)	(2)	(8)	(8)	(30)	(22)	(17)	(15)	(4)	(3)	
<i>Col</i>	min-max	10-11	7-11	11-12	6-12	8-9	11-11	9-12	8-12	6-14	7-12	8-14	8-12	7-11	7-12	
	mean ± SD	10.88±0.35	9.33±2.08	11.33±0.57	8.6±2.19	8.5±0.7	11±0	10.5±1.19	9.75±1.28	9.72±1.98	9.36±1.29	9.75±1.43	10.13±1.12	9.8±1.64	9.5±3.53	
	N	(35)	(8)	(57)	(8.6±2.19)	(8.5±0.7)	(11±0)	(10.5±1.19)	(9.75±1.28)	(9.72±1.98)	(9.36±1.29)	(9.75±1.43)	(10.13±1.12)	(9.8±1.64)	(9.5±3.53)	

		<i>Mesalina</i> sp. nov.			<i>M. simoni</i> ssp. nov.			<i>M. simoni</i>			<i>M. olivieri</i>			<i>M. pasteuiri</i>		
		M	F	J	M	F	J	M	F	M	F	J	M	F	J	
	N	(8)	(3)	(3)	(5)	(2)	(2)	(8)	(8)	(29)	(22)	(16)	(15)	(5)	(2)	
<i>EL</i>	min-max	5-6	5-5	5-6	6-10	8-5	-	9-12	5-12	3-10	5-12	4-8	1-7	5-6	5-5	
	mean ± SD	5.11±0.3 3	5±0	5.33±0.5 77	7.5±1.6	6.5±2.12	-	10.5±1.1 9	8.38±2.4 4	6±1.78	6.86±2.0 3	5.83±1.3 2	4.83±1.6 4	5.25±0.5	5±0	
	N	(9)	(5)	(3)	(8)	(2)	-	(8)	(8)	(17)	(14)	(6)	(12)	(4)	(1)	
<i>NTS</i>	min-max	11-13	10-13	10-13	8-10	10-11	8-11	9-15	8-12	7-13	8-12	7-10	6-11	7-10	8-9	
	mean ± SD	12.36±0. 67	11.6±1.1 4	12±1.73	8.71±0.7 5	10.5±0.7	9.33±1. 52	10.9±1.9 1	9.7±1.41	10±1.06	9.68±1.0 3	9.17±0.9 2	8.57±1.4 3	8.89±1.2 6	8.67±0.5 7	
	N	(11)	(5)	(3)	(7)	(2)	(3)	(10)	(10)	(36)	(25)	(18)	(21)	(9)	(3)	
<i>Pf (Sx)</i>	min-max	12-18	12-17	14-15	10-12	11-12	12-13	10-14	10-14	11-18	10-16	9-14	11-17	10-13	9-12	
	mean ± SD	14.6±1.8 3	14.25±2. 06	14.33±0. 57	11.6±0.8 9	11.5±0.7	12.5±0. 7	12.44±1. 23	12±1.19	13.19±1. 75	12.45±1. 77	12.2±1.6 9	13.44±1. 65	11.67±1. 03	11±1.73	
	N	(10)	(4)	(3)	(5)	(2)	(2)	(9)	(8)	(27)	(19)	(15)	(18)	(6)	(3)	
<i>Pf (Dx)</i>	min-max	12-17	14-15	14-14	12-13	11-12	12-13	5-13	10-14	11-18	4-15	10-15	11-17	8-13	9-13	
	mean ± SD	14.6±1.8 3	14.25±0. 95	14±0	12.2±0.8 3	11.5±0.7	12.5±0. 7	11.33±2. 55	12±1.41	13.29±1. 75	11.5±2.4 1	12.38±1. 41	13.44±1. 65	11.33±1. 75	11.33±2. 08	
	N	(10)	(4)	(3)	(5)	(2)	(2)	(9)	(8)	(28)	(20)	(16)	(18)	(6)	(3)	
<i>Lam</i>	min-max	18-23	20-24	23-23	22-24	21-25	23-23	18-23	19-22	17-29	16-24	10-15	11-17	8-13	16-24	
	mean ± SD	22.14±1. 86	21.5±1.9 1	23±0	22.75±0. 95	23±2.82	23±0	20±1.65	20.25±1. 5	21.44±3. 05	19.5±2.3	12.38±1. 41	13.44±1. 65	11.33±1. 75	19.93±2. 63	
	N	(7)	(4)	(1)	(4)	(2)	(1)	(9)	(4)	(25)	(20)	(16)	(18)	(6)	(15)	

249 **Table 2.3** Loading scores and percentage of variance explained in the first two principal components extracted according
 250 to the Principal Components Analysis using morphological characters comparing male and female individuals of
 251 *Mesalina* sp. nov. with the other species of the *Mesalina olivieri* species complex.

Characters	<i>Mesalina</i> sp. nov. VS <i>M. olivieri</i>			<i>Mesalina</i> sp. nov. VS <i>M. simoni</i>			<i>Mesalina</i> sp. nov. VS <i>M. pasteuri</i>		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
Males									
SVL	0.944	0.123	-0.171	-0.181	0.942	0.059	0.956	0.059	-0.177
HL	0.211	0.155	0.262	-0.030	0.194	-0.008	0.214	-0.058	0.037
HW	0.177	-0.159	0.303	-0.025	0.149	-0.017	0.140	-0.065	0.755
HH	0.152	-0.266	0.355	-0.026	0.106	0.037	0.131	0.037	0.453
TE	0.021	0.069	0.785	-0.006	0.058	-0.026	-0.019	0.863	0.010
RN	-0.035	-0.113	0.238	0.510	0.049	0.858	-0.024	0.232	0.415
PS	-0.093	0.921	0.104	0.839	0.189	-0.508	-0.040	0.435	-0.138
% variance	95.009	2.273	1.155	97.701	2.021	0.213	96.853	1.471	0.986
Females									
Characters	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
SVL	0.985	-0.032	-0.130	0.015	0.956	0.214	0.980	0.113	-0.034
HL	0.130	0.222	0.665	0.017	0.164	0.077	0.167	-0.467	0.108
HW	0.069	0.084	0.518	0.003	0.079	0.031	0.086	0.120	-0.175
HH	0.045	-0.238	0.475	-0.003	0.017	0.064	0.037	-0.558	-0.312
TE	-0.046	0.142	0.163	-0.006	0.002	-0.014	-0.042	0.524	-0.371
RN	0.067	-0.069	-0.082	0.584	0.174	-0.791	0.033	0.007	0.821
PS	0.020	0.928	-0.120	0.811	-0.147	0.564	-0.002	0.411	0.218
% variance	90.752	4.559	2.013	97.682	2.142	0.125	98.441	0.793	0.426

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254 **Table 2.4** Loading scores and percentage of variance explained in the first two principal components extracted according
 255 to the Principal Components Analysis using ploidosis characters comparing male and female individuals of *Mesalina* sp.
 256 nov. with the other species of the *Mesalina olivieri* species complex.

Characters	<i>Mesalina</i> sp. nov. VS <i>M. olivieri</i>		<i>Mesalina</i> sp. nov. VS <i>M. simoni</i>		<i>Mesalina</i> sp. nov. VS <i>M. pasteuri</i>	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Males						
V	0.312	0.012	0.579	0.469	0.298	-0.186
D	-0.714	-0.051	0.486	-0.475	-0.637	0.171
DS	0.049	-0.159	-0.082	0.057	-0.275	0.154
TR	0.213	0.179	0.221	0.066	0.194	0.018
SL(Sx)	0.047	0.075	-0.177	-0.049	0.194	-0.038
SL(Dx)	0.067	0.101	-0.171	-0.026	0.171	-0.054
IL(Sx)	0.052	0.050	0.134	0.103	0.079	0.139
IL(Dx)	0.064	0.059	0.097	0.152	0.098	0.110
G	0.426	-0.694	-0.397	0.283	0.266	-0.354
Col	0.190	0.048	-0.157	-0.403	-0.042	0.049
EL	0.161	0.385	-0.007	-0.191	-0.109	0.100
NTS	0.101	-0.031	0.210	-0.044	-0.227	-0.082
Pf(Sx)	-0.024	0.112	-0.107	-0.034	0.035	-0.380
Pf(Dx)	-0.059	-0.011	-0.218	0.120	-0.023	-0.296
Lam	0.272	0.522	-0.028	0.462	0.414	0.707
% variance	43.313	17.317	92.216	3.601	46.810	18.483
Females						
Characters	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
V	-0.040	-0.512	0.627	0.404	0.297	0.087
D	-0.403	-0.185	0.482	-0.582	-0.624	-0.243
DS	-0.008	0.092	-0.080	0.044	-0.117	-0.009
TR	-0.173	0.664	0.185	0.199	0.242	0.144
SL(Sx)	-0.003	0.036	-0.159	0.032	0.068	-0.055
SL(Dx)	0.017	0.109	-0.169	0.030	0.221	-0.031
IL(Sx)	-0.078	0.112	0.108	0.034	0.140	-0.004
IL(Dx)	-0.031	0.041	0.056	0.138	0.134	-0.189
G	0.392	0.388	-0.373	-0.164	0.418	-0.347
Col	0.131	-0.063	-0.108	-0.132	-0.053	0.422
EL	-0.542	0.258	-0.003	0.489	-0.034	-0.011
NTS	0.070	-0.020	0.193	0.107	-0.231	-0.259
Pf(Sx)	0.346	-0.013	-0.157	0.253	-0.064	0.486
Pf(Dx)	0.242	0.017	-0.222	0.273	-0.195	0.485
Lam	0.389	0.068	-0.047	0.029	0.290	0.192
% variance	27.494	20.650	94.817	2.501	51.127	20.854

257 **Table 2.5** Loading scores and percentage of variance explained in the first two principal components extracted according
 258 to the Principal Components Analysis using coloration characters comparing male and female individuals of *Mesalina* sp.
 259 nov. with the other species of the *Mesalina olivieri* species complex.

Characters	<i>Mesalina</i> sp. nov. VS <i>M. olivieri</i>		<i>Mesalina</i> sp. nov. VS <i>M. simoni</i>		<i>Mesalina</i> sp. nov. VS <i>M. pasteuri</i>	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Males						
EBL	-0.191	-0.063	0.964	-0.203	0.196	-0.104
DBF	0.080	-0.669	0.157	0.241	0.392	-0.209
PSDBF	0.337	0.214	-0.053	-0.123	0.179	0.339
PDLL	0.254	0.152	0.055	0.227	-0.465	0.238
SPDLL	-0.124	0.517	0.106	0.368	-0.216	0.044
DDSL	-0.047	-0.215	0.089	0.287	-0.336	-0.663
SDDL	-0.254	-0.136	0.087	0.768	0.552	0.012
PSDDSL	0.689	0.147	-0.061	-0.100	0.231	-0.055
DSO	-0.409	0.353	0.084	0.080	-0.062	0.565
TC	-0.233	0.029	0.051	-0.100	0.196	-0.104
% variance	49.928	14.493	78.780	9.658	50.541	26.395
Females						
Characters	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
EBL	-0.112	-0.062	0.935	-0.076	0.183	-0.009
DBF	0.008	0.423	0.172	0.240	0.446	0.369
PSDBF	0.186	-0.014	0.027	0.054	0.227	0.074
PDLL	0.319	0.086	0.042	-0.225	-0.487	-0.243
SPDLL	0.269	-0.022	0.209	-0.562	-0.204	0.639
DDSL	-0.063	0.233	0.055	0.199	-0.377	-0.184
SDDL	-0.809	0.158	0.206	0.703	0.471	-0.547
PSDDSL	-0.177	-0.594	-0.013	0.180	0.182	-0.119
DSO	0.180	0.505	-0.004	0.020	0.078	0.072
TC	0.238	-0.348	0.072	0.033	0.184	0.197
% variance	39.872	16.950	79.353	11.635	55.148	25.457

2.3.5 TAXONOMIC IMPLICATIONS

Given its genetic, morphological and ecological divergence and lack of gene flow with *M. pasteuri* and *M. simoni*, we assign species level to the new lineage of the *olivieri* complex from Mauritania. Moreover, both mtDNA and nuclear DNA data unambiguously group the populations of “*Mesalina olivieri*” from southern and southwestern Morocco with *M. simoni*, and confirm that *M. simoni* is a valid species that is highly divergent from *M. olivieri* (distributed from eastern Morocco to Israel, see Fig. 2.1). The formal description of these two lineages was not included here to do not compromise the future publication on peer-reviewed scientific journal.

2.3.6 DISTRIBUTION MODELLING AND CONSERVATION STATUS

The 20 replicate ecological models exhibited good predictive accuracy (average AUC=0.906). The most important environmental predictors were terrain ruggedness index (42.6% contribution) and Land-cover (35.4%) (Table S8; Fig. 2.6). The highest probability of occurrence is at an intermediate levels of terrain ruggedness and in bare rock habitats (Fig. S8). The predicted range of *Mesalina* sp. nov. encompassed the mountain rocky areas of the Adrar Atar in Mauritania, further extending to the north up to the plateau around F'derick, to the north-west up to Koudiet Lagnem (Morocco), and to the south down to the central Tagant mountain.

The Area of Occupancy (AOO) calculated from the ecological models was of 34,766 km², while the Extent of Occurrence (EOO) was of 175,445 km². Following IUCN guidelines, it is here proposed the status of Near Threatened for *Mesalina* sp. nov. according to the following parameters: i) EOO below 20,000 km², ii) the high degree of uncertainty in the population size; iii) the rarity of the species, and iv) the general fragmented distribution. The taxon is restricted to the rocky highlands of the Adrar and neighbouring highlands with northern disjunct populations apparently separated from the distribution by wide unsuitable habitats (sandy desert) (Fig. 2.6).

2.3.7 HABITAT COMPARISON

There are significant differences in number of observations in each land-cover category (χ^2 ; $p=0.037$; $df=39$). *Mesalina* sp. nov. selects (70% of observations) a specific land cover habitat that has a restricted availability in the study area (6.3% of study area) being most frequently found in bare rocks units. *Mesalina simoni* was most frequently found in rocky plateau, while *M. olivieri* and *M. pasteuri* occur in almost all units. Bs measure of niche breadth was lower for *Mesalina* sp. nov. and *M. simoni*, and higher for *M. olivieri* and *M. pasteuri*, indicating that the former pair are more specialized than the latter (Table S8).

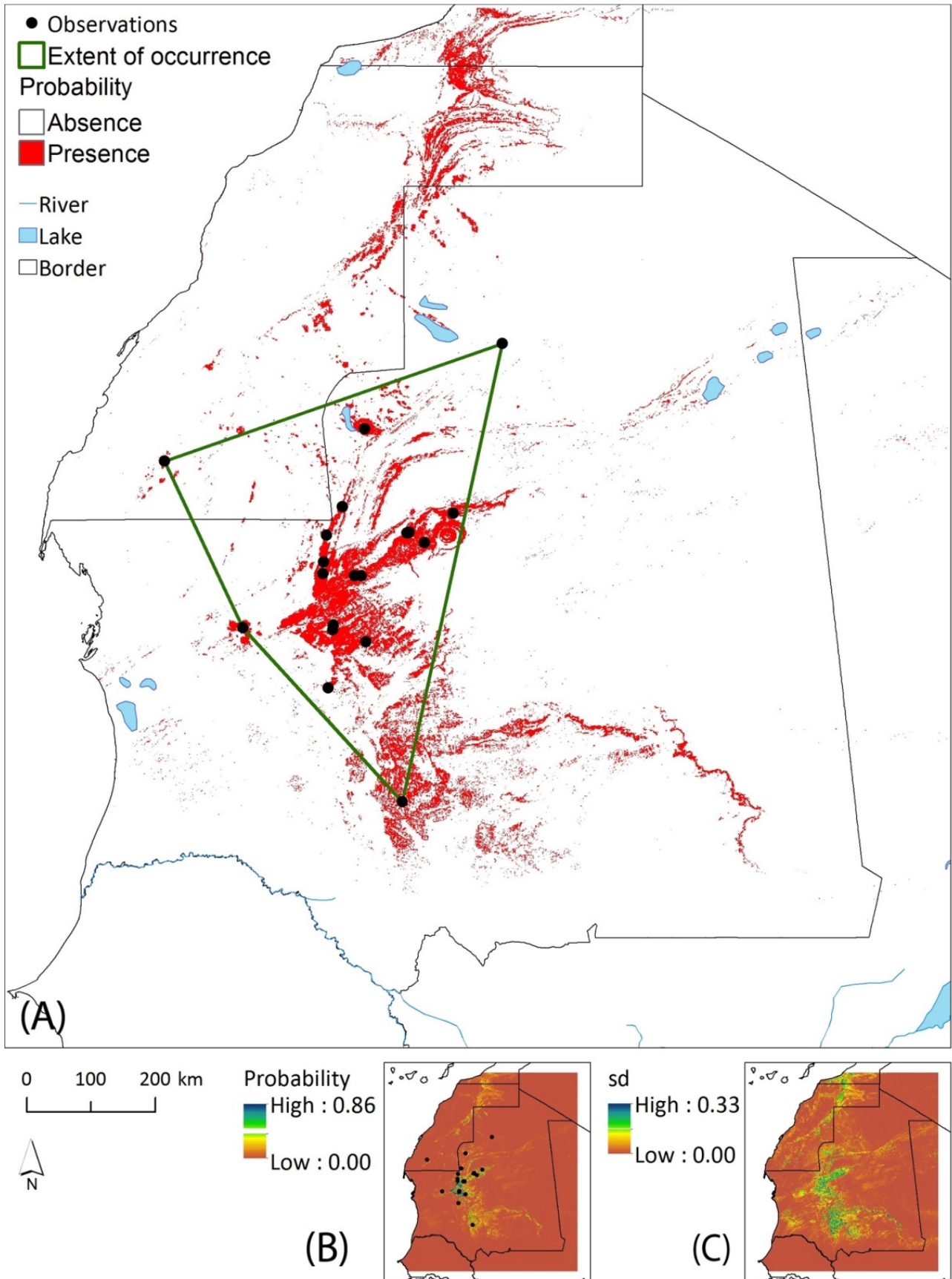


Fig. 2.5 Ecological modelling of *Mesalina* sp. nov. (A) Binary predictions of suitable habitats for the taxon. (B) Average probability of occurrence and (C) standard deviation from 20 individual model replicates.

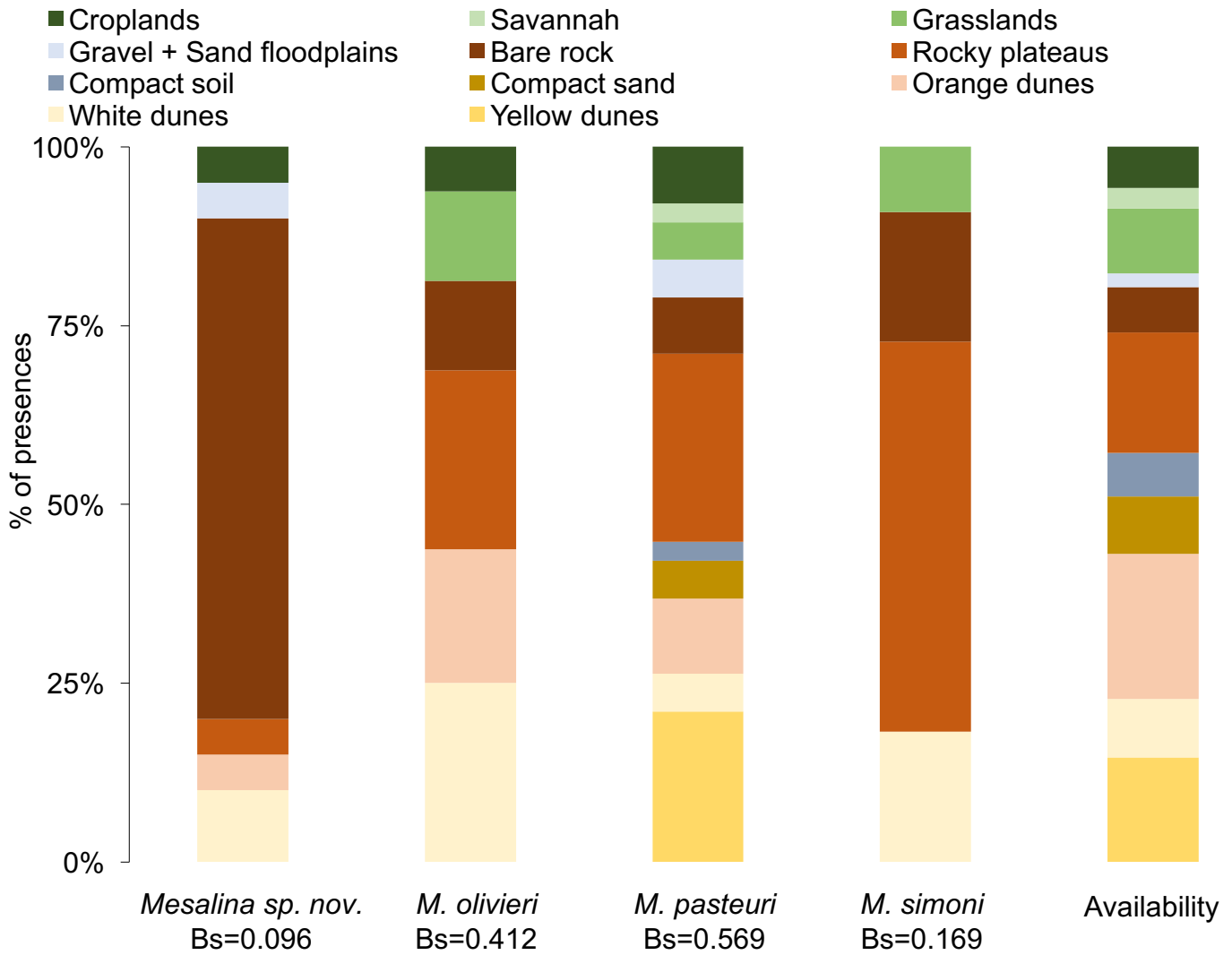


Fig. 2.6 Results on the habitat analysis on the five species of the *olivieri* complex in North West Africa. Bs is the standardized Levin's measure ranging from 0.0 to 1.0; high B means no discrimination between land-cover units, meanwhile low Bs value means selection among land-cover units.

2.4. DISCUSSION

The integrative taxonomy methodology used in this study offers further evidence about how multidisciplinary approaches are pivotal for better understanding and describing a new species. Our study describes a new species within the *M. olivieri* species complex and solves other taxonomic problems within this group. Moreover, this study unveils much more intraspecific diversity within this last two species than previously described. Our integrative taxonomy assessment on *Mesalina sp. nov.* and *M. simoni* provide additional evidences about how highlands, hydrographic systems, and coastal areas can work as refugia and centre of diversification during the humid and dry cycles that characterised the Sahara Desert (Brito et al., 2014; Gonçalves et al., 2018a,b; Velo-Antón et al., 2018).

2.4.1 PHYLOGENETIC RELATIONSHIPS AND SYSTEMATICS OVERVIEW

Our phylogenetic results unveil *Mesalina sp. nov.*, as an independent evolving lineage, while the *olivieri* lineages from the Atlas Mountain and Atlantic Sahara evolved together with *M. simoni* as another independent evolving lineage. However, we found mitonuclear discordances in *M. martini* and the Algerian *M. olivieri*. *Mesalina martini* resulted to be basal to the *olivieri* species complex when more data were included in the analysis, higher number of genes in the cytonuclear tree (dataset 3) or higher number of samples in the mitochondrial tree including all the species of the genus available in GeneBank (dataset 1). The unclear phylogenetic situation of *M. martini* was previously highlighted by other studies. It was for instance found to be basal to the *M. olivieri* species complex (Kapli et al., 2008; 2015), but also basal to the other species, except for *M. watsonana* in Sindaco et al. (2018) and Simó-Riudalbas et al. (2019). Seen the low support recorded in any of the cases, this result could be due to incomplete lineage sorting caused by the discrepancy between the amount of data present for *M. martini* included in the analysis. Despite the efforts here developed to sequence additional nDNA genes in comparison to previous studies, further research is needed to better clarify the relativeness of *M. martini* with the other species of the genus, including samples covering the complete distribution area of the species and possibly more genes, both mitochondrial and nuclear.

Regarding the cytonuclear discordance for the *olivieri* clade from Algeria (*M. olivieri* ALG1 in Fig 2.2 and S2; samples BEV.9225 and BEV.T3038 in Fig. S3), just two were the studies including this clade in their Bayesian inference phylogenetic analysis. The study of Kapli et al. (2015) and in the study of Simó-Riudalbas et al. (2019). Both the studies

analysed the same fragments of mitochondrial DNA (16S and *Cyt-b*). As it is recorded in this study, the Algerian clade is recovered to be sister taxa of the *M. pasteuri* from Mauritania. This discordance between the nuclear and mitochondrial scenario, could be due to an higher number of variable characters in mtDNA that may consequently express cases of homoplasy. Another potential explanation could be a a relatively recent hybridization event that led to gradual mitochondrial introgression between the Algerian *M. olivieri* and a lineage of *M. pasteuri* from Mauritania, Niger and Algeria. Incongruences on the genetic divergence between mtDNA and nDNA have been also reported in other taxa, like *Drosophila simulans*, *Podarcis muralis* and *Tarentola mauritanica* (Ballard et al., 2007; Pinho et al., 2007; Rato et al., 2010) explained by incomplete lineage sorting or ongoing gene flow between the two lineages (García-Paris et al., 2008; Rato et al., 2010). The results of the cytonuclear concatenated tree (Fig. 2.2) agree with the nuclear DNA results where the Algerian lineage results to be an independent evolving lineage, basal to *M. olivieri* and *M. pasteuri*. Sampling gaps from the central region of North Africa, especially from the contact zones between *M. olivieri* and *M. pasteuri*, hamper the validation of a putative broader contact zone between *M. pasteuri* and *M. olivieri* over southern Algeria, north-eastern Mauritania, Mali and Niger, and/or the presence of a new species from Algeria.

2.4.2 SPATIAL STRUCTURE OF GENETIC VARIABILITY

2.4.2.1 Biogeography of *Mesalina sp. nov.*

The *M. olivieri* species complex started to diversify in the Late Miocene (ca. 12.08 - 6.38 Mya). This dating is congruent with the beginning of the arid period that originated the current Sahara Desert (Holmes, 2008). Mountain chains, highland and coastal areas worked as refugia during the arid and humid cycles of the Sahara-Sahel (Brito et al., 2014; Gonçalves et al., 2018a,b; Velo-Antón et al., 2018). The progressing desertification in the area likely forced the ancestor of the *M. olivieri* species complex to contract its distribution in the several refugia present in the Sahara (e.g. Adrar-Atar highlands and the Atlantic coastal area). This contraction could have leaved the ancestor of *Mesalina sp. nov.* and *M. simoni* isolated from the other species of *M. olivieri*. This hypothesis is supported by the low genetic divergence between these two taxa and the high divergence observed with the remaining species included in our study (Table 2.1). *Mesalina sp. nov.* and *M. simoni* started their indipend evolution around 8.9 Mya. The high genetic divergence between the Atlantic lineage of *M. simoni ssp. nov.* and *Mesalina sp. nov.* could indicate an early split

between the *M. simoni* group and *Mesalina sp. nov.* occurred in that area (north to the current distribution of *Mesalina sp. nov.*). It is still unclear what was the geological situation of the area at that time. Signs, as the low elevation above the sea level and the presence of sand in the area even before the Sahara's desertification started (Swezey, 2008), point to the possibility that the area was probably flooded and that the today's mountain chains and plateau (i.e. Adrar-Atar) were islands. This potential scenario matches with the phylogeographical pattern of this new species and *M. simoni* and some species of reptiles as *Agama sp.* (Gonçalves et al., 2018a). These species may have contracted their distribution in the Adrar-Atar and Tagant mountains or to the Atlas Mountain chain respectively to then expand again once the ocean retracted. This diversification could be also explained by the vicariance effect due to the formation of numerous hydrological networks in the Western Sahara (e.g. Tamanrasset paleo river; Skonieczny et al., 2015) that worked as genetic barrier between the two species. This large hydrological system likely acted as barrier to dispersal in some species (e.g. *Psammophis schokari*, Gonçalves et al., 2018b), cutting the region longitudinally with its massive amount of water during the humid periods, and the vast sandy area left behind it during the arid periods. The Atlantic coast of the Sahara Desert has also been proposed to act as Trans-Sahara corridor and refugia for several species (Brito et al., 2014, 2016; Gonçalves et al., 2018b; Velo-Antón et al., 2018) given its stable climate, high humidity and vegetation cover when compared to the continental areas (Dinerstein et al., 2017). However, the shifts in the local hydrological regime have likely worked as landscape barriers that isolated different populations, which promoted high diversification levels through vicariant effects (Gonçalves et al., 2018b; Velo-Antón et al., 2018) and led to the formation of multiple endemic taxa (Crochet et al., 2003; Vogel et al., 2006; Sindaco and Jeremcenko, 2008; Ndiaye et al., 2012; Trape et al., 2012), among which *M. simoni* (Schleich et al., 1996). The latitudinal genetic structure recorded for *Mesalina sp. nov.* and *M. simoni* could be due to more recent contraction and expansion of the lineages due to adverse and favourable climatic condition (Swezey, 2009; Brito et al., 2014; Gonçalves et al., 2018a) and/or because of the isolation by temporary geographical features as rivers or dry river basins (Gonçalves et al., 2018b; Velo-Antón et al., 2018).

Moreover, the historical demography results show an overall reduction in the population density of *Mesalina sp. nov.* starting around 2.5 Mya in concomitance with the beginning of the Sahara Green Phase occurred during the Holocene. This shrink in the population density matches also in time with results on the time of divergence that show a high

intraspecific diversification in the four species of the complex during the Plio-Pleistocene transition.

2.4.2.2 *The hidden diversity within M. olivieri and M. pasteuri*

For what concerns the *M. olivieri* lineages, the North African genetic diversity highlighted in this study matches the continuous latitudinal distribution of the species. From the results, at least five potential different lineages can be discerned: i) one from the Atlas Mountain in the eastern part of Morocco; ii) a well-supported (PP>95%) lineage from the western part of Algeria basal to both *M. olivieri* and *M. pasteuri* and iii) another Algerian lineage from the eastern part of the country; iv) one from Tunisia and v) one including the *M. olivieri* from Egypt and Israel. Regarding *M. pasteuri* two well supported lineages (PP=100%) have been unveiled in North West Africa: i) one mostly distributed on the Atlantic Sahara region; and ii) a second one including specimens from the inland of Mauritania, Niger and Algeria. This noteworthy amount of diversity has been already hypnotised in numerous studies (Arnold et al., 1986, 2007; Kapli et al., 2015). Although this study increases the resolution of the systematic background of *M. olivieri* and *M. pasteuri*, additional data are needed for an integrative approach on the description of these lineages.

2.4.3 HABITAT COMPARISON AND DISTRIBUTION OF MESALINA SIMONI AND MESALINA SP. NOV.

The habitat comparison among the four species of the complex gives additional support to the validity of *Mesalina sp. nov.* as a new species, showing that the latter selects among land cover units and exhibits narrow niche breadth (low Bs). For instance, *Mesalina sp. nov.* dwells almost exclusively on steep and rocky areas (Fig. 2.6 Table S8), contrary to *M. pasteuri* and *M. olivieri* that are more generalist species (Table S8 and Fig. 2.6) and mostly occur in sandy areas (Bons, 1960; Sindaco and Jeremcenko, 2008; Trape et al., 2012). The relatively low Levin's measure recorded for *M. simoni* indicates that the latter is also a habitat selective species. As *Mesalina sp. nov.*, *M. simoni* also prefers rocky areas but contrary to the former it inhabits plateaus with sparse vegetation, from sea level to above 900 meters. *Mesalina simoni* is an endemic species from the central Atlantic coast of Morocco. It has been previously considered as a subspecies of the Moroccan lineage of *M. olivieri* (Shcherbak, 1975) and later elevated to species level (Schleich et al., 1996) based on morphological features. The new *M. simoni* subspecies distribution matches with the hypothesised Trans-Sahara Atlantic corridor that worked as refugia and centre of lineage diversification for mesic species (e.g. Gonçalves et al., 2018b; Velo-Antón et al., 2018), from the South-Eastern part of the Atlas Mountains, along the Atlantic coast of Sahara, to the border with Mauritania.

2.4.4 CONCLUSIONS AND FUTURE RESEARCH

This study allowed a better understanding of the systematic and phylogeography of the *M. olivieri* species complex, providing also new observation for all the species of the complex extending their current distributions. Here it is demonstrated that the use of a combination of molecular, morphological and environmental data is crucial to clarify taxonomy, ecology and distribution of a species, and unveiling from a molecular point of view the existence of previously undescribed lineages (Arnold, 1986). This study also provides evidences that the single use of mtDNA or nDNA could lead to misleading results. Moreover, while assessing the diversification within the *M. olivieri* species complex, this study gives additional evidences on the validity of the Trans-Sahara Atlantic corridor and the Adrar and Tagant highlands as valid refugia during the climatic oscillation since the Miocene. With the inclusion of more samples and molecular markers, future research will be conducted to understand the taxonomic situation of the *Mesalina olivieri* species complex. These studies will be focused on the clarification of the phylogeographic pattern highlighted in this study and on the description of potential new species.

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3 DISCUSSION AND FINAL REMARKS

Since the beginning of the Pliocene that North-West Africa has been shaped by arid and humid cycles, which have characterised the history of the Sahara-Sahel ecoregions (Holmes, 2008; Kröpelin *et al.*, 2008; Brito *et al.*, 2014). The complex paleogeographic and climatic events lead to a peculiar topographical, hydrographical and environmental variation that drove the current biodiversity patterns and induced high levels of diversity and endemism in the area (Sindaco *et al.*, 2008; Brito *et al.*, 2014; Velo-Antón *et al.*, 2018). The ever-changing character of the region has attracted the attention of the scientific community. The arid and hot climate and the remoteness of the area always challenged research activities. The most hindering concern currently is the political instability and social insecurity that is growing in the region over the last decades (Brito *et al.*, 2018). It has been highlighted that the increasing warfare and political instability is inversely related to the research efforts in North West Africa (Brito *et al.*, 2014). This, together with remoteness and harsh climatic conditions that characterise the region results in a huge gap of knowledge on the amount of biodiversity inhabiting the area. Fortunately, this gap is being filled by numerous studies that included North West Africa (Geniez, 2004; Sindaco *et al.*, 2008; Brito *et al.*, 2014; Velo-Antón *et al.*, 2018; Freitas *et al.*, 2018; Gonçalves *et al.*, 2018; Karssene *et al.*, 2019; Demos *et al.*, 2019).

Previous studies on the genus *Mesalina* recovered strong patterns of genetic and morphological differentiation (Arnold, 1989; Joger & Mayer, 2002; Moravec, 2004; Kapli *et al.*, 2008; Yousefkhani *et al.*, 2015; Šmíd *et al.*, 2017; Sindaco *et al.*, 2018) and suggested that past geological and climatic events had a profound effect in its biogeographic history and speciation of the genus (Kapli *et al.*, 2015; Simó-Riudalbas *et al.*, 2019). However, no study has deeply addressed the *M. olivieri* species complex leaving a big lack of knowledge on the systematics, morphology and the geographical genetic diversity of the complex. In this work, it was addressed the interspecific variability of the *M. olivieri* species complex using an integrative approach that combined genetic, ecological and morphological variability analyses. This study gives a multidisciplinary overview about the phylogeography, morphology and distribution of two new undescribed taxa from Mauritania and Atlantic Sahara, validating the status of a new species and as new subspecies of *M. simoni*.

Integrative taxonomy is a powerful tool that allows obtaining broader and resolute pictures of the ecological role, natural history and the evolution of a species (Padiál *et al.*, 2010; Crottini *et al.*, 2011; Heinrichs *et al.*, 2015; Ghielmi *et al.*, 2016; Sloan *et al.*, 2017; Šmíd *et al.*, 2017; Sindaco *et al.*, 2018). Here it was also provided for the first time information regarding high diversity of the *M. olivieri* species complex in North West Africa, increasing knowledge on genetic variability. Despite

the new data regarding the interspecific and intraspecific patterns of genetic variation in the complex, more studies are needed on its morphological and ecological variation.

3.1. INTERSPECIFIC DIVERSITY WITHIN *MESALINA OLIVIERI* SPECIES COMPLEX

3.1.1. GENETICS

The evidences given by the accumulation of the phylogenetic results (concatenated cytonuclear Bayesian tree and species tree), genetic divergences, and haplotype networks give strong genetic support to the recognition of the lineage of *M. olivieri* from Mauritania as a valid species and the inclusion of the two lineages of *M. olivieri* from the Atlantic Sahara and Atlas Mountain as subspecies of *M. simoni*. These results expand the currently known distribution from Figuig in North-eastern Morocco until the North-western border of Mauritania.

The results obtained here also provide evidences on the high intraspecific diversity within the *Mesalina olivieri* species complex putting forward the possibility of an additional valid species from Algeria. Moreover, this study also adds evidences that the single use of mtDNA or nDNA could lead to misleading results.

3.1.2. MORPHOLOGY

The results for the PCA pointed to some morphologic differences between the species of the complex and the new species from Mauritania, as for instance the number, shape and disposition of the scales composing the eyelid and in the number of rows of the temporal granulae (Fig. S6). This species is also discernible from its fragmented but linear and organized dorsal pattern and, In vivo, its pearly coloration stronger on the ventral part of the body (Fig. 3.1 and 3.2). Unfortunately, also the most updated dichotomic key available for the genus *Mesalina* (Trape *et al.*, 2012; Yousefkhani *et al.*, 2015) were found to be not completely accurate or of little use for the species belonging to the *M. olivieri* species complex (e.g. Trape *et al.*, 2012). Future studies to define dichotomous characters that can better discern the species within this complex are necessary. It would be interesting to take into consideration also internal characters, such as hemipenis anatomy because differences in their length have already been highlighted by Arnold (1986a and 1986b).



Fig 3.1. Dorsal and ventral prospective of an adult of the new species from the Adrar Atar (Mauritania). Pictures from P.-A. Geniez

Despite this, it is here highlighted the strong morphologic modification during the ontogenesis that characterise individuals of this new species. The evidences given by the phylogenetic analysis and haplotype networks (Fig. 2.2 and 2.3) recovered the two juvenile specimens (147.3 and 147.4; Fig. 3.2) previously misrecognised as *M. pasteuri* in Kapli *et al.* (2015), as belonging to this new species from Mauritania and neighbouring regions. This finding provides a good overview of what most likely are the morphological steps that characterise the ontogenesis of this new species, but also solves the paraphyly of *M. pasteuri* and extends the known distribution of the species (previously restricted to the plateau of the Adrar Atar in Mauritania) to the southern Tagant plateau.



Fig 3.2. Juveniles of the new species previously recognized as *M. pasteuri* on the left and in the middle (Codes from Kapli *al.*, 2015) and an adult from the Adrar on the right. The specimen on the left is a new-born displaying the typical striped coloration meanwhile on the right a juvenile. It is evident how the striped-like pattern is stronger in the first stage of the ontogenesis to than shade first in the juveniles and totally disappear in the adults. Pictures from Cristian Pizzigalli (left) and José Carlos Brito (middle and right).

3.1.3. ECOLOGICAL ANALYSIS AND CONSERVATION STATUS

The ecological niche-based analysis situates the new species in habitats characterised by intermediate levels of ruggedness and bare rocks. The predicted distribution encompasses the mountain rocky areas of the Adrar Atar in Mauritania, further extending to the north up to the plateau around F'derick, to the north-west up to Koudiet Lagnem (Morocco), and to the south down to the central Tagant mountain. The new species is confirmed to be sympatric to *M. pasteuri*, *M. rubropunctata* and *M. guttulata* (Trape *et al.*, 2012; Sindaco *et al.*, 2018). While *M. pasteuri* is

well known to inhabit mostly sand dunes, the latter two species share the same habitats with the new species in some localities (Trape *et al.*, 2012), but haplotype networks confirm that they do not hybridise (results not showed). The fine scale distribution of *Mesalina* sp. nov. and *M. pasteuri* in the Adrar Atar plateau in relation to main categories of land-cover (Fig. 3.2) shows that the former species is exclusively found on the upper rocky parts of the plateau (sometimes isolated by kilometres of sandy desert), being absent from the lower sandy and dune valleys where the latter species occurs (Bons, 1960; Sindaco and Jeremcenko, 2008). Although no evident contact zones are known, additional local studies are needed to better understand habitat partition between the two species and potential interactions with the other species of the genus *Mesalina* present in the region.

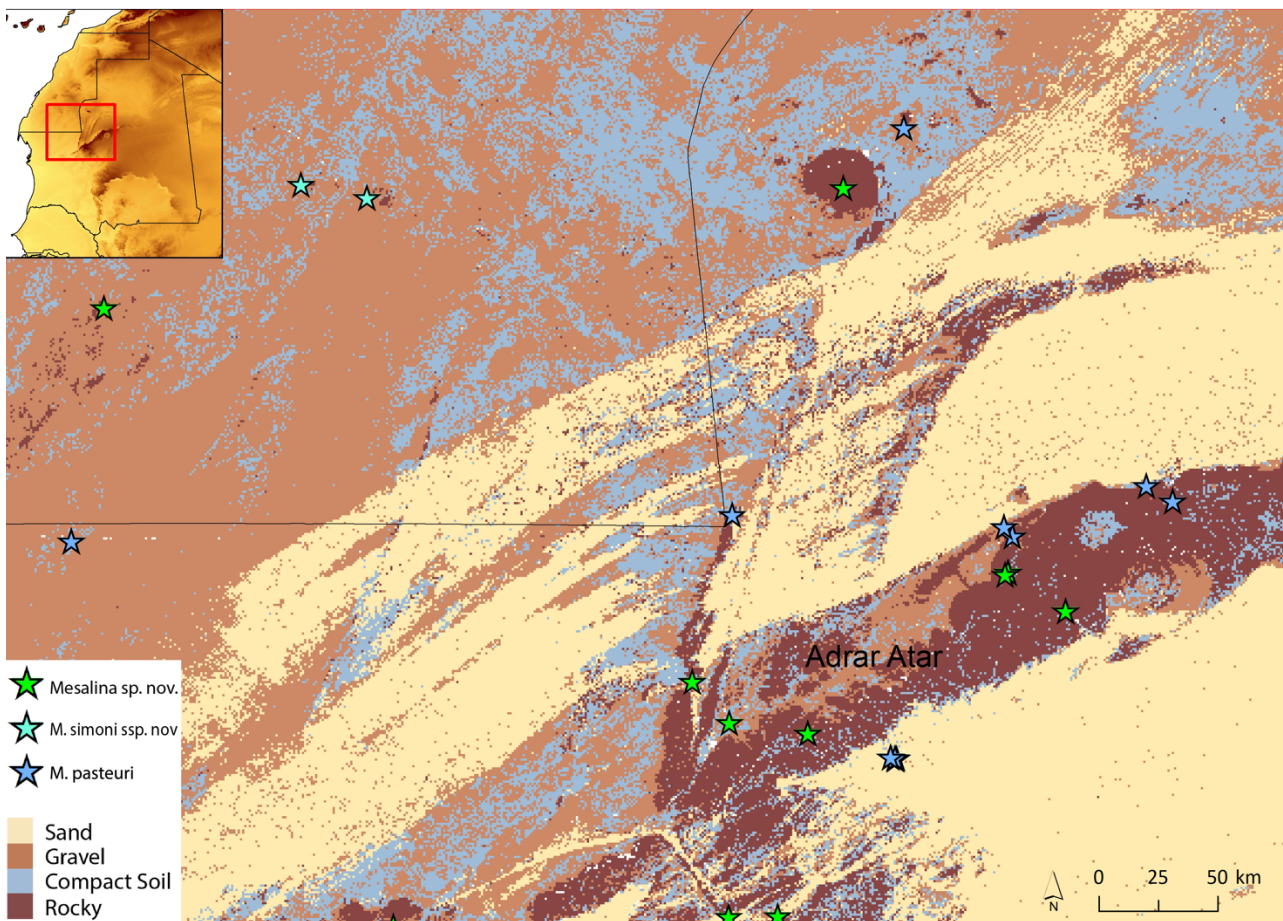


Fig 3.3 Distribution of *Mesalina* sp. nov. (light green), *M. simoni* ssp. nov. (light blue), *M. pasteuri* (dark blue), and main land-cover categories (adapted from Campos and Brito, 2018) in the Adrar Atar (Mauritania) and adjacent northern regions.

The conservation status of the new species can be considered as Least Concern according to the IUCN Red List categories (2019). This classification was based on the high values recorded for the area of occupancy (AOO = 34,766 km²) and extend of occurrence (EOO = 175,445 km²). Still, it is important to consider the scarce currently available knowledge about the new species, the

remoteness of its distribution area, and its apparent extreme habitat fragmentation. Thus, local studies are needed to confirm the correct assignment of the conservation status.

3.2 PAST CLIMATIC CHANGES AS DRIVERS FOR SPECIATION WITHIN *MESALINA OLIVIERI* SPECIES COMPLEX.

The analysis on the time of divergence show that high intraspecific diversification occurred during the Pliocene-Pleistocene transition, and the same pattern was found in the mtDNA historical demography simulations. A demographic contraction was predicted to have started around 4 Mya and a bottleneck period from 2 Mya until 0.1 Mya. This initial contraction was preceded by a period population stabilisation and followed by an expansion starting at about 0.1 Mya. The climatic oscillations that characterised the Sahara-Sahel during the Pliocene and Pleistocene affected the region after the beginning of the desertification process. These climatic oscillations resulted in arid and humid periods that drove the population expansion (during dry periods) and contraction (during humid periods) of the xeric species inhabiting the area, leading to the formation of new lineages and contact zones (Brito *et al.*, 2014). This pattern has been found in several reptile species, including *Tarentola* sp. (Rato *et al.*, 2012), *Stenodactylus* sp. (Metallinou *et al.*, 2012), and *Agama* sp. (Gonçalves *et al.*, 2018). Although additional data analysis are needed to support this hypothesis, the new species from Mauritania could be considerate another good model to test the diversification through aridity-induced vicariance in North-West Africa and how highlands, hydrographic systems, and coastal areas can work as refugia and centers of diversification for xeric species during the humid and dry cycles that characterised the Sahara Desert. Moreover, the assessment of the diversification within the *M. olivieri* species complex developed in this study gave additional evidence on the validity of the Trans-Sahara Atlantic corridor and the Adrar and Tagant highlands as valid refugia during the climatic oscillation from the Miocene until now.

Still, it remains to be clarified the taxonomic situation of the other species of the *M. olivieri* species complex, understand their biogeographic histories, and describe the potential new species highlighted in this work.

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4. APPENDIX SUPPLEMENTARY MATERIAL

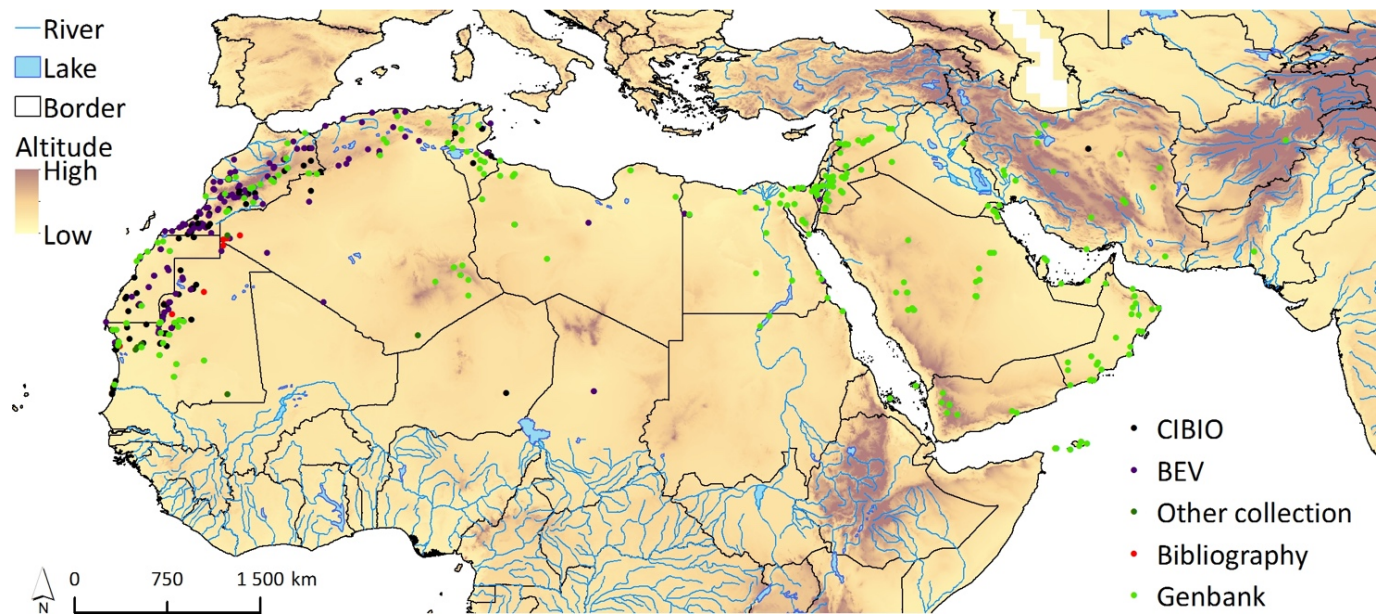


Fig S1. Sampling localities and sources of the *Mesalina* specimens used in this study.

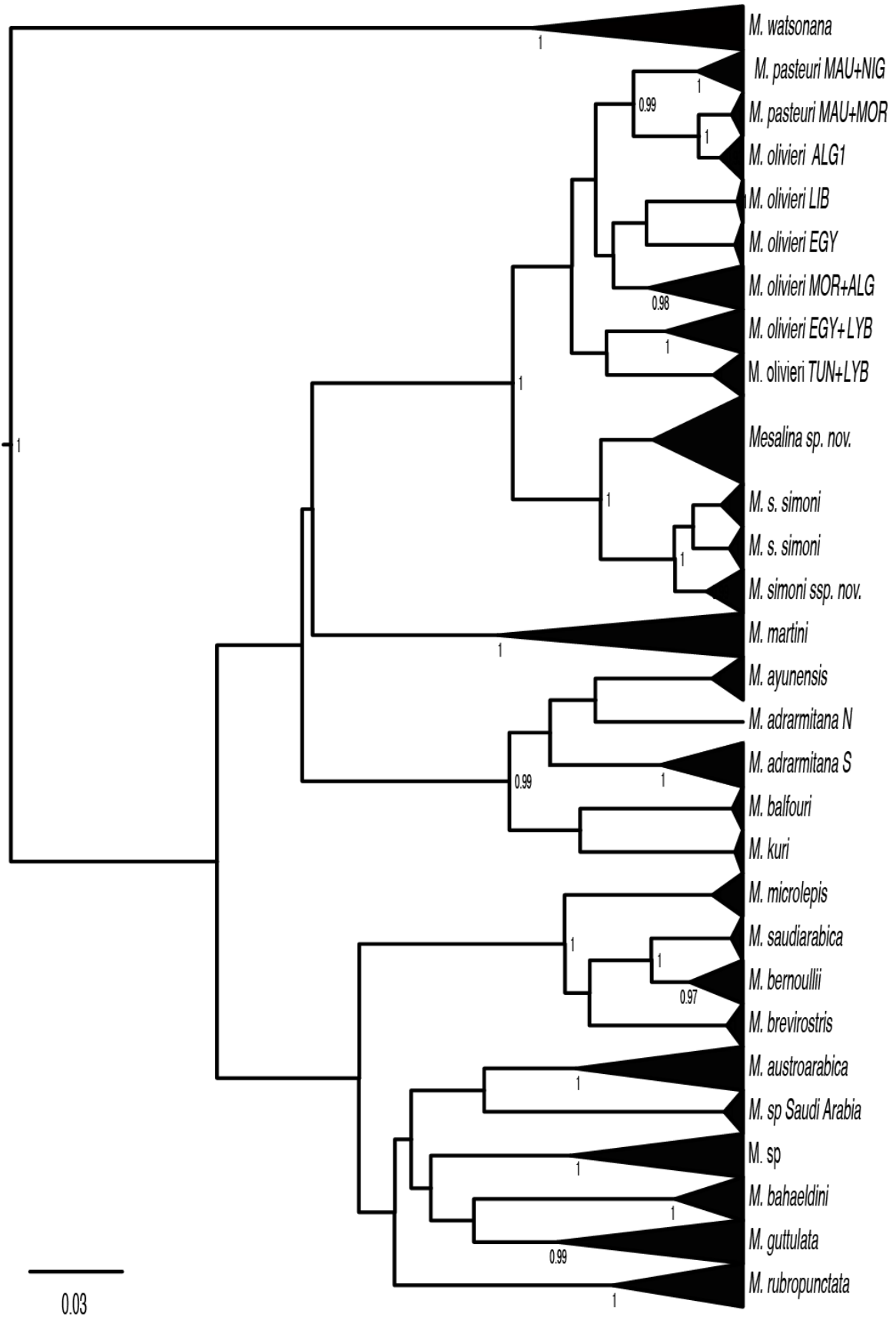


Fig S2. Results of the BI analysis of mtDNA dataset 1. Only posterior probabilities ≥ 0.95 are shown in the branches. Sample codes correspond to those in Table S1.

Phylogeography and systematics of the *Mesalina olivieri* species complex (*Squamata: Lacertidae*) from North-West Africa

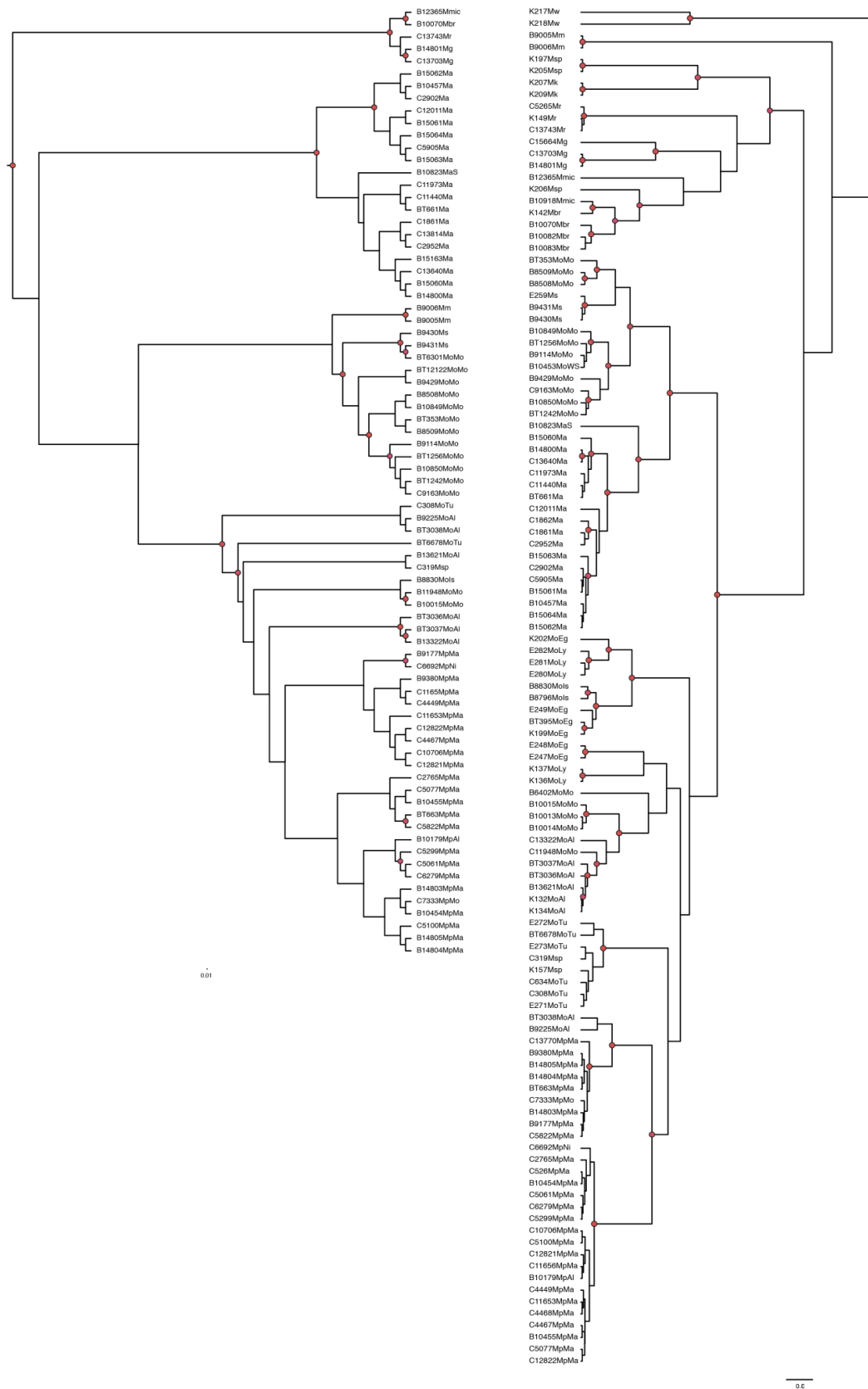


Fig S3. Mirrored results of the BI analysis of multilocus nuclear dataset 0 (left) and mitochondrial dataset 2 (right). Only posterior probabilities ≥ 0.95 are shown in the branches. Sample codes correspond to those in Table S1.

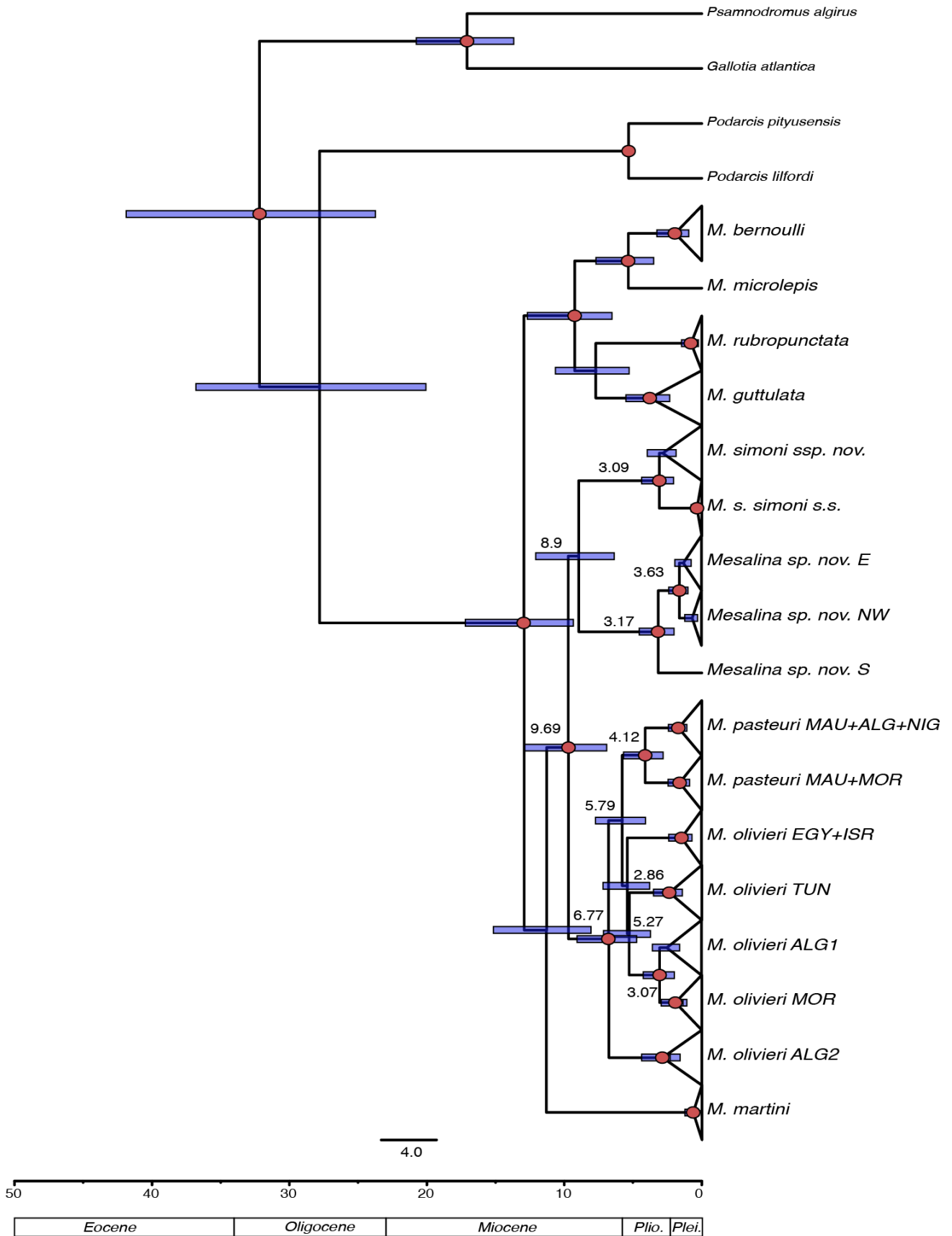


Fig S4. Calibrated phylogenetic tree obtained from cytonuclear Dataset 3. Support values represent posterior probability values from BEAST (PP<95% not showed). Blue horizontal bars represent the 95% confidence intervals for age estimate.

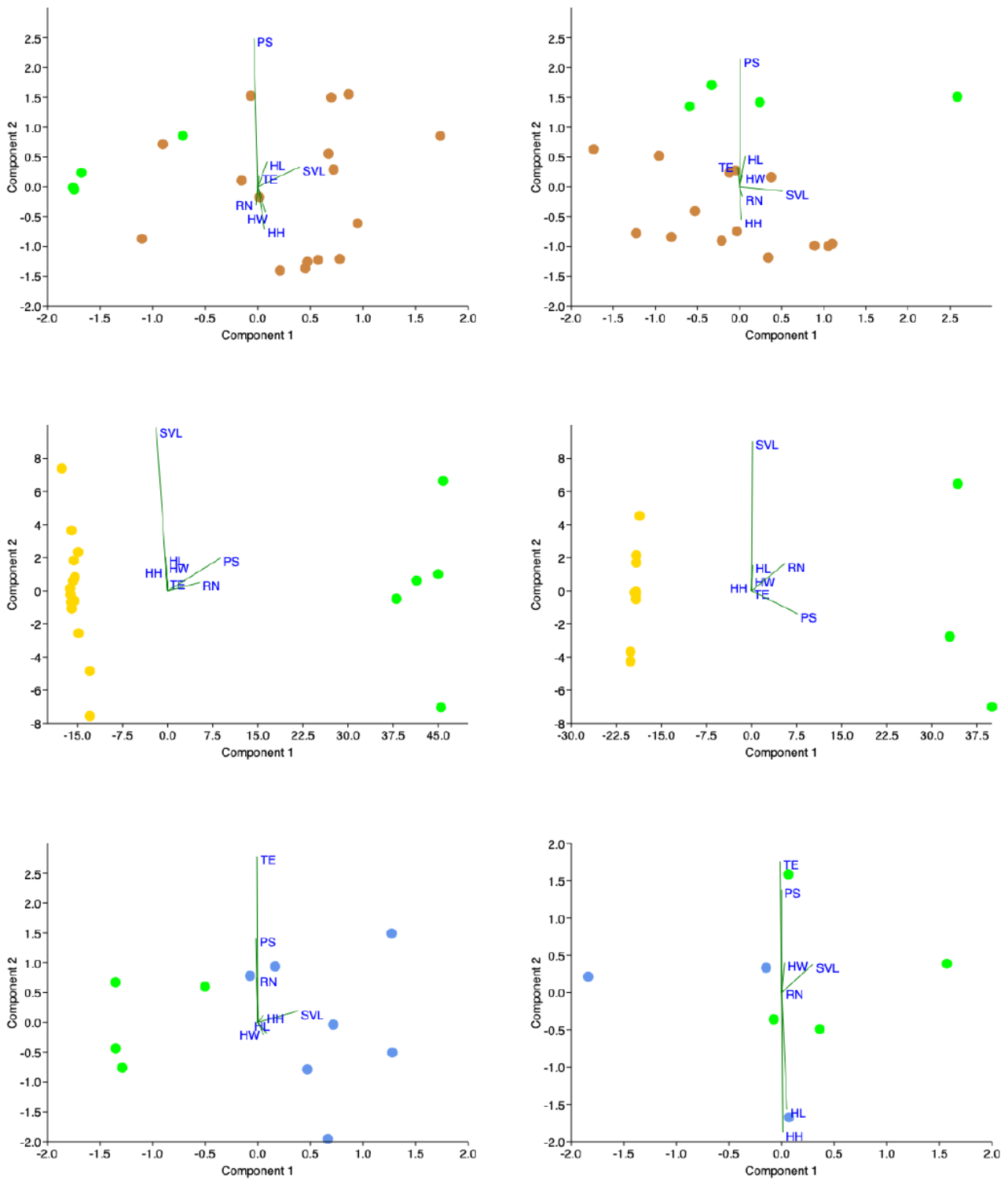


Fig. S5. Principal Component Analysis (PCA) of the morphological variables selected from the heating map analysis from male (above) and female (below) individuals of *Mesalina olivieri* species complex. The main morphological variables are superimposed to the graphs. Colours are the same previously used in Fig 2.1, and represent *M. olivieri* from Mauritania (green), *M. pasteuri* (blue), *M. simoni* (yellow), and *M. olivieri* (brown).

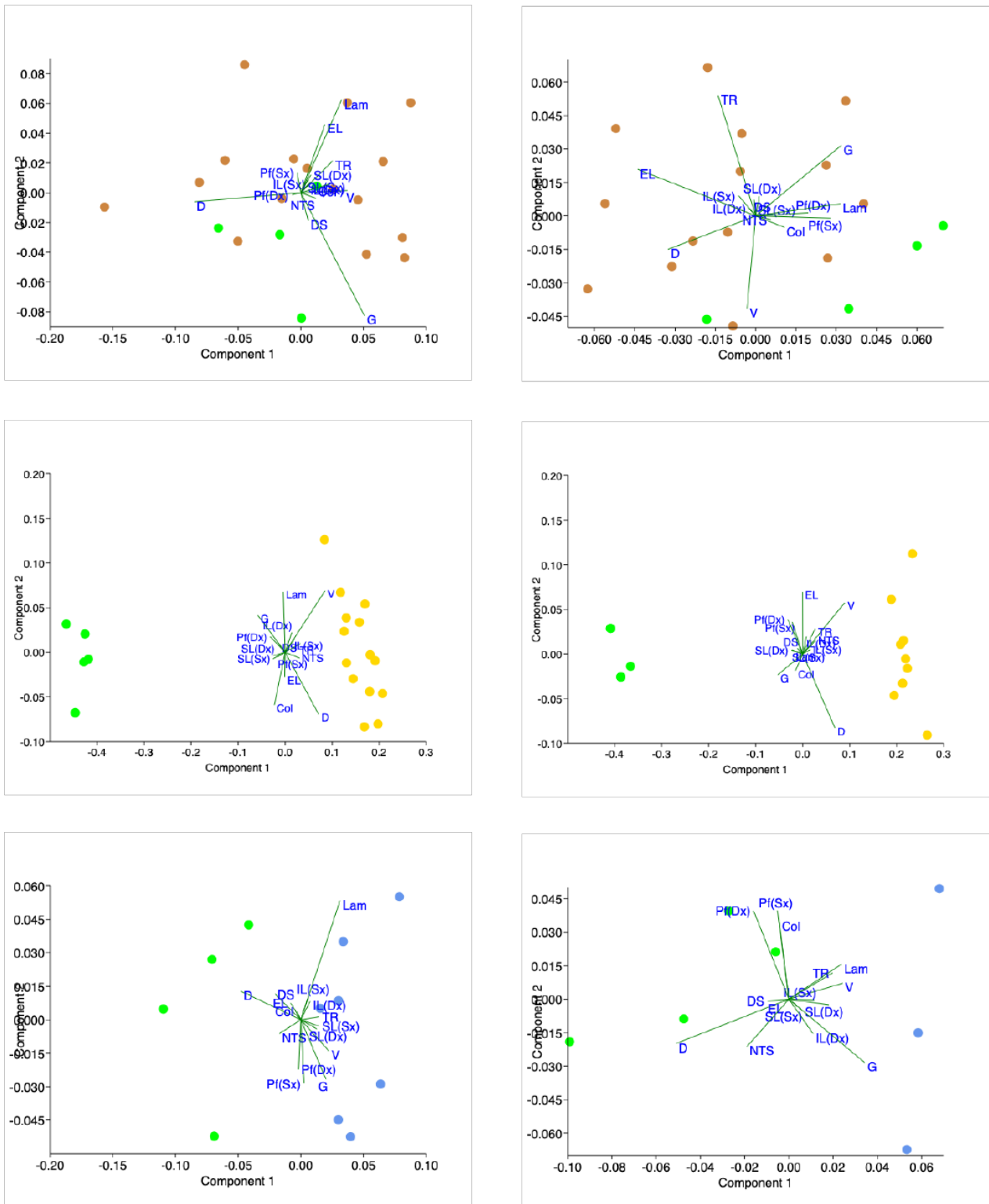


Fig. S6. Principal Component Analysis (PCA) of the pholidosis variables selected from the heating map analysis from male (above) and female (below) individuals of *Mesalina olivieri* species complex. The main morphological variables are superimposed to the graphs. Colours are the same previously used in Fig 2.1, and represent *M. olivieri* from Mauritania (green), *M. pasteuri* (blue), *M. simoni* (yellow), and *M. olivieri* (brown).

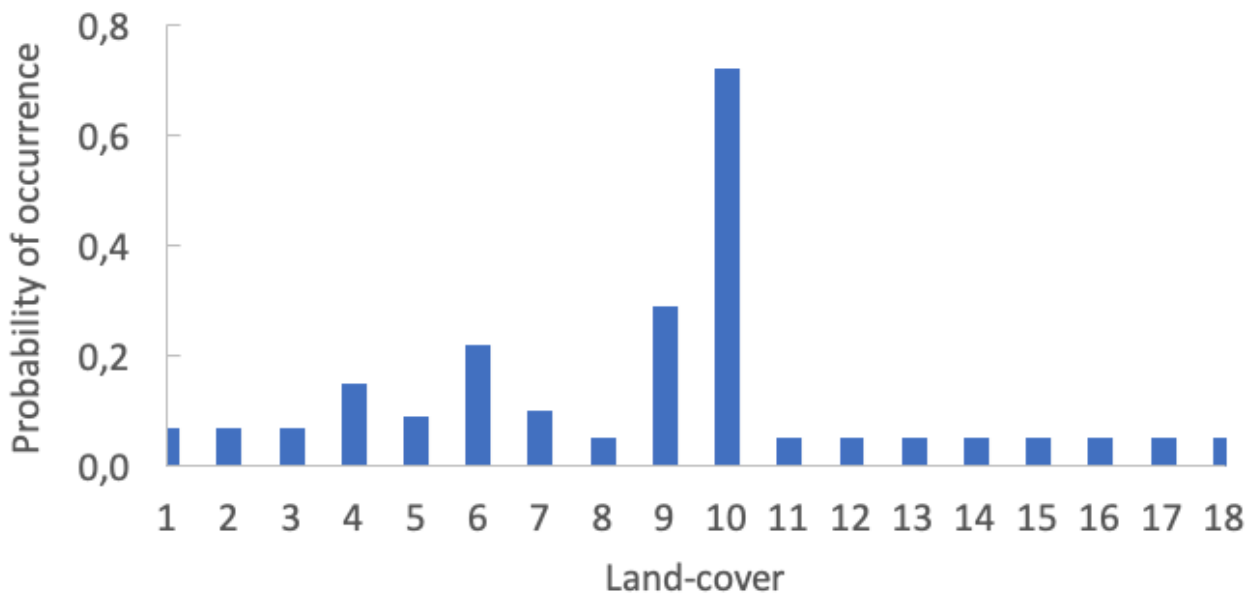
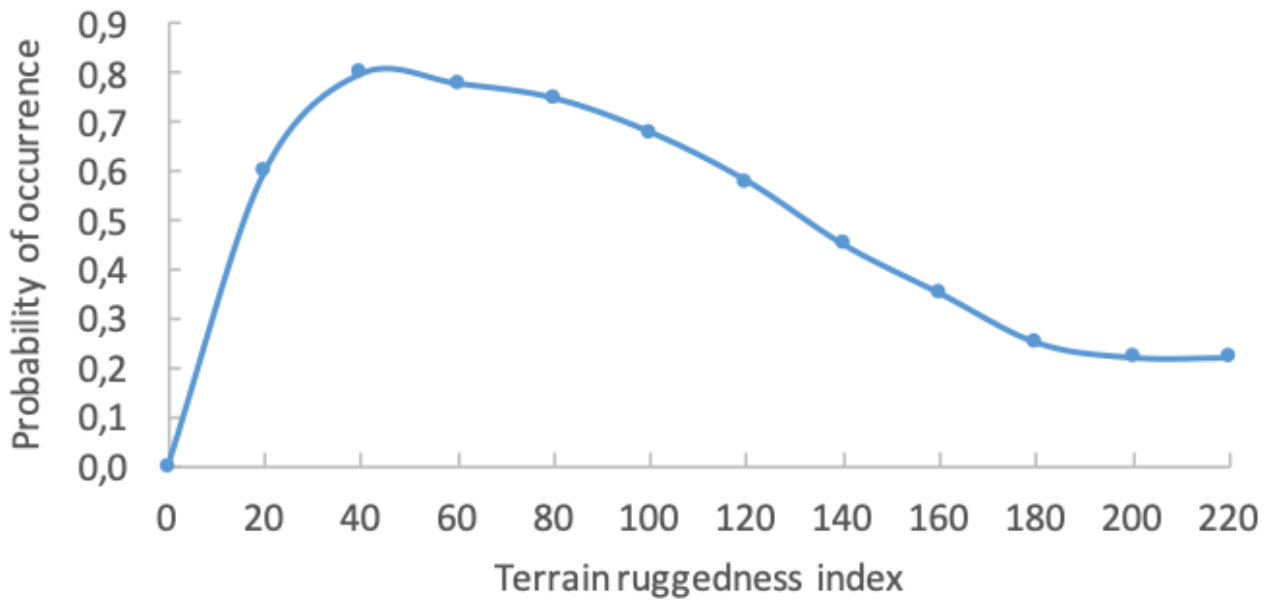


Fig S8. Response curves for the most important environmental predictors related to the distribution of *Mesalina* sp. nov. .

Table S1. Data on the gene fragments used in this study, including their lengths and the primers used (with their orientation, sequences, references and PCR conditions).

Gene	Primers	Reference	Sequence 5'- 3'	PCR cycling
<i>MC1R</i>	MC1RF	Pinho et al. (2009)	GGCNGCCATYGTCAAGAACCGGAACC	95° (5 :00) ; [94° (0 :30) ; 58° (1 :30)- 72° (1 :00)] for 40 cycles ; 72° (7 :00)
	MC1RR		CTCCGRAAGGCRTAAATGATGGGGTCCAC	
<i>PgD7</i>	PgDP8R	Pinho et al. (2008)	GAG TCC AGC TCA GTC TTA TTC CAC	95° (5 :00) ; [94° (0 :30) ; 58° (1 :30)- 72° (1 :00)] for 40 cycles ; 72° (7 :00)
	PgDP7F		GAC ATG CAG CTG ATC TGT GAG GCC	
<i>OD</i>	ODIez R		CCACCAATATCAAGCAGGTAC	95° (5 :00) ; [94° (0 :30) ; 56 to 58° (1 :30)- 72° (1 :00)] for 40 to 42 cycles ; 72° (7 :00)
	ODIez F		GCTACACTAAAAACCAGCAG	
<i>Cyt b</i>	Mes_cytb_F	Kapli et al. (2015)	CGWAAACAACACCCVATCCT	95° (5 :00) ; [95° (0 :30) ; 50 to 53° (0:45)- 72° (1 :00)] for 45 cycles ; 60° (10 :00)
	Mes_cytb_R	Kapli et al. (2015)	GATATTTGTCCTCADGGHA	
<i>B-fib7</i>	BFXF	Sequeira et al. (2008)	CAGGGAGAGCTACTTTTGATTAGAC	95° (10 :00) ; [95° (0 :30) ; 52° (0:30)- 72° (1 :00)] for 38 cycles ; 60° (10 :00)
	BF8	Pinho et al. (2006)	CACCACCGTCTTCTTTGGAACACTG	

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Table S2. Information about the samples used for the genetic analyses including Genbank accession codes.

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
CN1 ^{abc}	<i>M. adramitana</i>	Oman	23.7861	57.7977	MK551691	--	--	MK551616	--
CN10639 ^{ab}	<i>M. adramitana</i>	Oman	22.365	59.7011	---	--	--	---	--
CN10649 ^b	<i>M. adramitana</i>	Oman	22.365	59.7011	---	--	--	MK551662	--
CN10674 ^{ab}	<i>M. adramitana</i>	Oman	22.3937	59.6855	---	--	--	MK551663	--
CN10693 ^b	<i>M. adramitana</i>	Oman	22.365	59.7011	---	--	--	MK551664	--
CN10712 ^{ab}	<i>M. adramitana</i>	Oman	22.365	59.7011	---	--	--	MK551665	--
CN2632 ^{ab}	<i>M. adramitana</i>	Oman	22.4405	57.822	---	--	--	MK551618	--
CN3819 ^b	<i>M. adramitana</i>	Oman	20.6824	58.5296	---	--	--	MK551619	--
CN4089 ^b	<i>M. adramitana</i>	Oman	22.3098	59.2202	---	--	--	MK551615	--
CN7493 ^b	<i>M. adramitana</i>	Oman	21.9253	57.719	---	--	--	MK551617	--
CN7835 ^b	<i>M. adramitana</i>	Oman	21.8839	58.2575	---	--	--	MK551614	--
OM04/2010-101 ^b	<i>M. adramitana</i>	Oman	23.2543	57.9315	---	--	--	MK551622	--
OM04/2010-98 ^b	<i>M. adramitana</i>	Oman	23.2543	57.9315	---	--	--	MK551621	--
S3219 ^{ab}	<i>M. adramitana</i>	Oman	22.7238	58.014	---	--	--	MK551620	--
SPM001457U ^b	<i>M. adramitana</i>	UAE	24.16	55.84	---	--	--	MK551623	--
577 ^b	<i>M. adramitana</i>	Saudi Arabia	22.2371	41.8428	---	--	--	---	--
CN7935 ^{abc}	<i>M. adramitana</i>	Oman	18.8911	54.8119	MK551683	--	--	MK551606	--
CN8005 ^{ab}	<i>M. adramitana</i>	Oman	18.2627	55.1938	MH040005	--	--	MH040050	--
CN8009 ^{ab}	<i>M. adramitana</i>	Oman	18.4416	55.2722	MK551684	--	--	MK551607	--
CN8021 ^{ab}	<i>M. adramitana</i>	Oman	17.8778	53.0862	MK551685	--	--	MK551608	--
CN8360 ^{ab}	<i>M. adramitana</i>	Oman	18.464	53.0678	MK551690	--	--	MK551613	--
NHMC80.3.142.2 ^a	<i>M. adramitana</i>	Saudi Arabia	22.2445	41.432	KM411197	--	--	---	--
NHMC80.3.142.3 ^a	<i>M. adramitana</i>	Saudi Arabia	22.2421	41.4478	KM411196	--	--	---	--
NHMC80.3.164.8 ^{ac}	<i>M. adramitana</i>	Saudi Arabia	22.2525	41.8796	KM411205	--	--	---	--
S2807 ^{ab}	<i>M. adramitana</i>	Oman	19.5626	57.6233	KY967144	--	--	KY967099	--
S7640 ^{ab}	<i>M. adramitana</i>	Oman	20.7264	58.2622	MK551686	--	--	MK551609	--
S7642 ^{ab}	<i>M. adramitana</i>	Oman	19.0311	57.5285	MK551687	--	--	MK551610	--
S7916 ^b	<i>M. adramitana</i>	Oman	20.2584	56.581	MK551688	--	--	MK551611	--
S7976 ^{ab}	<i>M. adramitana</i>	Oman	19.0311	57.5285	MK551689	--	--	MK551612	--
BEV.10457	<i>Mesalina</i> sp. nov.	Mauritania	21.015000	-11.718000	Pending	Pending	Pending	Pending	Pending
BEV.10823	<i>Mesalina</i> sp. nov.	Mauritania	17.398228	-12.030510	Pending	Pending	Pending	Pending	Pending
BEV.14800	<i>Mesalina</i> sp. nov.	Mauritania	22.608563	-12.556853	Pending	Pending	Pending	Pending	Pending
BEV.15060	<i>Mesalina</i> sp. nov.	Mauritania	20.553695	-12.691632	Pending	Pending	Pending	Pending	Pending
BEV.15061	<i>Mesalina</i> sp. nov.	Mauritania	21.159582	-11.936230	Pending	Pending	Pending	Pending	Pending
BEV.15062	<i>Mesalina</i> sp. nov.	Mauritania	21.159582	-11.936230	Pending	Pending	Pending	Pending	Pending

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
BEV.15063	<i>Mesalina</i> sp. nov.	Mauritania	21.159582	-11.936230	Pending	Pending	Pending	Pending	Pending
BEV.15064	<i>Mesalina</i> sp. nov.	Mauritania	21.159582	-11.936230	Pending	Pending	Pending	Pending	Pending
BEV.15163	<i>Mesalina</i> sp. nov.	Mauritania	20.553695	-12.691632	Pending	Pending	Pending	Pending	Pending
BEV.T661	<i>Mesalina</i> sp. nov.	Mauritania	20.748540	-13.127550	Pending	Pending	Pending	Pending	Pending
CIBIO11973	<i>Mesalina</i> sp. nov.	Mauritania	19.826485	-14.255477	Pending	Pending	Pending	Pending	Pending
CIBIO11440	<i>Mesalina</i> sp. nov.	Morocco	22.155680	-15.346780	Pending	Pending	Pending	Pending	Pending
CIBIO1861	<i>Mesalina</i> sp. nov.	Mauritania	19.797180	-12.998011	Pending	Pending	Pending	Pending	Pending
CIBIO12011	<i>Mesalina</i> sp. nov.	Mauritania	21.159582	-11.936230	Pending	Pending	Pending	Pending	Pending
CIBIO12018	<i>Mesalina</i> sp. nov.	Mauritania	21.150235	-11.962342	Pending	Pending	Pending	Pending	Pending
CIBIO13640	<i>Mesalina</i> sp. nov.	Mauritania	22.608563	-12.556853	Pending	Pending	Pending	Pending	Pending
CIBIO13814	<i>Mesalina</i> sp. nov.	Mauritania	19.628933	-12.534387	Pending	Pending	Pending	Pending	Pending
CIBIO1862	<i>Mesalina</i> sp. nov.	Mauritania	19.863228	-12.990913	Pending	Pending	Pending	Pending	Pending
CIBIO2902	<i>Mesalina</i> sp. nov.	Mauritania	21.428225	-11.313882	Pending	Pending	Pending	Pending	Pending
CIBIO2952	<i>Mesalina</i> sp. nov.	Mauritania	18.984935	-13.064730	Pending	Pending	Pending	Pending	Pending
CIBIO5865	<i>Mesalina</i> sp. nov.	Mauritania	20.553695	-12.691632	Pending	Pending	Pending	Pending	Pending
CIBIO5905	<i>Mesalina</i> sp. nov.	Mauritania	21.152082	-11.946980	Pending	Pending	Pending	Pending	Pending
JEM015 ^a	<i>M. arnoldi</i>	Yemen	15.36	44.47	MH040006	--	--	---	--
JEM4 ^{a,c}	<i>M. arnoldi</i>	Yemen	15.38	44.45	MH040007	--	--	MH040051	--
MCCI-R890 ^{a,c}	<i>M. arnoldi</i>	Yemen	15.51	43.88	MH040008	--	--	---	--
S3615 ^{a,c}	<i>M. arnoldi</i>	Yemen	14.78	44.28	MH040009	--	--	MH040052	--
S4049	<i>M. arnoldi</i>	Yemen	14.78	44.28	MH040010	--	--	MH040053	--
CN11196 ^a	<i>M. austroarabica</i>	Saudi Arabia	16.7543	41.9985	MK551727	--	--	MK551656	--
CN11197 ^a	<i>M. austroarabica</i>	Saudi Arabia	16.7543	41.9985	MK551728	--	--	MK551657	--
CN11198 ^a	<i>M. austroarabica</i>	Saudi Arabia	16.7543	41.9985	MK551729	--	--	MK551658	--
CN11199 ^{a,c}	<i>M. austroarabica</i>	Saudi Arabia	16.7543	41.9985	MK551730	--	--	MK551659	--
CN7392 ^a	<i>M. austroarabica</i>	Oman	17.1494	54.9757	MH040011	--	--	MH040054	--
CN7638	<i>M. austroarabica</i>	Oman	17.1597	54.8069	MH040012	--	--	MH040055	--
CN7641	<i>M. austroarabica</i>	Oman	17.1494	54.9757	MH040013	--	--	MH040056	--
JEM109 ^{a,c}	<i>M. austroarabica</i>	Yemen	14.9	49.03	MH040014	--	--	MH040057	--
JIR70 ^a	<i>M. austroarabica</i>	Oman	16.8014	53.2783	MH040015	--	--	MH040058	--
NHMC80.3.72.108 ^{a,c}	<i>M. austroarabica</i>	Yemen	16.2333	43.9667	KM411144	--	--	---	--
NHMC80.3.72.109 ^{a,c}	<i>M. austroarabica</i>	Yemen	14.65	45.05	KM411145	--	--	---	--
S2421	<i>M. austroarabica</i>	Oman	17.1139	54.7137	MH040016	--	--	MH040059	--
S2599 ^a	<i>M. austroarabica</i>	Oman	17.1139	54.7137	MH040017	--	--	MH040060	--
S2701	<i>M. austroarabica</i>	Oman	17.1139	54.7137	MH040018	--	--	MH040061	--
S2725 ^a	<i>M. austroarabica</i>	Oman	17.1139	54.7137	MH040019	--	--	MH040062	--
S2838 ^a	<i>M. austroarabica</i>	Oman	17.1139	54.7137	MH040020	--	--	MH040063	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
S7324 ^{a,c}	<i>M. austroarabica</i>	Oman	17.1214	54.714	MH040021	--	--	MH040064	--
JEM634 ^{a,b}	<i>M. ayunensis</i>	Yemen	14.78	49.37	MK551693	--	--	MK551625	--
JIR104 ^{a,b,c}	<i>M. ayunensis</i>	Oman	17.9335	55.5275	MK551692	--	--	MK551624	--
HUJR-19066 ^a	<i>M. bahaeldini</i>	Israel	31.254	35.163	MH040022	--	--	MH040065	--
HUJR-TAIL-26 ^a	<i>M. bahaeldini</i>	Israel	31.987	35.436	MH040023	--	--	---	--
HUJR-TAIL-27 ^a	<i>M. bahaeldini</i>	Israel	31.208	34.771	MH040024	--	--	MH040066	--
HUJR-TAIL-28 ^a	<i>M. bahaeldini</i>	Israel	31.204	34.793	MH040025	--	--	MH040067	--
HUJR-TAIL-29 ^a	<i>M. bahaeldini</i>	Israel	31.327	35.228	MH040026	--	--	MH040068	--
HUJR-TAIL-30	<i>M. bahaeldini</i>	Israel	31.327	35.228	MH040027	--	--	---	--
J66/04 ^a	<i>M. bahaeldini</i>	Jordan	30.7622	36.6803	MH040028	--	--	MH040069	--
NHMC80.3.108.1	<i>M. bahaeldini</i>	Egypt	28.5408	33.981	EF555285	--	--	---	--
NHMC80.3.108.2 ^a	<i>M. bahaeldini</i>	Egypt	28.5408	33.981	EF555286	--	--	---	--
NHMC80.3.108.3 ^a	<i>M. bahaeldini</i>	Egypt	28.5408	33.981	EF555287	--	--	---	--
NHMC80.3.108.4 ^a	<i>M. bahaeldini</i>	Egypt	28.5408	33.981	EF555288	--	--	---	--
NHMC80.3.108.5 ^a	<i>M. bahaeldini</i>	Egypt	28.7064	33.748	EF555283	--	--	---	--
NHMC80.3.72.10 ^a	<i>M. bahaeldini</i>	Jordan	31.2531	35.6135	EF555293	--	--	---	--
NHMC80.3.72.100 ^a	<i>M. bahaeldini</i>	Jordan	31.5615	35.7827	KM411182	--	--	---	--
NHMC80.3.72.11 ^a	<i>M. bahaeldini</i>	Jordan	31.2531	35.6135	EF555294	--	--	---	--
NHMC80.3.72.111 ^a	<i>M. bahaeldini</i>	Jordan	30.3289	35.4426	KM411201	--	--	---	--
NHMC80.3.72.13 ^a	<i>M. bahaeldini</i>	Jordan	30.7022	35.5841	EF555295	--	--	---	--
NHMC80.3.72.14 ^a	<i>M. bahaeldini</i>	Jordan	31.9116	36.6168	EF555317	--	--	---	--
NHMC80.3.72.15 ^a	<i>M. bahaeldini</i>	Jordan	31.9116	36.6168	EF555318	--	--	---	--
NHMC80.3.72.16 ^a	<i>M. bahaeldini</i>	Jordan	31.9116	36.6168	EF555319	--	--	---	--
NHMC80.3.72.17	<i>M. bahaeldini</i>	Jordan	31.9116	36.6168	EF555320	--	--	---	--
NHMC80.3.72.20 ^a	<i>M. bahaeldini</i>	Jordan	31.2531	35.6135	EF555292	--	--	---	--
NHMC80.3.72.22 ^a	<i>M. bahaeldini</i>	Egypt	29.9651	33.1606	EF555284	--	--	---	--
NHMC80.3.72.24 ^a	<i>M. bahaeldini</i>	Jordan	29.5704	35.4113	EF555321	--	--	---	--
NHMC80.3.72.47 ^a	<i>M. bahaeldini</i>	Jordan	31.2149	35.9653	KM411174	--	--	---	--
NHMC80.3.72.48 ^a	<i>M. bahaeldini</i>	Jordan	31.2149	35.9653	KM411175	--	--	---	--
NHMC80.3.72.49 ^a	<i>M. bahaeldini</i>	Jordan	31.5989	35.9934	KM411176	--	--	---	--
NHMC80.3.72.50 ^a	<i>M. bahaeldini</i>	Jordan	31.8773	35.6834	KM411177	--	--	---	--
NHMC80.3.72.88 ^a	<i>M. bahaeldini</i>	Israel	30.6242	34.8233	KM411100	--	--	---	--
NHMC80.3.72.93 ^a	<i>M. bahaeldini</i>	Israel	30.7077	34.7845	KM411093	--	--	---	--
NHMC80.3.72.94 ^a	<i>M. bahaeldini</i>	Israel	30.7077	34.7845	KM411094	--	--	---	--
NHMC80.3.72.95 ^a	<i>M. bahaeldini</i>	Israel	31.0648	34.8406	KM411095	--	--	---	--
NHMC80.3.72.96 ^a	<i>M. bahaeldini</i>	Israel	31.0648	34.8406	KM411096	--	--	---	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
NHMC80.3.72.98 ^a	<i>M. bahaeldini</i>	Jordan	29.6864	35.426	KM411180	--	--	---	--
NHMC80.3.72.99 ^a	<i>M. bahaeldini</i>	Jordan	29.647	35.434	KM411181	--	--	---	--
S10345 ^{a,c}	<i>M. bahaeldini</i>	Saudi Arabia	27.3243	41.43	MH040029	--	--	MH040070	--
S2496 ^{a,c}	<i>M. bahaeldini</i>	Egypt	28.5528	33.9492	MH040030	--	--	MH040071	--
S2835	<i>M. bahaeldini</i>	Egypt	28.7946	33.7321	MH040031	--	--	MH040072	--
S3746 ^a	<i>M. bahaeldini</i>	Jordan	30.168	35.673	MH040032	--	--	---	--
TAU.R16256 ^a	<i>M. bahaeldini</i>	Israel	31.19	34.805	KY967145	--	--	KY967100	--
TAU.R16263 ^a	<i>M. bahaeldini</i>	Israel	31.256	35.171	MH040033	--	--	MH040073	--
TAU.R16293 ^a	<i>M. bahaeldini</i>	Israel	30.863	34.442	MH040034	--	--	MH040074	--
TAU.R16294 ^{a,c}	<i>M. bahaeldini</i>	Israel	30.85	34.451	MH040035	--	--	MH040075	--
NHMC80.3.143.1 ^a	<i>M. balfouri</i>	Yemen	12.65	54.0333	KM411213	--	--	---	--
NHMC80.3.143.2 ^a	<i>M. balfouri</i>	Yemen	12.65	54.0333	KM411214	--	--	---	--
NHMC80.3.143.3 ^a	<i>M. balfouri</i>	Yemen	12.65	54.0333	KM411215	--	--	---	--
NHMC80.3.143.4 ^a	<i>M. balfouri</i>	Yemen	12.65	54.0333	KM411216	--	--	---	--
S2500 ^{a,b}	<i>M. balfouri</i>	Yemen	12.1224	53.2748	MH040036	--	--	MH040076	--
S5187 ^{a,b}	<i>M. balfouri</i>	Yemen	12.546	54.4974	MK551681	--	--	MK551604	--
S5292 ^{a,b}	<i>M. balfouri</i>	Yemen	12.1224	53.2748	MK551680	--	--	MK551603	--
S5650 ^{a,b,c}	<i>M. balfouri</i>	Yemen	12.3635	53.9329	KY967146	--	--	KY967101	--
I01 ^{a,c}	<i>M. bernoullii</i>	Iran	34.3893	45.4705	KY967154	--	--	KY967112	--
I02 ^a	<i>M. bernoullii</i>	Iran	34.3893	45.4705	KY967155	--	--	KY967113	--
IRA600 ^a	<i>M. bernoullii</i>	Iran	32.03333	48.5	KY967156	--	--	---	--
MB_Azraq ^a	<i>M. bernoullii</i>	Jordan	31.8333	36.8167	KY967157	--	--	---	--
MB_Azraq2 ^a	<i>M. bernoullii</i>	Jordan	31.8333	36.8167	KY967158	--	--	---	--
MB03 ^a	<i>M. bernoullii</i>	Jordan	31.8333	36.8167	KY967159	--	--	---	--
MB04 ^a	<i>M. bernoullii</i>	Jordan	30.9233	36.569	KY967159	--	--	---	--
MB05 ^a	<i>M. bernoullii</i>	Jordan	32.4582	38.0368	KY967160	--	--	---	--
MB07 ^a	<i>M. bernoullii</i>	Syria	34.628	38.5609	KY967162	--	--	---	--
MB08	<i>M. bernoullii</i>	Syria	34.628	38.5609	KY967161	--	--	---	--
MB09 ^a	<i>M. bernoullii</i>	Syria	32.7221	36.9376	KY967165	--	--	---	--
MB10	<i>M. bernoullii</i>	Syria	32.7221	36.9376	KY967166	--	--	---	--
MB11 ^a	<i>M. bernoullii</i>	Syria	34.3111	36.9072	KY967167	--	--	---	--
MB14 ^a	<i>M. bernoullii</i>	Syria	34.2667	37.0667	KY967163	--	--	---	--
MB15	<i>M. bernoullii</i>	Syria	34.2667	37.0667	KY967168	--	--	---	--
MB16 ^a	<i>M. bernoullii</i>	Jordan	31.9667	35.9667	KY967169	--	--	---	--
MB17 ^a	<i>M. bernoullii</i>	Jordan	31.9667	35.9667	KY967170	--	--	---	--
MB19 ^a	<i>M. bernoullii</i>	Iraq	33.0212	40.2769	---	--	--	---	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
MB21	<i>M. bernoullii</i>	Iraq	33.0212	40.2769	---	--	--	---	--
NHMC80.3.69.1 ^a	<i>M. bernoullii</i>	Syria	34.3619	38.174	EF555302	--	--	---	--
NHMC80.3.69.10 ^a	<i>M. bernoullii</i>	Syria	35.4268	40.0278	EF555307	--	--	---	--
NHMC80.3.69.11 ^a	<i>M. bernoullii</i>	Syria	35.4268	40.0278	EF555308	--	--	---	--
NHMC80.3.69.14 ^a	<i>M. bernoullii</i>	Saudi Arabia	26.4185	47.4792	KM411190	--	--	---	--
NHMC80.3.69.15 ^a	<i>M. bernoullii</i>	Saudi Arabia	26.4147	47.4773	KM411191	--	--	---	--
NHMC80.3.69.2 ^a	<i>M. bernoullii</i>	Syria	34.6	37.8315	EF555303	--	--	---	--
NHMC80.3.69.21 ^a	<i>M. bernoullii</i>	Kuwait	29.3678	47.8102	KM411234	--	--	---	--
NHMC80.3.69.22 ^a	<i>M. bernoullii</i>	Kuwait	29.0144	47.9773	KM411235	--	--	---	--
NHMC80.3.69.23 ^a	<i>M. bernoullii</i>	Kuwait	29.8433	48.1131	KM411236	--	--	---	--
NHMC80.3.69.24	<i>M. bernoullii</i>	Kuwait	29.3794	47.8422	KM411237	--	--	---	--
NHMC80.3.69.25 ^a	<i>M. bernoullii</i>	Kuwait	29.8236	47.2502	KM411183	--	--	---	--
NHMC80.3.69.3 ^a	<i>M. bernoullii</i>	Syria	34.6	37.8315	EF555304	--	--	---	--
NHMC80.3.69.30 ^a	<i>M. bernoullii</i>	Syria	33.6831	36.4953	KM411142	--	--	---	--
NHMC80.3.69.6 ^a	<i>M. bernoullii</i>	Syria	34.8142	38.7897	EF555305	--	--	---	--
S15 ^a	<i>M. bernoullii</i>	Syria	34.5247	38.2856	KY967172	--	--	KY967114	--
S4	<i>M. bernoullii</i>	Syria	34.3111	36.9072	KY967160	--	--	KY967115	--
S5 ^a	<i>M. bernoullii</i>	Syria	34.3111	36.9072	KY967173	--	--	KY967115	--
S7 ^a	<i>M. bernoullii</i>	Syria	34.3111	36.9072	KY967174	--	--	KY967111	--
S8 ^{a,c}	<i>M. bernoullii</i>	Syria	34.3111	36.9072	KY967175	--	--	KY967115	--
S9 ^a	<i>M. bernoullii</i>	Syria	34.3111	36.9072	KY967164	--	--	KY967110	--
Sherif10708 ^a	<i>M. bernoullii</i>	Egypt	27.7472	34.2287	KY967171	--	--	---	--
868 ^{a,c}	<i>M. breviostris</i>	Iran	26.6878	54.4221	---	--	--	---	--
Mb_UAE ^a	<i>M. breviostris</i>	UAE	24.3865	54.547	---	--	--	---	--
QAT1	<i>M. breviostris</i>	Qatar	26.0112	51.3901	---	--	--	---	--
QAT2 ^a	<i>M. breviostris</i>	Qatar	25.8234	51.5739	---	--	--	---	--
SPM001455U ^{a,c}	<i>M. breviostris</i>	UAE	24.1719	52.6109	KY967153	--	--	KY967109	--
SPM002959(97) ^a	<i>M. breviostris</i>	Bahrain			KY967152	--	--	KY967108	--
BEV.10070	<i>M. breviostris</i>	Kuwait	28.584400	18.167300	Pending	Pending	Pending	Pending	Pending
BEV.10082	<i>M. breviostris</i>	Kuwait	29.555900	47.741000	Pending	Pending	Pending	Pending	Pending
NHMC80.3.109.12 ^a	<i>M. cf. simoni</i>	Morocco	30.6811	-8.2834	KM411125	--	--	---	--
NHMC80.3.72.1 ^{a,c}	<i>M. guttulata</i>	Tunisia	33.5225	9.9925	EF555310	--	--	---	--
NHMC80.3.72.18 ^a	<i>M. guttulata</i>	Morocco	31.0882	-6.4673	EF555299	--	--	---	--
NHMC80.3.72.2 ^a	<i>M. guttulata</i>	Tunisia	33.5225	9.9925	EF555311	--	--	---	--
NHMC80.3.72.21 ^a	<i>M. guttulata</i>	Morocco	31.7146	-4.9221	EF555300	--	--	---	--
NHMC80.3.72.25 ^a	<i>M. guttulata</i>	Libya	32.1245	12.8076	KM411130	--	--	---	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
NHMC80.3.72.26 ^a	<i>M. guttulata</i>	Libya	32.1247	12.8068	KM411129	--	--	---	--
NHMC80.3.72.28 ^a	<i>M. guttulata</i>	Libya	31.9756	12.6724	KM411131	--	--	---	--
NHMC80.3.72.31 ^a	<i>M. guttulata</i>	Libya	32.0601	12.7227	KM411133	--	--	---	--
NHMC80.3.72.35 ^a	<i>M. guttulata</i>	Libya	32.1245	12.8076	KM411135	--	--	---	--
NHMC80.3.72.44 ^{a,c}	<i>M. guttulata</i>	Algeria	25.3483	8.3791	KM411165	--	--	---	--
NHMC80.3.72.45 ^a	<i>M. guttulata</i>	Algeria	34.4176	3.4798	KM411167	--	--	---	--
NHMC80.3.72.46 ^a	<i>M. guttulata</i>	Algeria	25.35	8.3911	KM411173	--	--	---	--
NHMC80.3.72.5 ^a	<i>M. guttulata</i>	Morocco	32.0472	-4.4088	EF555297	--	--	---	--
NHMC80.3.72.51 ^{a,c}	<i>M. guttulata</i>	Morocco	32.586	-3.7605	KM411178	--	--	---	--
NHMC80.3.72.53 ^a	<i>M. guttulata</i>	Morocco	29.3698	-8.1993	KM411210	--	--	---	--
NHMC80.3.72.54 ^a	<i>M. guttulata</i>	Morocco	30.3918	-6.8817	KM411211	--	--	---	--
NHMC80.3.72.55 ^a	<i>M. guttulata</i>	Morocco	29.4523	-8.0597	KM411212	--	--	---	--
NHMC80.3.72.57 ^a	<i>M. guttulata</i>	Libya	28.4433	12.78	KM411222	--	--	---	--
NHMC80.3.72.7 ^a	<i>M. guttulata</i>	Tunisia	33.1502	10.2899	EF555312	--	--	---	--
NHMC80.3.72.8 ^a	<i>M. guttulata</i>	Libya	30.4659	24.5366	EF555296	--	--	---	--
NHMC80.3.72.82 ^a	<i>M. guttulata</i>	Morocco	33.2894	-3.8437	KM411092	--	--	---	--
NHMC80.3.72.83 ^a	<i>M. guttulata</i>	Morocco	33.2894	-3.8437	KM411088	--	--	---	--
NHMC80.3.72.84 ^a	<i>M. guttulata</i>	Morocco	32.1193	-1.5799	KM411089	--	--	---	--
NHMC80.3.72.85 ^{a,c}	<i>M. guttulata</i>	Morocco	32.1193	-1.5799	KM411090	--	--	---	--
NHMC80.3.72.87 ^a	<i>M. guttulata</i>	Algeria	34.6805	3.2499	KM411099	--	--	---	--
NHMC80.3.72.89 ^a	<i>M. guttulata</i>	Algeria	24.4441	9.4138	KM411101	--	--	---	--
NHMC80.3.72.9 ^a	<i>M. guttulata</i>	Morocco	31.4018	-5.7276	EF555298	--	--	---	--
NHMC80.3.72.90 ^a	<i>M. guttulata</i>	Algeria	25.5012	8.9996	KM411102	--	--	---	--
NHMC80.3.72.91 ^a	<i>M. guttulata</i>	Algeria	23.313	9.4302	KM411103	--	--	---	--
NHMC80.3.72.92 ^a	<i>M. guttulata</i>	Egypt	23.1141	35.5882	KM411091	--	--	---	--
NHMC80.3.72.97 ^a	<i>M. guttulata</i>	Morocco	30.078	-6.2365	KM411097	--	--	---	--
S3612 ^{a,c}	<i>M. guttulata</i>	Libya	30.3132	10.4496	MH040037	--	--	MH040077	--
S3907 ^a	<i>M. guttulata</i>	Libya	30.3131	10.4495	MH040038	--	--	---	--
SPM001477U ^a	<i>M. guttulata</i>	Morocco			MH040039	--	--	MH040078	--
SPM002367(7) ^a	<i>M. guttulata</i>	Egypt	22.1831	36.6657	MH040040	--	--	MH040079	--
SPM002368(93) ^a	<i>M. guttulata</i>	Egypt	22.1831	36.6657	MH040041	--	--	MH040080	--
SPM002382(8) ^{a,c}	<i>M. guttulata</i>	Egypt	30.832	29.2037	MH040042	--	--	MH040081	--
SPM003430 ^{a,c}	<i>M. guttulata</i>	Morocco	27.14	-13.18	MH040043	--	--	MH040082	--
SUD12/2010-68 ^a	<i>M. guttulata</i>	Sudan	21.072	30.6938	MH040044	--	--	MH040083	--
BEV.14801	<i>M. guttulata</i>	Mauritania	24.462253	-11.351480	Pending	Pending	Pending	Pending	Pending
CIBIO15664	<i>M. guttulata</i>	Algeria	30.923680	-2.031399	Pending	Pending	Pending	Pending	Pending

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
CIBIO13703	<i>M. guttulata</i>	Mauritania	25.156463	-11.534827	Pending	Pending	Pending	Pending	Pending
NHMC80.3.165.1 ^a	<i>M. kuri</i>	Yemen	12.1867	52.1528	KM411207	--	--	---	--
NHMC80.3.165.2 ^a	<i>M. kuri</i>	Yemen	12.1867	52.1528	KM411208	--	--	---	--
NHMC80.3.165.3 ^a	<i>M. kuri</i>	Yemen	12.1867	52.1528	KM411209	--	--	---	--
S5169 ^{a b c}	<i>M. kuri</i>	Yemen	12.1996	52.2658	MK551682	--	--	MK551605	--
S5368 ^{a b}	<i>M. kuri</i>	Yemen	12.1996	52.2658	KY967147	--	--	KY967102	--
NHMC80.3.166.1 ^{a c}	<i>M. martini</i>	Egypt	24.9629	34.9357	KM411104	--	--	MK551653	--
NHMC80.3.166.2	<i>M. martini</i>	Egypt	24.4929	35.1594	KM411105	--	--	MH040084	--
NHMC80.3.166.3 ^{a c}	<i>M. martini</i>	Eritrea	15.8009	40.1271	KM411204	--	--	---	--
BEV.9005	<i>M. martini</i>	Egypt	24.361320	35.292090	Pending	Pending	Pending	Pending	Pending
BEV.9006	<i>M. martini</i>	Egypt	24.395590	35.237350	Pending	Pending	Pending	Pending	Pending
L32 ^{a c}	<i>M. microlepis</i>	Lebanon	34.3656	36.4026	KY967149	--	--	KY967105	--
L33 ^a	<i>M. microlepis</i>	Lebanon	34.3656	36.4026	KY967150	--	--	KY967106	--
L34	<i>M. microlepis</i>	Lebanon	34.3656	36.4026	KY967150	--	--	KY967107	--
MB12 ^a	<i>M. microlepis</i>	Syria	34.3111	36.9072	KY967151	--	--	---	--
MB13 ^a	<i>M. microlepis</i>	Syria	34.3111	36.9072	KY967151	--	--	---	--
NHMC80.3.69.12 ^a	<i>M. microlepis</i>	Syria	34.2931	36.7655	EF555309	--	--	---	--
NHMC80.3.69.9 ^a	<i>M. microlepis</i>	Syria	35.4174	40.3198	EF555306	--	--	---	--
BEV.10918	<i>M. microlepis</i>	Jordan	31.598900	35.993400	Pending	Pending	Pending	Pending	Pending
BEV.12365	<i>M. microlepis</i>	Lebanon	34.316359	36.413579	Pending	Pending	Pending	Pending	Pending
NHMC80.3.119.10 ^a	<i>M. olivieri</i>	Tunisia	32.1287	10.5638	EF555314	--	--	---	--
NHMC80.3.119.108	<i>M. olivieri</i>	Algeria	35.4151	4.519	KM411132	--	--	---	--
NHMC80.3.119.109 ^a	<i>M. olivieri</i>	Egypt	27.83	31.1068	KM411202	--	--	---	--
NHMC80.3.119.14 ^a	<i>M. olivieri</i>	Tunisia	33.7531	9.335	EF555315	--	--	---	--
NHMC80.3.119.16 ^{a c}	<i>M. olivieri</i>	Egypt	29.9651	33.1606	EF555289	--	--	---	--
NHMC80.3.119.19 ^{a c}	<i>M. olivieri</i>	Egypt	29.9651	33.1606	EF555290	--	--	---	--
NHMC80.3.119.2 ^a	<i>M. olivieri</i>	Libya	32.3912	21.2404	EF555322	--	--	---	--
NHMC80.3.119.20 ^{a c}	<i>M. olivieri</i>	Egypt	29.9797	32.1187	EF555291	--	--	---	--
NHMC80.3.119.21 ^{a c}	<i>M. olivieri</i>	Libya	32.1247	12.8068	KM411136	--	--	---	--
NHMC80.3.119.22 ^a	<i>M. olivieri</i>	Libya	32.1247	12.8068	KM411137	--	--	---	--
NHMC80.3.119.23 ^a	<i>M. olivieri</i>	Algeria	35.4151	4.519	KM411134	--	--	---	--
NHMC80.3.119.29 ^a	<i>M. olivieri</i>	Tunisia	35.6895	10.1501	KM411225	--	--	---	--
NHMC80.3.119.3 ^a	<i>M. olivieri</i>	Libya	32.3912	21.2404	EF555323	--	--	---	--
NHMC80.3.119.35 ^a	<i>M. olivieri</i>	Morocco	33.2894	-3.8437	KM411106	--	--	---	--
NHMC80.3.119.36 ^a	<i>M. olivieri</i>	Morocco	33.2894	-3.8437	KM411107	--	--	---	--
NHMC80.3.119.37 ^a	<i>M. olivieri</i>	Morocco	31.5739	-4.7417	KM411108	--	--	---	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
NHMC80.3.119.38 ^a	<i>M. olivieri</i>	Morocco	27.2369	-12.8208	KM411109	--	--	---	--
NHMC80.3.119.39 ^a	<i>M. olivieri</i>	Morocco	25.7847	-14.7328	KM411110	--	--	---	--
NHMC80.3.119.40 ^a	<i>M. olivieri</i>	Egypt	30.5965	32.2715	KM411199	--	--	---	--
NHMC80.3.119.41 ^a	<i>M. olivieri</i>	Morocco	22.5709	-14.3544	KM411164	--	--	---	--
NHMC80.3.119.42 ^a	<i>M. olivieri</i>	Morocco	26.5298	-12.3364	KM411166	--	--	---	--
NHMC80.3.119.43 ^{a,c}	<i>M. olivieri</i>	Morocco	26.4925	-13.9198	KM411170	--	--	---	--
NHMC80.3.119.44 ^a	<i>M. olivieri</i>	Algeria	36.3333	4.25	KM411163	--	--	---	--
NHMC80.3.119.46 ^a	<i>M. olivieri</i>	Algeria	36.3413	4.2509	KM411168	--	--	---	--
NHMC80.3.119.5 ^a	<i>M. olivieri</i>	Libya	32.3912	21.2404	EF555324	--	--	---	--
NHMC80.3.119.50 ^a	<i>M. olivieri</i>	Morocco	33.2894	-3.8437	KM411172	--	--	---	--
NHMC80.3.119.51 ^a	<i>M. olivieri</i>	Morocco	26.1256	-14.4799	KM411227	--	--	---	--
NHMC80.3.119.80 ^{a,c}	<i>M. olivieri</i>	Morocco	31.1755	-6.2374	KM411112	--	--	---	--
NHMC80.3.119.81 ^{a,c}	<i>M. olivieri</i>	Morocco	32.19	-2.2037	KM411113	--	--	---	--
NHMC80.3.119.82 ^a	<i>M. olivieri</i>	Morocco	32.175	-2.1667	KM411114	--	--	---	--
NHMC80.3.119.85 ^{a,c}	<i>M. olivieri</i>	Egypt	31.1319	33.8032	KM411117	--	--	---	--
NHMC80.3.119.87 ^a	<i>M. olivieri</i>	Israel	30.7077	34.7845	KM411115	--	--	---	--
NHMC80.3.119.9 ^a	<i>M. olivieri</i>	Tunisia	34.4076	7.9448	EF555313	--	--	---	--
NHMC80.3.119.91 ^a	<i>M. olivieri</i>	Israel	31.0858	34.631	KM411116	--	--	---	--
NHMC80.3.119.92 ^a	<i>M. olivieri</i>	Tunisia	35.5667	8.4667	KM411228	--	--	---	--
NHMC80.3.119.93 ^a	<i>M. olivieri</i>	Tunisia	34.0009	8.2847	KM411229	--	--	---	--
NHMC80.3.164.19 ^a	<i>M. olivieri</i>	Libya	33.0956	11.7626	KM411157	--	--	---	--
NHMC80.3.164.2 ^a	<i>M. olivieri</i>	Tunisia	32.9974	10.608	KM411233	--	--	---	--
S2596 ^a	<i>M. olivieri</i>	Tunisia	32.5349	10.2712	MK551715	--	--	MK551644	--
S2808 ^a	<i>M. olivieri</i>	Egypt	31.1111	33.4399	MK551708	--	--	MK551639	--
S3322 ^{a,c}	<i>M. olivieri</i>	Morocco	35.0983	-2.4593	MK551716	--	--	MK551645	--
S3344 ^a	<i>M. olivieri</i>	Libya	32.0055	11.727	MK551723	--	--	---	--
S3608 ^{a,c}	<i>M. olivieri</i>	Egypt	31.0698	33.4523	MK551712	--	--	---	--
S3748 ^a	<i>M. olivieri</i>	Tunisia	35.409	8.9508	MK551714	--	--	MK551643	--
S3765 ^a	<i>M. olivieri</i>	Egypt	31.1111	33.4399	MK551707	--	--	---	--
S3928 ^{a,c}	<i>M. olivieri</i>	Egypt	31.0698	33.4523	MK551709	--	--	---	--
S5404	<i>M. olivieri</i>	Egypt	31.07	33.45	MH040045	--	--	MH040085	--
S5407	<i>M. olivieri</i>	Egypt	31.11	33.44	MK551733	--	--	MK551661	--
SPM002917 ^{a,c}	<i>M. olivieri</i>	Egypt			MK551705	--	--	MK551637	--
SPM002920	<i>M. olivieri</i>	Egypt			MK551704	--	--	MK551636	--
SPM002954(28) ^{a,c}	<i>M. olivieri</i>	Egypt	30.832	29.2037	MK551711	--	--	MK551641	--
SPM002981(55) ^{a,c}	<i>M. olivieri</i>	Egypt	31.0512	32.8878	MK551706	--	--	MK551638	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
SPM003875 ^a	<i>M. olivieri</i>	Morocco	34.3589	-3.7495	MK551717	--	--	MK551646	--
T31-34_Mesaoliv1 ^{a,c}	<i>M. olivieri</i>	Tunisia	34.5854	8.9445	MK551713	--	--	MK551642	--
TAU.R16257 ^{a,c}	<i>M. olivieri</i>	Israel	31.124	34.809	MK551710	--	--	MK551640	--
BEV.10013	<i>M. olivieri</i>	Morocco	33.186000	-3.990000	Pending	Pending	Pending	Pending	Pending
BEV.10014	<i>M. olivieri</i>	Morocco	33.186000	-3.990000	Pending	Pending	Pending	Pending	Pending
BEV.10015	<i>M. olivieri</i>	Morocco	33.186000	-3.990000	Pending	Pending	Pending	Pending	Pending
BEV.10849	<i>M. olivieri</i>	Morocco	26.529800	-12.336400	Pending	Pending	Pending	Pending	Pending
BEV.10850	<i>M. olivieri</i>	Morocco	22.570900	-14.354400	Pending	Pending	Pending	Pending	Pending
BEV.11948	<i>M. olivieri</i>	Morocco	32.9297	-5.0465	Pending	Pending	Pending	Pending	Pending
BEV.13322	<i>M. olivieri</i>	Algeria	36.6245	4.8517	Pending	Pending	Pending	Pending	Pending
BEV.13621	<i>M. olivieri</i>	Algeria	35.88019	1.68412526	Pending	Pending	Pending	Pending	Pending
BEV.5925	<i>M. olivieri</i>	Morocco	28.350000	-9.840000	Pending	Pending	Pending	Pending	Pending
BEV.6402	<i>M. olivieri</i>	Morocco	31.194000	-6.210000	Pending	Pending	Pending	Pending	Pending
BEV.8508	<i>M. olivieri</i>	Morocco	32.190030	-2.203730	Pending	Pending	Pending	Pending	Pending
BEV.8509	<i>M. olivieri</i>	Morocco	32.175000	-2.165000	Pending	Pending	Pending	Pending	Pending
BEV.8830	<i>M. olivieri</i>	Israel	31.085800	34.631000	Pending	Pending	Pending	Pending	Pending
BEV.9114	<i>M. olivieri</i>	Morocco	26.492500	-13.919800	Pending	Pending	Pending	Pending	Pending
BEV.9225	<i>M. olivieri</i>	Algeria	33.591400	2.950800	Pending	Pending	Pending	Pending	Pending
BEV.9429	<i>M. olivieri</i>	Morocco	30.707600	-8.357700	Pending	Pending	Pending	Pending	Pending
BEV.T12122	<i>M. olivieri</i>	Morocco	28.487590	-11.336590	Pending	Pending	Pending	Pending	Pending
BEV.T1242	<i>M. olivieri</i>	Morocco	21.396300	-16.957900	Pending	Pending	Pending	Pending	Pending
BEV.T1256	<i>M. olivieri</i>	Morocco	26.492500	-13.919800	Pending	Pending	Pending	Pending	Pending
BEV.T3036	<i>M. olivieri</i>	Algeria	36.341300	4.250883	Pending	Pending	Pending	Pending	Pending
BEV.T3037	<i>M. olivieri</i>	Algeria	36.341300	4.250883	Pending	Pending	Pending	Pending	Pending
BEV.T3038	<i>M. olivieri</i>	Algeria	35.858500	6.490833	Pending	Pending	Pending	Pending	Pending
BEV.T353	<i>M. olivieri</i>	Morocco	31.574000	-4.738000	Pending	Pending	Pending	Pending	Pending
BEV.T395	<i>M. olivieri</i>	Egypt	31.120000	33.760000	Pending	Pending	Pending	Pending	Pending
BEV.T6678	<i>M. olivieri</i>	Tunisia	35.800637	11.036123	Pending	Pending	Pending	Pending	Pending
CIBIO308	<i>M. olivieri</i>	Tunisia	35.582150	8.482633	Pending	Pending	Pending	Pending	Pending
CIBIO9163	<i>M. olivieri</i>	Morocco	22.621538	-14.604377	Pending	Pending	Pending	Pending	Pending
NHMC80.3.147.10 ^a	<i>M. pasteuri</i>	Mauritania	20.7972	-16.2221	KM411162	--	--	---	--
NHMC80.3.147.11 ^a	<i>M. pasteuri</i>	Algeria	24.7839	8.8719	KM411171	--	--	---	--
NHMC80.3.147.12 ^a	<i>M. pasteuri</i>	Mauritania	21.2777	-15.4703	KM411230	--	--	---	--
NHMC80.3.147.13 ^a	<i>M. pasteuri</i>	Mauritania	21.2777	-15.4703	KM411231	--	--	---	--
NHMC80.3.147.14 ^a	<i>M. pasteuri</i>	Mauritania	21.2777	-15.4703	KM411232	--	--	---	--
NHMC80.3.147.17 ^a	<i>M. pasteuri</i>	Mauritania	21.3321	-11.9512	KM411118	--	--	---	--
NHMC80.3.147.18 ^a	<i>M. pasteuri</i>	Mauritania	20.4606	-12.362	KM411119	--	--	---	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
NHMC80.3.147.19 ^a	<i>M. pasteuri</i>	Mauritania	20.4641	-12.379	KM411120	--	--	---	--
NHMC80.3.147.2 ^a	<i>M. pasteuri</i>	Mauritania	20.8061	-16.4561	KM411226	--	--	---	--
NHMC80.3.147.20	<i>M. pasteuri</i>	Mauritania	20.4641	-12.379	KM411121	--	--	---	--
NHMC80.3.147.3 ^{a,c}	<i>M. pasteuri</i>	Mauritania	17.3982	-12.0305	KM411138	--	--	---	--
NHMC80.3.147.4 ^a	<i>M. pasteuri</i>	Mauritania	18.9849	-13.0647	KM411139	--	--	---	--
NHMC80.3.147.6 ^a	<i>M. pasteuri</i>	Mauritania	16.8484	-16.3503	KM411158	--	--	---	--
NHMC80.3.147.7 ^a	<i>M. pasteuri</i>	Mauritania	19.6851	-16.0641	KM411159	--	--	---	--
NHMC80.3.147.8 ^a	<i>M. pasteuri</i>	Mauritania	19.7795	-16.039	KM411160	--	--	---	--
NHMC80.3.147.9 ^a	<i>M. pasteuri</i>	Mauritania	19.9197	-16.028	KM411161	--	--	---	--
NHMC80.3.164.17 ^a	<i>M. pasteuri</i>	Mauritania	21.015	-11.718	KM411140	--	--	---	--
NHMC80.3.164.18 ^a	<i>M. pasteuri</i>	Mauritania	21.4282	-11.3139	KM411141	--	--	---	--
NHMC80.3.164.20 ^{a,c}	<i>M. pasteuri</i>	Mauritania	20.5936	-12.9883	KM411098	--	--	---	--
NHMC80.3.164.21 ^a	<i>M. pasteuri</i>	Mauritania	19.8652	-12.8055	KM411223	--	--	---	--
NHMC80.3.164.22 ^a	<i>M. pasteuri</i>	Mauritania	19.8652	-12.8055	KM411224	--	--	---	--
RIM113 ^a	<i>M. pasteuri</i>	Mauritania	21.3776	-12.9764	MK551722	--	--	MK551651	--
RIM171 ^a	<i>M. pasteuri</i>	Mauritania	18.5748	-9.8064	MK551720	--	--	MK551649	--
RIM201 ^{a,c}	<i>M. pasteuri</i>	Mauritania	18.3334	-11.8334	MK551718	--	--	MK551647	--
RIM202 ^a	<i>M. pasteuri</i>	Mauritania	18.3334	-11.8334	MK551719	--	--	MK551648	--
SPM002372(98) ^{a,c}	<i>M. pasteuri</i>	Egypt	29.19	25.51	MK551721	--	--	MK551650	--
NHMC80.3.119.47 ^a	<i>M. pasteuri</i>	Algeria	35.8585	6.4908	KM411169	--	--	---	--
NHMC80.3.119.52 ^a	<i>M. pasteuri</i>	Algeria	33.4992	3.0106	KM411111	--	--	---	--
BEV.10179	<i>M. pasteuri</i>	Algeria	24.783900	8.871900	Pending	Pending	Pending	Pending	Pending
BEV.10454	<i>M. pasteuri</i>	Mauritania	21.277733	-15.470317	Pending	Pending	Pending	Pending	Pending
BEV.10455	<i>M. pasteuri</i>	Mauritania	21.277733	-15.470317	Pending	Pending	Pending	Pending	Pending
BEV.14803	<i>M. pasteuri</i>	Mauritania	21.486580	-11.413930	Pending	Pending	Pending	Pending	Pending
BEV.14804	<i>M. pasteuri</i>	Mauritania	21.296970	-11.919850	Pending	Pending	Pending	Pending	Pending
BEV.14805	<i>M. pasteuri</i>	Mauritania	21.296970	-11.919850	Pending	Pending	Pending	Pending	Pending
BEV.5926	<i>M. pasteuri</i>	Algeria	30.130000	-2.170000	Pending	Pending	Pending	Pending	Pending
BEV.5927	<i>M. pasteuri</i>	Morocco	29.970000	-5.520000	Pending	Pending	Pending	Pending	Pending
BEV.5928	<i>M. pasteuri</i>	Algeria	22.800000	-1.100000	Pending	Pending	Pending	Pending	Pending
BEV.9177	<i>M. pasteuri</i>	Mauritania	21.332140	-11.951210	Pending	Pending	Pending	Pending	Pending
BEV.9380	<i>M. pasteuri</i>	Mauritania	20.460000	-12.356000	Pending	Pending	Pending	Pending	Pending
BEV.T662	<i>M. pasteuri</i>	Mauritania	20.456280	-12.360220	Pending	Pending	Pending	Pending	Pending
BEV.T663	<i>M. pasteuri</i>	Mauritania	20.464100	-12.379000	Pending	Pending	Pending	Pending	Pending
CIBIO10706	<i>M. pasteuri</i>	Mauritania	16.205077	-16.503377	Pending	Pending	Pending	Pending	Pending
CIBIO11653	<i>M. pasteuri</i>	Mauritania	16.607197	-16.441810	Pending	Pending	Pending	Pending	Pending
CIBIO11656	<i>M. pasteuri</i>	Mauritania	16.655410	-16.424157	Pending	Pending	Pending	Pending	Pending

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
CIBIO12821	<i>M. pasteuri</i>	Mauritania	16.130688	-16.511242	Pending	Pending	Pending	Pending	Pending
CIBIO12822	<i>M. pasteuri</i>	Mauritania	16.130688	-16.511242	Pending	Pending	Pending	Pending	Pending
CIBIO13770	<i>M. pasteuri</i>	Mauritania	23.369895	-11.669612	Pending	Pending	Pending	Pending	Pending
CIBIO2765	<i>M. pasteuri</i>	Mauritania	20.806070	-16.456107	Pending	Pending	Pending	Pending	Pending
CIBIO4449	<i>M. pasteuri</i>	Mauritania	17.067378	-16.255501	Pending	Pending	Pending	Pending	Pending
CIBIO4467	<i>M. pasteuri</i>	Mauritania	16.848397	-16.350311	Pending	Pending	Pending	Pending	Pending
CIBIO4468	<i>M. pasteuri</i>	Mauritania	16.848397	-16.350311	Pending	Pending	Pending	Pending	Pending
CIBIO5061	<i>M. pasteuri</i>	Mauritania	19.685135	-16.064098	Pending	Pending	Pending	Pending	Pending
CIBIO5077	<i>M. pasteuri</i>	Mauritania	19.779490	-16.038992	Pending	Pending	Pending	Pending	Pending
CIBIO5100	<i>M. pasteuri</i>	Mauritania	19.919693	-16.028018	Pending	Pending	Pending	Pending	Pending
CIBIO5299	<i>M. pasteuri</i>	Mauritania	20.797217	-16.222065	Pending	Pending	Pending	Pending	Pending
CIBIO5822	<i>M. pasteuri</i>	Mauritania	22.835012	-12.329155	Pending	Pending	Pending	Pending	Pending
CIBIO5849	<i>M. pasteuri</i>	Mauritania	21.832925	-12.810607	Pending	Pending	Pending	Pending	Pending
CIBIO6279	<i>M. pasteuri</i>	Mauritania	19.351447	-16.200417	Pending	Pending	Pending	Pending	Pending
CIBIO6692	<i>M. pasteuri</i>	Niger	16.217758	12.198542	Pending	Pending	Pending	Pending	Pending
CIBIO7333	<i>M. pasteuri</i>	Morocco	23.218518	-15.446822	Pending	Pending	Pending	Pending	Pending
NHMC80.3.99.1 ^a	<i>M. rubropunctata</i>	Egypt	24.4	33.017	EF555316	--	--	---	--
NHMC80.3.99.13 ^a	<i>M. rubropunctata</i>	Egypt	24.9294	30.3897	KM411122	--	--	---	--
NHMC80.3.99.17 ^a	<i>M. rubropunctata</i>	Algeria	24.3264	7.0058	KM411203	--	--	---	--
NHMC80.3.99.18 ^a	<i>M. rubropunctata</i>	Libya	25.9666	15.1574	KM411146	--	--	---	--
NHMC80.3.99.21 ^a	<i>M. rubropunctata</i>	Egypt	30.0457	31.2402	KM411147	--	--	---	--
NHMC80.3.99.25 ^a	<i>M. rubropunctata</i>	Mauritania	19.5518	-14.3706	KM411148	--	--	---	--
NHMC80.3.99.26 ^a	<i>M. rubropunctata</i>	Mauritania	19.5518	-14.3706	KM411149	--	--	---	--
NHMC80.3.99.27 ^a	<i>M. rubropunctata</i>	Mauritania	21.2985	-13.0674	KM411150	--	--	---	--
NHMC80.3.99.28 ^a	<i>M. rubropunctata</i>	Libya	25.9666	15.1574	KM411143	--	--	---	--
NHMC80.3.99.29 ^{a,c}	<i>M. rubropunctata</i>	Egypt	29.8734	32.6497	KM411200	--	--	---	--
RIM092	<i>M. rubropunctata</i>	Mauritania	21.4968	-11.6168	MK551703	--	--	MK551635	--
RIM093 ^{a,c}	<i>M. rubropunctata</i>	Mauritania	21.4968	-11.6168	MK551702	--	--	MK551634	--
SPM002355(45) ^a	<i>M. rubropunctata</i>	Egypt	29.7095	30.3792	MK551701	--	--	MK551633	--
SUD12/2010-56 ^{a,c}	<i>M. rubropunctata</i>	Sudan	21.8008	31.3488	MK551699	--	--	MK551631	--
SUD12/2010-57	<i>M. rubropunctata</i>	Sudan	21.8008	31.3488	KY967148	--	--	KY967103	--
SUD12/2010-58	<i>M. rubropunctata</i>	Sudan	21.8008	31.3488	MK551700	--	--	MK551632	--
CIBIO13743	<i>M. rubropunctata</i>	Mauritania	24.081058	-10.395780	Pending	Pending	Pending	Pending	Pending
CIBIO5265	<i>M. rubropunctata</i>	Mauritania	20.975818	-15.415585	Pending	Pending	Pending	Pending	Pending
912	<i>M. saudiarabica</i>	Saudi Arabia	22.2371	41.8428	---	--	--	KY967104	--
NHMC80.3.164.16 ^{a,c}	<i>M. saudiarabica</i>	Saudi Arabia	22.3952	41.7529	KM411151	--	--	---	--
NHMC80.3.164.5 ^a	<i>M. saudiarabica</i>	Saudi Arabia	22.4	41.7333	KM411198	--	--	---	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
NHMC80.3.164.9 ^a	<i>M. saudiarabica</i>	Saudi Arabia	22.2525	41.8796	KM411206	--	--	---	--
NHMC80.3.69.17 ^a	<i>M. saudiarabica</i>	Saudi Arabia	23.5388	40.5893	KM411192	--	--	---	--
NHMC80.3.69.18	<i>M. saudiarabica</i>	Saudi Arabia	23.5038	41.3472	KM411193	--	--	---	--
NHMC80.3.69.19	<i>M. saudiarabica</i>	Saudi Arabia	24.2531	41.1539	KM411194	--	--	---	--
NHMC80.3.69.20 ^a	<i>M. saudiarabica</i>	Saudi Arabia	23.5114	41.422	KM411195	--	--	---	--
MC57Me1 ^{a,c}	<i>M. simoni</i>	Morocco	30.5194	-9.6856	MK551724	--	--	MK551652	--
NHMC80.3.109.1 ^a	<i>M. simoni</i>	Morocco	31.912	-7.505	EF555301	--	--	---	--
NHMC80.3.109.5 ^a	<i>M. simoni</i>	Morocco	31.8028	-8.037	KM411123	--	--	---	--
NHMC80.3.109.6	<i>M. simoni</i>	Morocco	31.8028	-8.037	KM411124	--	--	---	--
BEV.9430	<i>M. simoni</i>	Morocco	31.830100	-7.982900	Pending	Pending	Pending	Pending	Pending
BEV.9431	<i>M. simoni</i>	Morocco	31.812900	-8.013800	Pending	Pending	Pending	Pending	Pending
BEV.T6301	<i>M. simoni</i>	Morocco	32.301120	-7.530650	Pending	Pending	Pending	Pending	Pending
CN11193 ^a	<i>M. sp.</i>	Saudi Arabia	24.4441	46.6756	MK551725	--	--	MK551654	--
CN11194 ^a	<i>M. sp.</i>	Saudi Arabia	24.4441	46.6756	MK551732	--	--	MK551660	--
CN11195 ^{a,c}	<i>M. sp.</i>	Saudi Arabia	24.4441	46.6756	MK551726	--	--	MK551655	--
CN11200 ^a	<i>M. sp.</i>	Saudi Arabia	24.3236	46.3961	MK551731	--	--	---	--
J16/04	<i>M. sp.</i>	Jordan	32.169	37.0078	MH040047	--	--	MH040087	--
NHMC80.3.72.36	<i>M. sp.</i>	Saudi Arabia	26.4278	47.3789	KM411184	--	--	---	--
NHMC80.3.72.37 ^a	<i>M. sp.</i>	Saudi Arabia	26.4066	47.707	KM411185	--	--	---	--
NHMC80.3.72.38	<i>M. sp.</i>	Saudi Arabia	26.4153	47.4736	KM411186	--	--	---	--
NHMC80.3.72.39 ^a	<i>M. sp.</i>	Saudi Arabia	23.2786	46.3534	KM411187	--	--	---	--
NHMC80.3.72.40 ^a	<i>M. sp.</i>	Saudi Arabia	23.193	46.4223	KM411188	--	--	---	--
NHMC80.3.72.41 ^a	<i>M. sp.</i>	Saudi Arabia	23.2417	46.4537	KM411189	--	--	---	--
NHMC80.3.72.52 ^a	<i>M. sp.</i>	Jordan	31.8817	36.9133	KM411179	--	--	MH040088	--
NHMC80.3.72.59 ^a	<i>M. sp.</i>	Kuwait	29.4624	47.6407	KM411238	--	--	MH040089	--
S10332 ^a	<i>M. spp.</i>	Saudi Arabia	25.2681	46.6237	MH040048	--	--	MH040090	--
CIBIO312	<i>M. spp.</i>	Tunisia	34.000883	8.284733	Pending	Pending	Pending	Pending	Pending
CIBIO319	<i>M. spp.</i>	Tunisia	32.997433	10.607950	Pending	Pending	Pending	Pending	Pending
IR001 ^{a,c}	<i>M. watsonana</i>	Iran	35.1109	50.8977	MK551694	--	--	MK551626	--
IR006 ^a	<i>M. watsonana</i>	Iran	30.2702	57.1231	MK551696	--	--	MK551628	--
IR013 ^{a,c}	<i>M. watsonana</i>	Iran	30.0243	57.2848	MK551697	--	--	MK551629	--
KUSH12 ^a	<i>M. watsonana</i>	Iran	35.1109	50.8977	MK551695	--	--	MK551627	--
NHMC80.3.144.1 ^a	<i>M. watsonana</i>	Iran	35.6962	51.4229	KM411217	--	--	---	--
NHMC80.3.144.15 ^a	<i>M. watsonana</i>	Iran	26.1592	60.1861	KM411153	--	--	---	--
NHMC80.3.144.16 ^a	<i>M. watsonana</i>	Iran	26.1592	60.1861	KM411154	--	--	---	--
NHMC80.3.144.17 ^{a,c}	<i>M. watsonana</i>	Afghanistan	34.5833	68.95	KM411219	--	--	---	--

Sample code	Species	Country	Latitude	Longitude	Cyt-b	B-fib7	OD	MC1R	PgD7
NHMC80.3.144.18 ^a	<i>M. watsonana</i>	Pakistan	26.4948	66.6677	KM411221	--	--	---	--
NHMC80.3.144.19 ^a	<i>M. watsonana</i>	Pakistan	26.4948	66.6677	KM411220	--	--	---	--
NHMC80.3.144.2 ^a	<i>M. watsonana</i>	Iran	32.5777	59.7978	KM411218	--	--	---	--
NHMC80.3.144.4 ^a	<i>M. watsonana</i>	Iran	32.383	48.3982	KM411126	--	--	---	--
NHMC80.3.144.5 ^a	<i>M. watsonana</i>	Iran	31.6516	49.2775	KM411127	--	--	---	--
NHMC80.3.144.6 ^a	<i>M. watsonana</i>	Iran	31.6516	49.2775	KM411128	--	--	---	--
NHMC80.3.144.7 ^a	<i>M. watsonana</i>	Iran	32.3081	52.0158	KM411152	--	--	---	--
NHMC80.3.144.8 ^a	<i>M. watsonana</i>	Iran	34.4164	50.8608	KM411155	--	--	---	--
NHMC80.3.144.9 ^a	<i>M. watsonana</i>	Iran	31.1956	59.3201	KM411156	--	--	---	--
TAB11 ^{a,c}	<i>M. watsonana</i>	Iran	33.5993	56.9123	MK551698	--	--	MK551630	--
VAZ10 ^{a,c}	<i>M. watsonana</i>	Iran	28.9974	54.7813	MH040049	--	--	MH040091	--
	<i>Gallotia atlantica</i>				DQ298679	--	--	AY151999	--
	<i>Psammodromus algirus</i>				DQ298675	--	--	AY151998	--
	<i>Podarcis lilfordi</i>				KX658188	--	--	EF679323	--
	<i>Podarcis pityusensis</i>				KX658227	--	--	EF679328	--

Table S3. Information on all datasets used in the phylogenetic, calibration, and range reconstruction analyses, including partitions, models and parameters.

Dataset	Data	Analysis	Partition	Model	Clock Model	Tree model	Run Specification
0	mtDNA	Bayesian Inference [BEAST]	Cyt-b	HKY+G +I	Relaxed Lognormal	Uncorrelated Speciation: Process	Yule 3 runs; 100000000 generations; 10000 sampling frequency; 10% burn-in
	mtDNA (outgroups excluded)	Historical demography [BEAST]	Cyt-b	HKY+G +I	Relaxed Lognormal	Uncorrelated Coalescent-based: Bayesian skyline plot (BSP)	Yule 3 runs; 100000000 generations; 10000 sampling frequency; 10% burn-in
1	mtDNA GENE BANK	all Bayesian Inference [BEAST]	Cyt-b	HKY+G +I	Relaxed Lognormal	Uncorrelated Speciation: Process	Yule 3 runs; 100000000 generations; 10000 sampling frequency; 10% burn-in
2	nDNA (outgroups included)	Bayesian Inference [BEAST]	B-fib7 MC1R OD PgD7	HKY+G HKY+I HKY K80+G	Strict clock Strict clock Strict clock Strict clock	Speciation: Process	Yule 3 runs; 100000000 generations; 10000 sampling frequency; 10% burn-in
	nDNA (outgroups excluded)	Species Tree (<i>M. olivieri</i> sp. Complex) [*BEAST]	B-fib7 MC1R OD PgD7	HKY+G HKY+I HKY K80+G	Strict clock Strict clock Strict clock Strict clock	Speciation Process	Yule 3 runs; 100000000 generations; 10000 sampling frequency; 10% burn-in
3	Concatenated cytonuclear (Dataset 0+2) [BEAST]	Bayesian Inference [BEAST]	B-fib7 Cyt-b MC1R OD PgD7	HKY+G HKY+G +I HKY+I HKY K80+G	Strict clock Relaxed Lognormal Strict clock Strict clock Strict clock	Uncorrelated Speciation: Process	Yule 3 runs; 100000000 generations; 10000 sampling frequency; 10% burn-in
	Concatenated cytonuclear (Dataset 0+2) [BEAST]	Divergence time estimation	B-fib7 Cyt-b MC1R OD PgD7	HKY+G HKY+G +I HKY+I HKY K80+G	Strict clock Relaxed Lognormal Strict clock Strict clock Strict clock	Uncorrelated Speciation: Process	Yule 3 runs; 100000000 generations; 10000 sampling frequency; 10% burn-in

Table S4. Material examined for morphological comparisons and original measurements for each specimen. Codes of morphological characters are given section Material and Methods. M = Male; F = Female.

Code	Species	Sex	SVL	HL	HW	HH	TE	RN	PS
BEV.10457	<i>Mesalina sp. nov.</i>	F	53.04	11.45	6.65	3.86	1	2	3
BEV.14800	<i>Mesalina sp. nov.</i>	F	44.01	9.99	6.42	4.26	1	1	3
BEV.15060	<i>Mesalina sp. nov.</i>	M	33.23	8.44	4.92	3.16	2	2	3
BEV.15061	<i>Mesalina sp. nov.</i>	F	40.80	9.38	5.57	3.79	1	2	3
BEV.15062	<i>Mesalina sp. nov.</i>	M	33.15	8.49	5.38	3.24	3	2	3
BEV.15063	<i>Mesalina sp. nov.</i>	M	38.05	9.78	6.13	3.62	3	1	3
BEV.15064	<i>Mesalina sp. nov.</i>	M	33.53	8.72	5.06	3.09	2	1	3
BEV.15163	<i>Mesalina sp. nov.</i>	F	42	9.00	6	3	2	1	3
BEV.10013	<i>M. olivieri</i>	M	40.78	10.28	5.51	4.25	3	1	2
BEV.11948	<i>M. olivieri</i>	F	44.64	9.43	6.36	4.35	1	1	2
BEV.12808	<i>M. olivieri</i>	F	47.25	10.51	6.83	5.08	1	2	1
BEV.13621	<i>M. olivieri</i>	M	49.59	12.17	8.40	5.27	2	1	2
BEV.14833	<i>M. olivieri</i>	M	44.95	10.45	6.49	4.13	2	1	2
BEV.5925	<i>M. olivieri</i>	F	41.00	10.21	6.33	3.75	1	1	1
BEV.5861	<i>M. olivieri</i>	F	46.68	9.55	6.40	4.53	1	1	1
BEV.5864	<i>M. olivieri</i>	F	38.52	8.61	5.30	3.59	1	1	1
BEV.5867	<i>M. olivieri</i>	F	40.17	8.67	5.33	3.66	1	1	1
BEV.5870	<i>M. olivieri</i>	M	41.53	10.17	6.62	4.26	3	2	2
BEV.5871	<i>M. olivieri</i>	F	42.98	9.64	5.80	4.17	1	1	2
BEV.5875	<i>M. olivieri</i>	F	42.66	9.60	6.24	4.45	1	1	2
BEV.5876	<i>M. olivieri</i>	M	44.03	10.60	6.96	5.19	2	1	1
BEV.5877	<i>M. olivieri</i>	F	44.63	8.73	5.41	4.13	1	2	1
BEV.5879	<i>M. olivieri</i>	M	45.91	11.20	6.77	5.01	3	1	1
BEV.5880	<i>M. olivieri</i>	F	47.22	9.90	6.28	4.48	1	2	1
BEV.5881	<i>M. olivieri</i>	M	42.31	10.30	6.90	4.61	3	2	1
BEV.5882	<i>M. olivieri</i>	F	42.37	9.31	5.95	4.42	1	1	1
BEV.5888	<i>M. olivieri</i>	F	36.43	9.05	6.14	3.89	2	1	2
BEV.5889	<i>M. olivieri</i>	M	43.41	10.90	7.26	4.99	2	1	1
BEV.5890	<i>M. olivieri</i>	M	41.30	10.46	6.02	3.65	3	1	3
BEV.5899	<i>M. olivieri</i>	F	39.38	9.76	5.96	4.50	2	1	2
BEV.5956	<i>M. olivieri</i>	M	37.35	9.22	5.39	3.57	2	1	3
BEV.5959	<i>M. olivieri</i>	M	36.09	9.24	5.59	3.99	2	1	2
BEV.8830	<i>M. olivieri</i>	M	43.28	10.65	7.27	5.36	3	1	1
BEV.8796	<i>M. olivieri</i>	M	45.32	11.87	7.31	5.49	3	1	3
BEV.8797	<i>M. olivieri</i>	M	44.57	11.68	7.26	5.24	3	1	2
BEV.8798	<i>M. olivieri</i>	M	44.78	11.06	7.66	5.60	3	1	1
BEV.8829	<i>M. olivieri</i>	M	44.77	11.04	7.00	5.09	3	1	3
BEV.8975	<i>M. olivieri</i>	F	43.03	9.52	6.18	4.33	2	2	1

Code	Species	Sex	SVL	HL	HW	HH	TE	RN	PS
BEV.10453	<i>M. simoni</i>	M	35.74	8.27	4.86	3.17	2	1	3
BEV.10849	<i>M. simoni</i>	M	38.07	9.24	5.56	4.39	3	2	3
BEV.10850	<i>M. simoni</i>	F	42.46	8.47	5.28	3.60	2	1	1
BEV.11187	<i>M. simoni</i>	M	42.49	10.41	6.90	4.65	3	2	1
BEV.11586	<i>M. simoni</i>	M	44.74	11.08	7.44	4.95	2	1	2
BEV.11587	<i>M. simoni</i>	F	45.71	9.17	6.38	4.02	2	1	2
BEV.11588	<i>M. simoni</i>	F	46.10	9.69	6.27	4.43	1	1	2
BEV.11589	<i>M. simoni</i>	M	46.56	11.32	7.33	5.00	3	1	2
BEV.11590	<i>M. simoni</i>	M	45.23	10.45	7.11	4.70	3	1	3
BEV.11591	<i>M. simoni</i>	F	45.92	9.71	6.49	4.60	1	1	2
BEV.11594	<i>M. simoni</i>	F	47.88	10.06	6.26	3.99	1	1	2
BEV.14869	<i>M. simoni</i>	F	41.77	8.77	5.62	3.76	1	1	1
BEV.5922	<i>M. simoni</i>	M	50.79	11.08	7.00	5.43	3	1	1
BEV.5923	<i>M. simoni</i>	F	50.69	9.74	6.33	4.41	2	2	2
BEV.5924	<i>M. simoni</i>	F	48.25	10.30	6.67	4.50	1	1	2
BEV.8508	<i>M. simoni</i>	M	43.14	9.72	6.42	4.89	3	1	1
BEV.8509	<i>M. simoni</i>	F	45.75	9.45	6.26	4.36	1	2	1
BEV.9114	<i>M. simoni</i>	M	40.70	9.62	5.90	4.20	2	1	2
BEV.9225	<i>M. simoni</i>	M	42.39	10.23	7.09	5.35	3	1	1
BEV.9429	<i>M. simoni</i>	M	42.15	10.21	6.75	4.39	3	1	1
BEV.9430	<i>M. simoni</i>	M	43.89	10.29	6.83	4.68	3	1	2
BEV.9431	<i>M. simoni</i>	M	43.74	10.39	7.14	4.64	3	2	1
BEV.9432	<i>M. simoni</i>	M	43.34	10.71	6.61	4.52	3	1	1
BEV.10179	<i>M. pasteuri</i>	M	48.32	11.83	7.44	5.63	2	1	2
BEV.10454	<i>M. pasteuri</i>	M	45.41	11.04	5.98	4.10	2	1	3
BEV.10455	<i>M. pasteuri</i>	M	42.17	10.42	5.57	3.90	3	1	3
BEV.14803	<i>M. pasteuri</i>	M	48.31	12.01	7.74	5.44	3	2	3
BEV.14804	<i>M. pasteuri</i>	F	40.38	8.94	5.59	4.16	2	1	3
BEV.14805	<i>M. pasteuri</i>	M	40.61	9.95	6.44	4.05	3	1	3
BEV.5926	<i>M. pasteuri</i>	M	43.75	11.17	6.27	4.07	2	1	2
BEV.5927	<i>M. pasteuri</i>	F	41.81	10.09	5.56	4.25	1	1	2
BEV.9177	<i>M. pasteuri</i>	M	44.70	11.23	7.50	4.64	1	1	2
BEV.9380	<i>M. pasteuri</i>	F	27.77	7.19	4.54	2.99	2	1	3

Table S5. Material examined for pholidotic characters comparisons for each specimen. Codes of morphological characters are given section Material and Methods. M = Male; F = Female.

Code	Species	Sex	SVL	HL	HW	HH	TE	RN	PS	V	D	DS	TR	SL(Sx)	SL(Dx)	IL(Sx)	IL(Dx)	G	Col	EL	NTS	Pf(Sx)	Pf(Dx)
BEV.10457	<i>Mesalina sp. nov.</i>	F	53.04	11.45	6.65	3.86	1	2	3	34	44	4	15	4	4	7	7	28	11	5	12	14	15
BEV.14800	<i>Mesalina sp. nov.</i>	F	44.01	9.99	6.42	4.26	1	1	3	32	44	3	12	4	4	7	7	24	7	5	12	14	13
BEV.15060	<i>Mesalina sp. nov.</i>	M	33.23	8.44	4.92	3.16	2	2	3	31	45	4	14	4	4	7	8	25	11	5	11	12	13
BEV.15061	<i>Mesalina sp. nov.</i>	F	40.80	9.38	5.57	3.79	1	2	3	33	52	4	14	4	4	7	8	24	10	5	11	12	14
BEV.15062	<i>Mesalina sp. nov.</i>	M	33.15	8.49	5.38	3.24	3	2	3	33	52	4	16	4	4	9	7	29	11	5	12	13	13
BEV.15063	<i>Mesalina sp. nov.</i>	M	38.05	9.78	6.13	3.62	3	1	3	30	56	4	17	4	4	7	7	29	11	5	12	17	17
BEV.15064	<i>Mesalina sp. nov.</i>	M	33.53	8.72	5.06	3.09	2	1	3	31	49	4	16	4	4	9	9	32	11	5	12	15	16
BEV.15163	<i>Mesalina sp. nov.</i>	F	42	9.00	6	3	2	1	3	34	48	4	15	4	4	9	8	27	11	5	10	17	15
BEV.10013	<i>M. olivieri</i>	M	40.78	10.28	5.51	4.25	3	1	2	29	44	4	15	4	4	8	8	24	7	8	9	13	14
BEV.11948	<i>M. olivieri</i>	F	44.64	9.43	6.36	4.35	1	1	2	32	50	2	19	4	4	9	8	25	11	12	10	13	13
BEV.12808	<i>M. olivieri</i>	F	47.25	10.51	6.83	5.08	1	2	1	30	46	4	17	5	4	8	7	27	8	6	10	12	12
BEV.13621	<i>M. olivieri</i>	M	49.59	12.17	8.40	5.27	2	1	2	30	64	3	16	4	4	8	9	26	9	5	9	15	16
BEV.14833	<i>M. olivieri</i>	M	44.95	10.45	6.49	4.13	2	1	2	32	44	3	17	4	4	7	8	29	12	3	10	11	12
BEV.5925	<i>M. olivieri</i>	F	41.00	10.21	6.33	3.75	1	1	1	31	46	0	14	4	4	8	8	25	12	5	10	13	12
BEV.5861	<i>M. olivieri</i>	F	46.68	9.55	6.40	4.53	1	1	1	31	43	3	17	4	4	8	8	25	9	5	9	13	14
BEV.5864	<i>M. olivieri</i>	F	38.52	8.61	5.30	3.59	1	1	1	32	43	2	12	4	4	8	7	23	9	5	8	10	10
BEV.5867	<i>M. olivieri</i>	F	40.17	8.67	5.33	3.66	1	1	1	29	41	3	17	4	5	7	8	26	9	5	8	11	10
BEV.5870	<i>M. olivieri</i>	M	41.53	10.17	6.62	4.26	3	2	2	30	45	4	16	4	4	7	6	23	11	6	11	15	13
BEV.5871	<i>M. olivieri</i>	F	42.98	9.64	5.80	4.17	1	1	2	35	48	3	16	3	4	8	9	26	8	8	10	13	13
BEV.5875	<i>M. olivieri</i>	F	42.66	9.60	6.24	4.45	1	1	2	32	42	3	14	5	5	7	8	25	9	7	10	12	10
BEV.5876	<i>M. olivieri</i>	M	44.03	10.60	6.96	5.19	2	1	1	32	44	2	16	4	4	8	8	25	12	5	9	12	12
BEV.5877	<i>M. olivieri</i>	F	44.63	8.73	5.41	4.13	1	2	1	32	40	2	16	4	5	8	8	24	11	5	11	13	12
BEV.5879	<i>M. olivieri</i>	M	45.91	11.20	6.77	5.01	3	1	1	31	40	3	16	4	4	8	9	24	9	5	10	12	13
BEV.5880	<i>M. olivieri</i>	F	47.22	9.90	6.28	4.48	1	2	1	33	46	3	15	4	4	8	7	21	9	8	9	11	10
BEV.5881	<i>M. olivieri</i>	M	42.31	10.30	6.90	4.61	3	2	1	30	47	2	18	4	4	7	8	20	9	5	10	12	11
BEV.5882	<i>M. olivieri</i>	F	42.37	9.31	5.95	4.42	1	1	1	32	42	4	16	4	4	8	8	22	8	9	10	10	12

Code	Species	Sex	SVL	HL	HW	HH	TE	RN	PS	V	D	DS	TR	SL(Sx)	SL(Dx)	IL(Sx)	IL(Dx)	G	Col	EL	NTS	Pf(Sx)	Pf(Dx)
BEV.5888	<i>M. olivieri</i>	F	36.43	9.05	6.14	3.89	2	1	2	27	45	4	17	4	5	9	7	26	8	8	12	12	12
BEV.5889	<i>M. olivieri</i>	M	43.41	10.90	7.26	4.99	2	1	1	30	52	1	18	4	4	9	9	28	9	3	10	13	16
BEV.5890	<i>M. olivieri</i>	M	41.30	10.46	6.02	3.65	3	1	3	33	46	2	19	4	4	7	9	31	7	7	10	16	15
BEV.5899	<i>M. olivieri</i>	F	39.38	9.76	5.96	4.50	2	1	2	33	46	2	16	4	4	8	8	22	11	7	11	12	11
BEV.5956	<i>M. olivieri</i>	M	37.35	9.22	5.39	3.57	2	1	3	30	41	3	17	5	5	9	8	30	9	7	11	14	13
BEV.5959	<i>M. olivieri</i>	M	36.09	9.24	5.59	3.99	2	1	2	30	40	4	17	4	4	7	6	29	10	5	10	11	12
BEV.8830	<i>M. olivieri</i>	M	43.28	10.65	7.27	5.36	3	1	1	30	48	1	16	5	5	8	8	28	8	6	10	14	13
BEV.8796	<i>M. olivieri</i>	M	45.32	11.87	7.31	5.49	3	1	3	30	57	1	16	6	5	9	8	27	10	6	11	13	14
BEV.8797	<i>M. olivieri</i>	M	44.57	11.68	7.26	5.24	3	1	2	30	42	2	20	5	5	9	10	26	14	9	11	13	13
BEV.8798	<i>M. olivieri</i>	M	44.78	11.06	7.66	5.60	3	1	1	30	48	2	17	4	4	9	8	20	8	6	10	16	16
BEV.8829	<i>M. olivieri</i>	M	44.77	11.04	7.00	5.09	3	1	3	28	42	2	16	5	6	8	7	23	12	10	10	11	12
BEV.8975	<i>M. olivieri</i>	F	43.03	9.52	6.18	4.33	2	2	1	30	45	2	17	4	5	8	9	23	9	6	8	12	12
BEV.10453	<i>M. simoni</i>	M	35.74	8.27	4.86	3.17	2	1	3	30	39	2	15	5	4	8	7	26	8	5	8	12	11
BEV.10849	<i>M. simoni</i>	M	38.07	9.24	5.56	4.39	3	2	3	34	42	1	15	4	4	9	8	24	8	8	9	12	12
BEV.10850	<i>M. simoni</i>	F	42.46	8.47	5.28	3.60	2	1	1	34	42	1	15	4	4	8	7	26	8	8	10	12	12
BEV.11187	<i>M. simoni</i>	M	42.49	10.41	6.90	4.65	3	2	1	30	47	2	15	4	4	8	8	22	10	9	9	12	12
BEV.11586	<i>M. simoni</i>	M	44.74	11.08	7.44	4.95	2	1	2	30	45	2	16	4	4	7	8	27	12	7	13	14	12
BEV.11587	<i>M. simoni</i>	F	45.71	9.17	6.38	4.02	2	1	2	31	42	2	15	4	3	7	8	24	8	8	8	11	10
BEV.11588	<i>M. simoni</i>	F	46.10	9.69	6.27	4.43	1	1	2	33	36	2	13	4	4	7	8	24	9	8	9	13	13
BEV.11589	<i>M. simoni</i>	M	46.56	11.32	7.33	5.00	3	1	2	30	49	2	18	4	4	8	8	21	12	10	11	12	12
BEV.11590	<i>M. simoni</i>	M	45.23	10.45	7.11	4.70	3	1	3	29	44	3	15	5	5	8	8	26	11	9	11	10	10
BEV.11591	<i>M. simoni</i>	F	45.92	9.71	6.49	4.60	1	1	2	31	45	4	14	4	4	7	7	24	9	7	12	12	12
BEV.11594	<i>M. simoni</i>	F	47.88	10.06	6.26	3.99	1	1	2	34	50	2	14	4	4	7	6	23	11	5	9	10	10
BEV.14869	<i>M. simoni</i>	F	41.77	8.77	5.62	3.76	1	1	1	35	36	4	16	4	4	7	7	20	9	12	10	12	12
BEV.5922	<i>M. simoni</i>	M	50.79	11.08	7.00	5.43	3	1	1	33	42	4	15	4	4	7	9	23	10	7	9	13	13
BEV.5923	<i>M. simoni</i>	F	50.69	9.74	6.33	4.41	2	2	2	34	42	4	14	4	4	8	7	24	10	6	9	12	12

Code	Species	Sex	SVL	HL	HW	HH	TE	RN	PS	V	D	DS	TR	SL(Sx)	SL(Dx)	IL(Sx)	IL(Dx)	G	Col	EL	NTS	Pf(Sx)	Pf(Dx)
BEV.5924	<i>M. simoni</i>	F	48.25	10.30	6.67	4.50	1	1	2	33	43	2	14	4	4	7	8	21	12	10	8	12	13
BEV.8508	<i>M. simoni</i>	M	43.14	9.72	6.42	4.89	3	1	1	31	46	4	15	4	4	8	7	28	9	6	9	12	12
BEV.8509	<i>M. simoni</i>	F	45.75	9.45	6.26	4.36	1	2	1	34	46	4	15	4	4	7	7	28	9	5	11	11	11
BEV.9114	<i>M. simoni</i>	M	40.70	9.62	5.90	4.20	2	1	2	28	34	4	15	4	5	7	9	25	6	5	8	10	13
BEV.9225	<i>M. simoni</i>	M	42.39	10.23	7.09	5.35	3	1	1	27	40	4	15	4	4	9	8	24	7	6	10	11	12
BEV.9429	<i>M. simoni</i>	M	42.15	10.21	6.75	4.39	3	1	1	30	54	4	16	4	4	7	8	24	12	8	9	12	13
BEV.9430	<i>M. simoni</i>	M	43.89	10.29	6.83	4.68	3	1	2	30	46	0	16	4	4	8	8	22	11	6	15	14	5
BEV.9431	<i>M. simoni</i>	M	43.74	10.39	7.14	4.64	3	2	1	32	46	1	16	4	4	8	8	23	9	6	11	12	12
BEV.9432	<i>M. simoni</i>	M	43.34	10.71	6.61	4.52	3	1	1	31	46	2	16	4	4	9	9	22	9	6	11	13	13
BEV.10179	<i>M. pasteuri</i>	M	48.32	11.83	7.44	5.63	2	1	2	31	39	1	15	5	5	7	6	30	9	1	7	12	15
BEV.10454	<i>M. pasteuri</i>	M	45.41	11.04	5.98	4.10	2	1	3	28	40	4	15	5	5	7	8	29	9	4	10	13	12
BEV.10455	<i>M. pasteuri</i>	M	42.17	10.42	5.57	3.90	3	1	3	33	40	0	15	6	6	8	7	27	10	4	11	17	15
BEV.14803	<i>M. pasteuri</i>	M	48.31	12.01	7.74	5.44	3	2	3	29	39	1	17	5	5	9	9	28	10	4	7	12	12
BEV.14804	<i>M. pasteuri</i>	F	40.38	8.94	5.59	4.16	2	1	3	34	38	3	16	4	6	8	8	24	10	4	7	13	12
BEV.14805	<i>M. pasteuri</i>	M	40.61	9.95	6.44	4.05	3	1	3	31	40	3	16	7	5	7	8	26	10	3	10	13	12
BEV.5926	<i>M. pasteuri</i>	M	43.75	11.17	6.27	4.07	2	1	2	32	43	0	18	5	5	6	8	31	9	5	9	16	13
BEV.5927	<i>M. pasteuri</i>	F	41.81	10.09	5.56	4.25	1	1	2	31	39	4	14	4	5	8	9	27	7	4	10	10	8
BEV.9177	<i>M. pasteuri</i>	M	44.70	11.23	7.50	4.64	1	1	2	29	42	0	16	5	5	9	8	27	8	5	9	14	13
BEV.9380	<i>M. pasteuri</i>	F	27.77	7.19	4.54	2.99	2	1	3	34	42	0	14	5	6	8	8	29	7	5	8	12	13

Table S6. Material examined for colouration characters comparisons for each specimen. Codes of morphological characters are given section Material and Methods. M = Male; F = Female.

Code	Species	Sex	EBL	DBF	PSDBF	PDLL	SPDLL	DDSLL	SDDLb	PSDDSLL	DSO	TC
BEV.10457	<i>Mesalina sp. nov.</i>	F	0	2	1	2	5	1	2	0	1	1
BEV.14800	<i>Mesalina sp. nov.</i>	F	1	3	1	1	2	2	6	1	1	1
BEV.15060	<i>Mesalina sp. nov.</i>	M	1	2	1	2	2	1	3	0	2	1
BEV.15061	<i>Mesalina sp. nov.</i>	F	1	2	2	1	2	1	4	1	0	1
BEV.15062	<i>Mesalina sp. nov.</i>	M	1	2	2	1	2	1	4	2	0	1
BEV.15063	<i>Mesalina sp. nov.</i>	M	1	2	0	1	1	2	4	0	1	1
BEV.15064	<i>Mesalina sp. nov.</i>	M	1	2	2	1	2	1	4	2	0	1
BEV.15163	<i>Mesalina sp. nov.</i>	F	0	0	0	3	2	1	4	1	1	0
BEV.10013	<i>M. olivieri</i>	M	0	4	2	1	2	1	4	2	2	0
BEV.11948	<i>M. olivieri</i>	F	0	4	2	3	3	2	5	2	0	2
BEV.12808	<i>M. olivieri</i>	F	0	0	2	2	2	0	0	2	0	2
BEV.13621	<i>M. olivieri</i>	M	0	2	2	2	3	1	4	0	2	2
BEV.14833	<i>M. olivieri</i>	M	0	3	2	2	2	1	4	2	0	0
BEV.5925	<i>M. olivieri</i>	F	0	2	2	2	2	1	1	0	1	0
BEV.5861	<i>M. olivieri</i>	F	1	2	2	0	3	1	4	2	0	0
BEV.5864	<i>M. olivieri</i>	F	0	2	2	2	3	1	5	2	0	0
BEV.5867	<i>M. olivieri</i>	F	0	2	2	2	2	1	4	0	2	0
BEV.5870	<i>M. olivieri</i>	M	0	2	2	2	2	1	4	2	0	0
BEV.5871	<i>M. olivieri</i>	F	0	2	2	2	2	1	1	0	2	0
BEV.5875	<i>M. olivieri</i>	F	0	2	2	1	2	1	4	2	1	0
BEV.5876	<i>M. olivieri</i>	M	0	2	2	2	2	1	4	2	0	0
BEV.5877	<i>M. olivieri</i>	F	0	2	2	2	2	1	3	0	0	0
BEV.5879	<i>M. olivieri</i>	M	0	2	2	2	2	1	1	2	0	0
BEV.5880	<i>M. olivieri</i>	F	0	2	2	2	3	1	3	0	2	0
BEV.5881	<i>M. olivieri</i>	M	0	2	2	1	2	1	4	2	2	1
BEV.5882	<i>M. olivieri</i>	F	0	2	2	2	2	1	2	0	2	2

Code	Species	Sex	EBL	DBF	PSDBF	PDLL	SPDLL	DDSLL	SDDLb	PSDDSLL	DSO	TC
BEV.5888	<i>M. olivieri</i>	F	0	4	1	3	4	2	2	1	1	0
BEV.5889	<i>M. olivieri</i>	M	0	0	2	2	2	1	3	2	2	0
BEV.5890	<i>M. olivieri</i>	M	0	2	2	2	3	1	4	2	0	0
BEV.5899	<i>M. olivieri</i>	F	0	2	2	2	1	2	5	2	2	0
BEV.5956	<i>M. olivieri</i>	M	0	2	2	2	3	1	4	2	1	0
BEV.5959	<i>M. olivieri</i>	M	0	4	1	1	1	2	4	0	0	0
BEV.8830	<i>M. olivieri</i>	M	1	2	2	1	4	1	7	1	2	1
BEV.8796	<i>M. olivieri</i>	M	1	3	2	1	3	1	4	0	2	0
BEV.8797	<i>M. olivieri</i>	M	2	3	2	2	4	2	5	1	2	0
BEV.8798	<i>M. olivieri</i>	M	1	2	2	2	7	2	6	0	2	0
BEV.8829	<i>M. olivieri</i>	M	0	2	2	1	6	1	7	0	2	2
BEV.8975	<i>M. olivieri</i>	F	0	2	2	2	2	2	3	0	2	2
BEV.10453	<i>M. simoni</i>	M	22	3	2	2	3	0	2	2	2	0
BEV.10849	<i>M. simoni</i>	M	22	3	2	2	2	1	1	0	0	0
BEV.10850	<i>M. simoni</i>	F	21	0	0	2	2	1	3	0	0	0
BEV.11187	<i>M. simoni</i>	M	19	0	2	2	2	1	4	2	0	0
BEV.11586	<i>M. simoni</i>	M	21	0	2	2	2	1	4	2	1	0
BEV.11587	<i>M. simoni</i>	F	18	0	2	2	3	2	4	1	2	1
BEV.11588	<i>M. simoni</i>	F	18	3	2	0	0	2	4	0	0	0
BEV.11589	<i>M. simoni</i>	M	18	2	2	2	2	1	5	2	1	0
BEV.11590	<i>M. simoni</i>	M	18	0	2	2	3	1	5	2	0	0
BEV.11591	<i>M. simoni</i>	F	20	0	2	2	2	2	4	1	2	1
BEV.11594	<i>M. simoni</i>	F	18	2	2	2	2	1	5	2	2	2
BEV.14869	<i>M. simoni</i>	F	19	2	2	3	4	1	3	2	0	0
BEV.5922	<i>M. simoni</i>	M	21	0	2	2	2	1	2	2	2	0
BEV.5923	<i>M. simoni</i>	F	19	2	0	1	1	2	4	2	2	0

Code	Species	Sex	EBL	DBF	PSDBF	PDLL	SPDLL	DDSLL	SDDLb	PSDDSLL	DSO	TC
BEV.5924	<i>M. simoni</i>	F	22	2	2	0	0	1	2	2	2	0
BEV.8508	<i>M. simoni</i>	M	23	2	2	2	3	1	8	0	2	0
BEV.8509	<i>M. simoni</i>	F	25	3	1	2	4	1	4	0	2	0
BEV.9114	<i>M. simoni</i>	M	24	2	2	0	2	0	1	2	1	1
BEV.9225	<i>M. simoni</i>	M	21	2	2	2	2	2	3	0	1	2
BEV.9429	<i>M. simoni</i>	M	21	3	2	2	3	1	6	1	2	0
BEV.9430	<i>M. simoni</i>	M	20	3	2	2	3	2	6	2	1	0
BEV.9431	<i>M. simoni</i>	M	19	2	2	2	3	2	6	2	0	1
BEV.9432	<i>M. simoni</i>	M	21	3	2	1	2	2	5	2	0	2
BEV.10179	<i>M. pasteuri</i>	M	0	0	1	3	2	0	1	0	2	0
BEV.10454	<i>M. pasteuri</i>	M	0	0	2	3	3	2	1	0	2	0
BEV.10455	<i>M. pasteuri</i>	M	0	0	0	3	3	3	1	0	0	0
BEV.14803	<i>M. pasteuri</i>	M	0	0	1	3	2	1	3	1	2	0
BEV.14804	<i>M. pasteuri</i>	F	0	0	2	3	2	2	3	0	0	0
BEV.14805	<i>M. pasteuri</i>	M	0	0	0	3	2	3	1	0	0	0
BEV.5926	<i>M. pasteuri</i>	M	0	0	0	3	2	3	2	0	1	0
BEV.5927	<i>M. pasteuri</i>	F	0	0	0	3	3	3	1	0	0	0
BEV.9177	<i>M. pasteuri</i>	M	0	0	2	3	2	0	5	0	2	0
BEV.9380	<i>M. pasteuri</i>	F	0	0	0	3	2	3	3	0	0	0

Table S7. Categories of the variable Land Cover used in the ecological models. Variable derived from Campos and Brito (2018).

Code	Category	Definition
LC_01	Yellow dunes	Frequently fixed dunes composed by yellow sand. Sparse shrubs with isolated <i>Acacia</i> sp. or no vegetation cover
LC_02	White dunes	Mobile dunes composed by white sand (e.g. barchan dunes). No vegetation cover
LC_03	Orange dunes	Frequently fixed dunes composed by orange sand. Sparse shrubs with isolated <i>Acacia</i> sp. or sometimes no vegetation cover
LC_04	Compact sand	Flat areas composed by consolidated sandy soils. Shrubs and sparse trees (e.g. <i>Acacia</i> sp.)
LC_05	Gravel + Sand floodplains	Soil composed by similar amounts of gravel and sand. Sparse vegetation or no vegetation cover
LC_06	Gravel floodplains	Large floodplains covered by gravel (locally known as Reg). Usually no vegetation cover
LC_07	Compact soil	Soils frequently composed by silt and/or clay. Sparse vegetation or no vegetation cover
LC_08	Rocky soil	Non-flat areas with soils composed by stones, silt and/or clay. Sparse vegetation or no vegetation cover
LC_09	Rocky plateaux	Flat areas totally covered by stones (locally known as Hammada). Isolated <i>Acacia</i> sp. or no vegetation cover
LC_10	Bare rock	Large rock outcrops
LC_11	Grasslands	Flat flooding areas covered by grasses (e.g. <i>Cenchrus biflorus</i>)
LC_12	Savannah	High vegetation cover (grasses, shrubs and trees)
LC_13	Croplands	Areas of crop cultivation (e.g. rice and sorghum)
LC_14	Permanent water	Permanent water features (rivers, lakes and mountain lagoons)
LC_15	Salt pans	Flat areas covered by salt (locally known as Sebkhah). No vegetation cover
LC_16	Railroads	Railroads and linear infra-structures
LC_17	Roads	Paved roads
LC_18	Urban	Major cities and villages

Campos, J.C., Brito, J.C. (2018) Mapping underrepresented land cover heterogeneity in arid regions: The Sahara-Sahel example. ISPRS J. Photogram. Rem. Sens. 146, 211-220.

Table S8. Details and metrics of the 20 model replicates developed for *Mesalina sp. nov.*, including average (standard deviation) training and tests Area under curve (AUC), average (standard deviation) percentage contribution of each variable to the model replicates.

	Maximum temperature of warmest month	Minimum temperature of coldest month	Temperature of annual range	Annual precipitation	total Land-cover	Terrain ruggedness index
% contribution	3.136 (2.180)	10.022 (3.766)	0.000 (0.003)	8.800 (4.505)	35.416 (11.808)	42.625 (13.414)
Permutation importance	6.098 (6.733)	15.762 (12.539)	0.037 (0.161)	21.808 (16.403)	24.962 (13.477)	31.332 (22.383)
Training gain without	3.069 (0.387)	2.931 (0.400)	3.096 (0.387)	2.892 (0.345)	2.458 (0.342)	2.404 (0.446)
Training gain with only	0.323 (0.110)	0.215 (0.095)	0.314 (0.101)	0.760 (0.226)	1.300 (0.370)	1.642 (0.307)
Test gain without	3.289 (1.029)	3.004 (1.192)	3.274 (1.077)	3.109 (1.092)	2.634 (1.041)	2.662 (1.086)
Test gain with only	0.350 (0.521)	0.351 (0.223)	0.348 (0.561)	0.837 (0.404)	1.528 (0.913)	1.694 (0.870)
AUC without	0.979 (0.019)	0.970 (0.036)	0.978 (0.022)	0.974 (0.025)	0.960 (0.039)	0.955 (0.051)
AUC with only	0.741 (0.145)	0.752 (0.090)	0.756 (0.145)	0.848 (0.079)	0.891 (0.107)	0.913 (0.080)

