

1 **Towards a global perspective for *Salvia* L: Phylogeny, diversification, and floral evolution**

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19 **Abstract**

20 *Premise of this study:* *Salvia* is the most species-rich genus in Lamiaceae, encompassing
21 approximately 1000 species distributed all over the world. We sought a new evolutionary
22 perspective for *Salvia* by employing macroevolutionary analyses to address the tempo and
23 mode of diversification. To study the association of floral traits with speciation and extinction,
24 we modeled and explored the evolution of corolla length and the lever-mechanism pollination
25 system across our *Salvia* phylogeny.

26 *Methods:* We reconstructed a multigene phylogeny for 366 species of *Salvia* in the broad
27 sense including all major recognized lineages and numerous species from Iran, a region
28 previously overlooked in studies of the genus. Our phylogenetic data in combination with
29 divergence time estimates were used to examine the evolution of corolla length, woody vs.
30 herbaceous habit, and presence vs. absence of a lever mechanism. We investigated the timing
31 and dependence of *Salvia* diversification related to corolla length evolution through a
32 disparity test and BAMM analysis. A HiSSE model was used to evaluate the dependency of
33 diversification on the lever-mechanism pollination system in *Salvia*.

34 *Key Results:* Based on recent investigations and classifications, *Salvia* is monophyletic and
35 comprises ~1000 species. Our inclusion, for the first time, of a comprehensive sampling for
36 Iranian species of *Salvia* provides higher phylogenetic resolution for southwestern Asian
37 species than obtained in previous studies. A medium corolla length (15-18mm) was
38 reconstructed as the ancestral state for *Salvia* with multiple shifts to shorter and longer
39 corollas. Macroevolutionary model analyses indicate that corolla length disparity is high
40 throughout *Salvia* evolution, significantly different from expectations under a Brownian
41 motion model during the last 28 million years of evolution. Our analyses show evidence of a
42 higher diversification rate of corolla length for some Andean species of *Salvia* compared to
43 other members of the genus. Based on our tests of diversification models, we reject the
44 hypothesis of a direct effect of the lever mechanism on *Salvia* diversification.

45 *Conclusions:* Using a broader species sampling than previous studies, we obtained a well-
46 resolved phylogeny for southwest Asian species of *Salvia*. Corolla length is an adaptive trait
47 throughout the *Salvia* phylogeny with a higher rate of diversification in the South American

48 clade. Our results suggest caution in considering the lever-mechanism pollination system as
49 one of the main drivers of speciation in *Salvia*.

50 *Key words: Salvia, phylogeny, diversification, corolla, pollination, lever mechanism*

51 **1. Introduction**

52 Integrating molecular data with organismal traits can be used to address a major question in
53 biology, “Is higher species diversity related to the presence of specific traits in that lineage?”
54 (Pyron and Tubrin, 2014). Recently developed model-based approaches for estimating
55 divergence times (BEAST: Drummond and Rambaut 2007; treePL: Smith and O’Meara 2010),
56 diversification rates (MEDUSA: Alfaro et al., 2009; BAMM: Rabosky et al., 2014), and the effect
57 of traits on diversification (FitzJohn et al., 2012; Beaulieu and O’Meara 2016; Caetano et al.,
58 2018; Landis et al., 2018; Han et al., 2020) provide new opportunities to address this question.
59 These methods have the advantage of providing estimates of the origin, divergence time, rate
60 of diversification, and drivers of diversification among species.

61 There has been considerable recent interest in studying the association of floral traits and
62 species richness in flowering plants (Vamosi et al., 2011; Van der Niet and Johnson 2014; Soltis
63 & Soltis 2014; Saquet et al., 2017; Landis et al., 2018; Onstein 2019; Hernández and Wiens
64 2020). Interactions between flowers and their pollinators have spurred speciation and the
65 evolution of novel floral variation (e.g., Stebbins 1970; Dodd et al., 1999; Crane et al., 1995;
66 Crepet 2000; Soltis and Soltis 2004; Soltis et al., 2008; Ambruster 2014; Fenster et al., 2004;
67 Smith 2010; Van der Niet and Johnson 2014). Some floral traits such as spur length, corolla
68 shape, corolla length, and number of flowers are more often influenced by selection than
69 other floral features (Yoshioka, 2007; Kacowski et al., 2012; Landis et al., 2016). Floral
70 specialization could potentially promote diversification by the evolution of adaptive floral
71 traits through the establishment of reproductive isolation (Kay and Sargent 2009, Armbruster
72 2014; Serrano-Serrano et al., 2015). Several studies have also shown a correlation between
73 flower specialization and rate of diversification (Fernández-Mazuecos et al., 2013; Ogutcen et
74 al., 2014; Lagomarsino et al., 2016). For example, in genera of Neotropical Gesneriaceae
75 including *Codonanthesis* Mansf, *Codonanthe* (Mart.) Hanst, and *Nematanthus* Schard,
76 species with hummingbird pollination syndromes have higher rates of diversification than
77 close relatives pollinated by insects (Serrano-Serrano et al., 2015).

78 Lamiaceae (the mints) are the sixth largest family of flowering plants with over 7000 species
79 distributed worldwide (Harley et al., 2004). Recently, Li et al. (2016, 2017) subdivided
80 Lamiaceae into ten subfamilies and four unplaced genera based on a large-scale, plastid-
81 based phylogenetic analysis, and this topology was largely corroborated by analysis of nuclear
82 transcriptomes (Mint Evolutionary Genomics Consortium 2018). Within Lamiaceae,
83 Nepetoideae is the largest subfamily with 105 genera and 3600 species, including well-known
84 genera such as *Thymus* L. (thyme), *Ocimum* L. (basil), *Nepeta* L. (catnip), *Salvia* L. (sage), and
85 *Lavandula* L. (lavender) (Harley et al., 2004).

86 *Salvia*, the largest genus in Lamiaceae as currently defined, includes approximately 1000
87 species, more than half of which are distributed in North and South America (Alziar, 1988-
88 1993). Morphologically, *Salvia* is highly diverse, particularly regarding specialized floral traits
89 such as corolla color, corolla and tube length, flower shape and stamen structure (Wester and
90 Claßen-Bockhoff, 2007; Reith et al., 2007; Will and Claßen-Bockhoff, 2015). Traditionally,
91 *Salvia* was separated from other genera in Lamiaceae by possessing two fertile stamens with
92 an elongated connective tissue. More than 80% of *Salvia* species are characterized by a special
93 pollination system referred to as a lever mechanism (Walker et al., 2004; Harely et al., 2004;
94 Claßen-Bockhoff et al., 2004; Walker and Sytsma, 2007). transfer to the stigma. The lever
95 mechanism has the advantage of promoting successful pollination. In addition, this approach
96 is efficient in pollen allocation and does not allow the pollinator to collect all of the pollen in
97 one visit (Claßen-Bockhoff et al., 2003; Reith et al., 2007; Celep et al., 2014). A staminal lever
98 is an advantage in *Salvia* due to the precise placement of pollen on bees while they are
99 accessing the restricted nectar (Claßen-Bockhoff et al., 2004; Zhang et al. (2011) showed that
100 removing the lever arms in *Salvia cyclostegia* resulted in lower fruit and seed set. Previous
101 morphological studies of *Salvia* pollinators and floral traits hypothesized that the lever
102 mechanism might play a role as a key innovation in promoting adaptive radiations (Claßen-
103 Bockhoff et al., 2004; Will and Claßen-Bockhoff 2014). Based on phylogenetic results, the
104 lever mechanism evolved in parallel in the Eastern and Western Hemispheres (Walker and
105 Sytsma, 2007).

106 Since the initial phylogenetic study on Menthineae (Wagstaff and Olmstead, 1995), several
107 studies have been performed based on nuclear and plastid regions with increasing taxonomic
108 sampling of *Salvia* species (Walker and Sytsma, 2007; Takano and Okado 2011; Will and

109 Claßen-Bockhoff, 2014; Drew and Sytsma, 2012; Will et al., 2015; Will and Claßen-Bockhoff,
110 2017; Hu et al., 2018; Drew et al., 2017; Fragoso-Martinez et al., 2017; Kriebel et al., 2019;
111 Wu et al., 2021). In the first molecular study of *Salvia* (based on *rbcl* and the *trnL-trnF*
112 regions), Walker and Sytsma (2004) found that *Salvia* is not monophyletic and recognized
113 three clades: clade I includes many species of *Salvia* from the Eastern Hemisphere along with
114 a Western Hemisphere lineage (8 species from former sect. *Heterosphacea* and subgen.
115 *Salviaostrum*), clade II comprises North and South American species and includes subgen.
116 *Calosphace* Benth. and subgen. *Audbertia* Benth, and clade III comprises species from eastern
117 North Africa and southwestern Asia. *Rosmarinus* L. and *Perovskia* Karel. were placed as sisters
118 to clade I, while *Dorystaechas* Boiss. & Heldr. ex Benth, distributed in Turkey, was placed with
119 clade II.

120 Walker and Sytsma (2007), with increased taxon sampling for *Salvia* and related genera in
121 Menthineae, found that *Meriandra* Benth and *Dorystaechas* formed the sister clade to North
122 and South American species of *Salvia* (clade II). They referred to *Zhumeria* Rech.f & Wendelbo
123 (a monotypic genus endemic to Iran) along with southwest and East Asian *Salvia* as clade III.
124 Will and Claßen-Bockhoff (2014) excluded the East Asian *Salvia* species from Walker and
125 Sytsma's (2007) clade III and considered them to represent an independent lineage (Clade IV).
126 Will and Claßen-Bockhoff (2017) suggested breaking the large *Salvia* group into six genera:
127 *Salvia sensu stricto*, *Ramonia* Raf., *Lasemia* Raf., *Glutinaria* Raf., *Pleudia*, and *Polakia*.
128 However, they did not provide a taxonomic revision. Drew et al. (2017) embedded these five
129 genera into a broadly defined *Salvia* and treated each as a subgenus. In recent phylogenetic
130 studies of *Salvia*, Hu et al. (2018) and Kriebel et al. (2019) followed and updated the Drew et
131 al. (2017) classification of *Salvia*, recognizing 11 subgenera. In this study, to maintain stability
132 in taxonomic definition and nomenclature, we follow the broad definition of *Salvia* (Drew et
133 al., 2017; Hu et al., 2018; Kriebel et al., 2019). A schematic diagram of changes in *Salvia*
134 delimitation based on previous phylogenetic studies is provided in **Figure 1**.

135 Frequent endemism and enormous morphological diversity have made interpretation of the
136 evolutionary patterns within *Salvia* challenging, particularly given the limited taxon sampling
137 for some areas, such as southwestern Asia. To improve taxon sampling for southwestern Asia
138 and to clarify patterns of morphological evolution and species diversification, we generated
139 new sequences for 50 Iranian species of *Salvia* and reconstructed a phylogeny for 351 species

140 overall. Notably, other recent phylogenetic analyses of *Salvia* differ in scope and emphasis
141 from our investigation. Kriebel et al. (2019) studied the effect of biome shifts and pollinators
142 on the radiation of *Salvia*. They found that shifts in pollination system are not correlated with
143 species diversification, except in subgen. *Calosphace* in the Western Hemisphere where
144 species are pollinated by hummingbirds. Kriebel et al. (2020) showed that the respective floral
145 morphospaces of the Western and Eastern Hemisphere *Salvia* are different. They inferred
146 that these differences in flower morphology are linked with shifts from bee to bird pollination.
147 In another recent study, Wester et al. (2020) found that shifts from bee- to bird-pollinated
148 *Salvia* are mostly associated with floral structure rather than floral colors.

149 Despite valuable contributions, the relationship between the evolution of floral traits and
150 patterns of *Salvia* diversification is not well understood. We used our new phylogenetic tree
151 for *Salvia* to trace patterns of both character evolution and diversification. We primarily focus
152 on the role of corolla length as one of the putative characters involved in *Salvia* diversification.
153 This is also the first attempt to trace the evolutionary history of corolla length in *Salvia* and
154 its association with diversification. Furthermore, we reconstructed the ancestral state for
155 lever mechanism and habitat with greater taxon sampling than in previous work (Will and
156 Claßen-Bockhoff 2014). In addition, we shed new light on the role of the pollination system
157 in *Salvia* diversification. We statistically examine the longstanding hypothesis that the lever
158 mechanism in *Salvia* flowers is correlated with high diversity and species richness.

159 **2. Materials & Methods**

160 **2.1. Taxon Sampling**

161 In total, 366 taxa representing 351 species covering all major areas of the geographic
162 distribution of *Salvia* were used to reconstruct the phylogeny. As noted, we considered *Salvia*
163 in the broad sense and included *Zhumeria*, *Meriandra*, *Rosmarinus*, and *Perovskia* (Drew et
164 al., 2017, Kriebel et al., 2019). Following Drew and Sytsma (2012), we selected *Melissa* and
165 *Lepechinia* as outgroups. We generated new sequences for many Iranian species of *Salvia*,
166 including 50 species (59 accessions) for the external transcribed spacer (ETS) region of nuclear
167 ribosomal DNA, 46 species (47 accessions) for ITS, and 35 species for the *ycf1-rps15* region of
168 the plastome. The remaining sequences used here (representing 216 species) were obtained
169 from GenBank. We concatenated all sequences for the three plastid regions (*rpl32*, *trnL-trnF*,

170 *ycf1-rps15*) and two nuclear regions (ITS, ETS); the plastid and nuclear data sets were each
171 analyzed separately and then combined, given the highly similar topologies obtained for each.
172 That is, there was no strongly supported incongruence or conflict (hard incongruence sensu
173 Seelanan et al., 1997) between nuclear and plastid trees. The newly generated sequences
174 were deposited in GenBank. Corresponding information for each voucher specimen is
175 provided in Table 1.

176 **2.2. DNA extraction, amplification, and sequencing**

177 Total DNA was extracted from herbarium and silica-dried material using a modified CTAB
178 method (Doyle & Doyle 1987) in which, to break down secondary metabolites, the mixture of
179 ground leaf tissue and CTAB solution was kept at room temperature for 24 hours. ITS, ETS,
180 and *ycf1* regions were amplified using the polymerase chain reaction (PCR) with each sample
181 prepared in 25- μ l volumes with the following components: 1 μ l of DNA solution (20 ng), 2.5
182 μ l of reaction buffer, 2 μ l dNTP mix (0.2 mM), 1 μ l of each primer (10 μ M), 1 μ l of MgCl₂, and
183 1.5 μ l of *Taq* DNA polymerase. The PCR conditions for the nuclear regions for most species
184 were: 95°C for 2 minutes, 32 cycles of denaturation for 20 seconds at 94°C, primer annealing
185 for 20 seconds at 50°C, and 2 minutes extension at 72°C, with a final extension of 7 minutes
186 at 72°C. For the *ycf1* region, we modified the annealing temperature to 52°C for 1 minute
187 (PCR optimization was set based on personal communication with B. Drew). High-quality PCR
188 products were sequenced on an ABI 3730 DNA Analyzer (Applied Biosystems, Inc.) at the
189 University of Florida Interdisciplinary Center for Biotechnology Research (ICBR).

190

191 **2.3. Alignment and phylogenetic analysis**

192 All consensus DNA sequences were generated using Geneious Pro v. 10.22 (Biomatters,
193 Auckland, New Zealand). Alignments were performed with the MAFFT plugin in Geneious with
194 manual adjustment. Maximum likelihood analysis was performed using the CIPRES Science
195 Gateway with RAxML HPC v.8 on XSEDE using the GTRGAMMA model with _Fa (rapid
196 bootstrapping analysis/search for the best ML tree) with 1000 iterations for bootstrapping.
197 Default settings were used for other options. Phylogenetic analyses were conducted for 1) all
198 plastid loci (*rpl32-trnI*, *trnI-trnf*, and *ycf1-rps15*), 2) both nuclear loci (ITS and ETS), and 3) a
199 combined data set of plastid and nuclear loci.

200

201 **2.4. BEAST analysis (divergence time estimation)**

202 We estimated divergence times using BEAST version 2.2.0 (Bouckaert et al., 2014) under the
203 uncorrelated lognormal model. Priors for the branch rate were assumed as a Yule process. A
204 node prior was calibrated for the most recent common ancestor (MRCA) of *Melissa* and
205 *Lepechinia* (28.4 Ma with a mean of 1.5 and a SD of 0.5; Drew and Sytsma 2012; Kriebel et al.,
206 2019) with a lognormal distribution. The BEAST analysis was performed with two independent
207 runs of Markov Chain Monte Carlo. Each run was performed for 2×10^8 generations, with
208 parameters logged every 1000 generations. We used Tracer v. 1.6 to evaluate the ESS
209 (Effective Sample Size) to assure that the chains were run sufficiently long. An ESS > 200
210 indicates that the two independent runs were adequate. Tree Annotator was used to find the
211 maximum clade credibility reporting median node ages after discarding the first 10% of the
212 generations as burn-in.

213

214 **2.5. Ancestral state reconstruction**

215 Two characters with discrete states were scored: mode of lever mechanism (present / absent)
216 and habit (woody / herbaceous). We treated shrubs and subshrubs as woody; however,
217 distinguishing woody from herbaceous is not always straightforward because some mostly
218 herbaceous plants may become woody in special climatic situations (FitzJohn et al., 2014;
219 Zanne et al., 2014). Therefore, we treated a species as woody if it is considered a shrub or
220 subshrub in the literature or if it was defined as having a woody rootstock. In addition, the
221 continuous character corolla length was measured from the joint of the calyx to the end of
222 the upper lip.

223 The relevant data for the discrete and continuous traits were collected from the literature:
224 *Flora of China* (www.efloras.org/flora_page.asp?flora_id=2), *California Salvia* (Epling, 1983),
225 *Flora of USSR* (Pobedimova, 1954), *Flora of Turkey and the East Aegeans* (Hedge, 1982), *Flora*
226 *Iranica* (Hedge, 1982), *Flora of Southern Africa* (Codd, 1985), *Flora of Madagascar* (Hedge,
227 1992), *Flora dels Paisos Catalans* (Bolos and Vigo, 1995; Wester and Claßen-Bockhoff, 2011),
228 and *Flora of Iran* (Jamzad, 2012). Additionally, we used online resources (www.gbif.org;
229 www.tropicos.org) as sources of data. For some species, the corolla length was measured
230 using the digitized type specimen available on JSTOR's Global Plants database
231 (<http://plants.jstor.org>).

232 For the discrete data, we used maximum likelihood to define the best model fitting our data
233 using the function ‘ace’ implemented in the R package ape v5. 3 (Paradis et al., 2004). We
234 tested “ER” (Equal Rates) and “ARD” (All Rates Different) on our data, and the best model was
235 selected based on the Akaike Information Criterion (AIC) (Akaike, 1974). We used the Akaike
236 weight using `aic.w` function in the R package `geiger` v2.0.6 to select the best model for those
237 data with low delta AIC between ER and ARD models. To reconstruct ancestral states, we used
238 stochastic character mapping with 1000 iterations using the `make.simmap` function in the
239 `phytools` v0.7.78 package (Revell, 2012). We also reconstructed the ancestral state of corolla
240 length using the `lik.anc` in `phytools` to calculate the likelihood of each ancestral state.
241 Ancestral states of corolla length and 95% confidence intervals were evaluated using the
242 function `anc.ML` with an OU (Ornstein-Unlenbeck) model in `phytools`.

243 **2.6. Macroevolutionary patterns within corolla length**

244 We focused on corolla length as one of the most important morphological traits that might
245 influence pollinator-flower interactions (Fernández- Mazuecos et al., 2013; Gómez et al.,
246 2016; Landis et al., 2018). To investigate the evolutionary dynamics of corolla length
247 throughout *Salvia* phylogeny, we applied three quantitative approaches based on the time-
248 calibrated phylogeny as follows:

249

250 **2.6.1. Diversification model**

251 We examined three evolutionary models with different patterns of phenotypic evolution
252 using the R package `geiger` v2.0.6 (Harmon et al., 2008) following three different models. 1)
253 The Brownian Motion model (BM): This model describes a “random walk” of evolution for
254 continuous characters. 2) The Ornstein-Uhlenbeck model (OU): This model describes the local
255 occurrence of stabilizing selection in which the trait is drawn toward optimal fitness (Hansen
256 1997). 3) The Early Burst model (EB): This model is known as a classic model of adaptive
257 radiation, in which the initial stage of morphological evolution is rapid with decreasing
258 morphological evolution after ecological spaces are filled (Harmon et al., 2010). Based on a
259 recent model of diversification reconstructed by Aguilée et al. (2018), after an initial phase of
260 geographic adaptive radiation, diversification rates can be affected not only by ecological
261 niches, but also by genetic processes, competition, and landscape dynamics. The best model
262 for explaining diversification of *Salvia* was selected based on the AIC (Akaike, 1974).

263

264 2.6.2. Disparity Through Time

265 Disparity Through Time (DTT) of the corolla length was modeled using the R package *geiger*
266 v2.0.6 (Harmon et al., 2008). This analysis uses corolla length of extant *Salvia* species to
267 reconstruct ancestral corolla length values and model disparity between species. This
268 approach estimates the pairwise Euclidean distance of the trait over time and compares it
269 with the expected value under a null model of Brownian motion by iterative simulation.
270 Phenotypic disparity refers to the phenotypic variation among related species (Harmon,
271 2003). We simulated corolla length evolution with 10,000 generations across the
272 phylogenetic tree built from the combined data set of plastid and nuclear sequences. The
273 Morphological Disparity Index (MDI) was calculated, and the average disparity of corolla
274 length from the real and simulated data was plotted. Negative MDI shows lower disparity of
275 the trait than expected, and positive MDI indicates strong overlap in morphospace and
276 higher disparity within subclades (Donoso et al., 2015).

277

278 2.6.3. Diversification rate

279 To assess variation in rates of diversification of corolla length across *Salvia*, we used the
280 phenotypic trait module in BAMM. We simulated 20,000,000 generations, and the priors
281 were set using the function “SetBAMMpriors” in the R package BAMMTools v.2.1.6 (Rabosky
282 et al., 2014). We specified the sampling fraction by accounting for the number of samples for
283 each of the four major clades. Sampling fractions were set as: 0.47 (clade I), 0.26 (clade II),
284 0.95 (clade III) and 0.56 (clade IV). We performed MCMC simulation with 20,000,000
285 generations by sampling every 1000 generations. We discarded the first 25% of runs as burn-
286 in. Effective Sample Size (ESS) > 200 was used to evaluate the convergence of four Markov
287 Chain Monte Carlo chains. The BAMM output was analyzed using BAMMtools.

288

289 **2.8. Lever-mechanism-dependent diversification**

290 To examine whether the diversification rate in *Salvia* is correlated with the presence of the
291 lever mechanism, we applied HiSSE (Hidden State Speciation and Extinction) implemented in
292 the R package *hisse* v2.1.1 (Beaulieu and O’Meara 2016), which is a modified method of BiSSE

293 (Binary State Speciation and extinction) (Maddison et al., 2014). Rabosky (2014) argued that
294 the BiSSE method suffers from type I and type II errors. In those cases, traits that are not
295 biologically correlated with speciation rates show significant effects on diversification
296 (Goldberg and Rabosky, 2015). In other words, rejecting the null hypothesis in BiSSE does not
297 mean the alternative is true.

298 Compared with the BiSSE model, the HiSSE model considers more free parameters and
299 assumes a hidden state for each of the observed states that potentially have independent
300 rates of diversification (OA, 1A, OB, 1B). The Character Independent Diversification (CID)
301 models, which assume independent evolution for binary characters, were also implemented.
302 The CID models explicitly test that the evolution of a binary character is independent of the
303 diversification process without forcing the diversification process to be constant. Different
304 subsets of the HiSSE model that differ in speciation, extinction, and transition rate
305 parameters, along with standard BiSSE models, were estimated (cf. Harrington and Reeder,
306 2017). We accounted for incomplete taxon sampling in our phylogeny by assigning the
307 sampling frequency of each state as 0.256 (presence of the lever mechanism) and 0.056
308 (absence of the lever mechanism). The model average of ancestral state and diversification
309 of all fitted models was plotted using the function “plot.hisse.state”. The advantage of this
310 function is that it accounts for both state and rate uncertainty of the models along plotted
311 branches. We also used FiSSE (Fast intuitive State-dependent Speciation Extinction) as a non-
312 parametric test for the lever-mechanism-dependent speciation rate. This method does not
313 depend on the character state, but considers the distribution of branch lengths (Rabosky and
314 Goldberg 2017).

315

316 **2.9. Diversity-dependent diversification**

317 We also used the R package DDD v2.7 (Etienne and Haegman, 2012) to test whether
318 diversification in *Salvia* is dependent or independent of diversity. DDD uses a hidden Markov
319 model to calculate the likelihood of phylogenetic history under a diversity-dependent birth-
320 death model of diversification. DDD estimates “ K ”, the maximum number of species that a
321 clade can have in a given environment; a value of K near the number of extant species
322 suggests that a clade is close to its ecological limit. The other two models are a density-
323 dependent logistic (DDL+E) model and a density-dependent exponential (DDE+E) model. The
324 model with the lowest AICc was selected as the best model. We also calculated the maximum

325 likelihood evolutionary history pattern with both a Yule model and a constant rate birth-death
326 (CrBD) model. The Maximum Clade Credibility (MCC) of the BEAST output was used to
327 perform this analysis. We also examined four model fits as an alternative method using the R
328 package *laser* v2. 4 (Rabosky 2006).

329

330 **3. Results**

331 **3.1. Characteristics of the phylogenetic data matrix and phylogenetic analysis**

332 In this study, 143 new DNA sequences were generated for 50 Iranian *Salvia* species, including
333 50 species (59 accessions) for the ETS region, 46 species (47 accessions) for ITS, and 34 species
334 for *ycf1*.

335 Maximum likelihood analyses of all three data combinations were conducted: 1) plastid loci
336 (*rpl32-trnI*, *trnI-trnF*, and *ycf1-rps15*), 2) nuclear loci (ITS and ETS), and 3) a combined data set
337 of plastid and nuclear loci. The overall topologies of the nuclear loci, plastid loci, and the
338 combined data set are similar in recovering major clades. Based on both nuclear and plastid
339 regions, the phylogenetic relationships among most of the Eurasian species in clade I are
340 unresolved. This result is not surprising given that we had more missing data in the plastid
341 partition than other partitions. The nuclear and combined data sets provide higher support
342 for most of the clades than plastid data. For example, clade III was recovered as fully resolved
343 based on nuclear regions and combined data, but based on plastid data, the relationship
344 between *S. majdae* and *S. macilenta* with the remain group in clade III was unresolved. Trees
345 based on the nuclear and combined data sets were highly similar, with only some minor
346 differences in support values for terminal clades. However, the combined data recovered a
347 more resolved phylogeny. For example, in clade I within Subgen. *Heterosphace*, the
348 relationship between the *S. verticillata* group with the remaining taxa was resolved based on
349 the combined data but not the nuclear data. As a result, we used the results from the
350 combined data set in subsequent analyses and in our discussion below.

351 We recovered four major clades of *Salvia* species: clade I (Eurasian and southern African
352 *Salvia*), clade II (South and North American *Salvia*), clade III (southwestern Asian and northern
353 African *Salvia*), and clade IV (Southeast Asian *Salvia*). With more taxon sampling, we provide
354 a new phylogeny for clade III with species that are primarily distributed in southwestern Asia.
355 However, we mostly focus here on newly recovered relationships for Iranian species of *Salvia*

356 and the clades to which they belong rather than on *Salvia* phylogeny as a whole. For more
357 straightforward comparisons, we also used both clade names provided in previous
358 phylogenetic studies of *Salvia* (Will and Claßen-Bockhoff, 2017) along with the recent
359 classification (Drew et al., 2017; Kriebel et al., 2019) in **Suppl. 1**.

360 Clade I

361 In this clade, species are mainly distributed in Europe, Central Asia, western Asia, and
362 southern Africa. This clade contains 140 species (170 accessions) out of the 250-300 species
363 described for these areas. They fall into four distinct subclades (subclades I-A, I-B, I-C, and I-
364 D) of Will and Claßen-Bockhoff (2017) including subgenera *Salvia* Benth., *Sclarea* Benth., and
365 *Heterosphace* Benth (Kriebel et al., 2019). For the first time, resolution within the *S*.
366 *verticillata* group was obtained. *Salvia taraxacifolia* was recovered as the sister to the *S*.
367 *verticillata* group (BS = 81%) consisting of *S. verticillata*, *S. judaica*, and *S. russellii*. This clade
368 was in turn sister (BS = 95%) to the southern African clade.

369 Subclade I-C and I-D: 26 species of Iranian *Salvia* sampled here were recovered as members
370 of subclades I-C, and six species were placed in subclade I-D, including subgen. *Sclarea* and
371 *Salvia* based on the updated subgeneric classification of *Salvia* (Will and Claßen-Bockhoff
372 2017; Drew et al., 2017; Kriebel et al., 2019). These subclades include *Salvia* distributed in
373 western Asia (Afghanistan, Iran, Iraq, and Turkey), Central Asia, Europe, and the Canary
374 Islands. Based on the combined data set of nuclear and plastid loci, the phylogenetic
375 relationships among most of the taxa were unresolved. However, several groups were
376 identified within this polytomy: 1) *S. jamzadaei*, *S. macrochlamys*, *S. bracteata*, and allied
377 species; 2) two species endemic to Iran (*S. leriifolia* and *S. hypochionaea*) along with *S*.
378 *montbretia*, *S. daghestanica*, and *S. phlomoides*; 3) *S. spinosa*, *S. sclareopsis*, *S. macrosiphon*,
379 *S. reuterana*, *S. perspolitiana*, and *S. palaestina* (a clade with BS = 60%); and 4) *S. nemorosa*
380 and *S. virgata* from southwestern Asia, the Caucasus, and Europe along with *S. deserta* and
381 *Salvia* × *sylvestris*.

382 Clade II

383 *Salvia* species in this clade are endemic to South and North America, and clade II includes
384 more than half of all *Salvia* species, with approximately 600 species in subg. *Calosphace* and

385 19 species in subg. *Audibertia*. Clade II is recovered with BS= 97%; however, relationships
386 among taxa in this clade are not fully resolved. Clade I is sister to clade II with BS= 74%.

387 Clade III

388 This clade contains species of *Salvia* from northern Africa and southwestern Asia. We provide
389 the most comprehensive taxon sampling for clade III to date by generating 13 new sequences
390 for members of this group from the region of Iran. Clade III was recovered with 100% BS
391 support with a well-resolved phylogeny in trees from nuclear and combined data. Based on
392 the combined nuclear and plastid tree, *S. majdae*, which was placed in subgen. *Zhumeria*
393 (Drew et al., 2017), was found instead to be sister with high support (BS = 97%) to the *S.*
394 *aristata* group, which includes *S. pterocalyx* (from northeastern Afghanistan) and *S. vvedenskii*
395 and *S. margaritae* (from Central Asia). *Salvia majdae* and the *S. aristata* group were placed as
396 the sister clade to a trichomy of *S. aegyptiaca*, *S. macilenta*, and *S. eremophila*.

397 Clade IV

398 *Salvia* species in this clade are restricted to eastern Asia, with the exception of *S. glutinosa*
399 and *S. plebeia*. We provide new sequence data for *S. glutinosa*, which is distributed in the
400 northern part of Iran and some parts of Europe. *Salvia plebeia* is reported from Iran and
401 Afghanistan and extends to Southeast Asia. Based on our results, *S. glutinosa* forms a clade
402 with *S. nubicola*, *S. koyamae*, *S. glabrescense*, and *S. nipponica* with BS = 88%.

403

404 **3.2. Divergence times**

405 Divergence times were estimated using the combined data set of nuclear and plastid loci. The
406 results are congruent with previous results (Drew et al., 2017; Kriebel et al., 2019). Our BEAST
407 analysis (**Fig. 3**) suggests that *Salvia* originated in the Oligocene ~34 Ma. Divergence time
408 estimation showed that the split between clade I and the rest of *Salvia* occurred
409 approximately 31 Ma (95% HPD = 37.6-27.5 Ma). In clade I, the North American clade diverged
410 from the African and Mediterranean clade approximately 15 Ma (95% HPD = 20.06-10.69)
411 during the middle Miocene. The age of the MRCA of most of the Iranian *Salvia* species in clade
412 I was estimated as 14.3 Ma (95%HPD = 18.74-10.47 Ma) near the end of the early Miocene.
413 Clade II diverged from clade III (mostly from southwestern Asia) in the early Miocene (95%

414 HPD = 27.8-17.8 Ma). The split between clade IV (eastern Asia) and clade III (southwestern
415 Asia and northern Africa) is estimated to have occurred during the late Oligocene (95%HPD =
416 31.5-20.26 Ma).

417 **3.3. Ancestral character reconstruction**

418 Corolla length varies from 4 mm in *S. aegyptiaca* in clade III to 51 mm in *S. patens* in clade II.
419 The most recent common ancestor for *Salvia* was reconstructed as having a corolla length of
420 approximately 15-18 mm (**Fig. 4**). Corolla length of ~20 mm was inferred as the ancestral state
421 for clade I. In clade I, within subg. *Sclarea*, multiple shifts from a corolla length of 20 mm to
422 smaller corollas occurred, but in subg. *Salvia*, all the species evolved corolla lengths longer
423 than 20 mm. In subg. *Heterosphace*, including bird-pollinated species of *Salvia* from southern
424 Africa (*S. africana-lutea*, *S. lanceolata*, *S. thermarum*), the corolla length is more variable,
425 ranging from ~7-41 mm. In clade II, shifts in the range of corolla size were much higher than
426 in other clades, especially in subg. *Calosphace*. In clade III, the ancestral state of corolla length
427 was recovered as ~15 mm. Within this clade, species of *Salvia* have small flowers (4-9 mm)
428 with shifts to larger flowers in subg. *Zhumeria* and the *S. aristata* group.

429 The ER model was selected as the best model for the evolution of the lever mechanism based
430 on the AIC value. However, the difference between the ER (Equal Rates) and the ARD (All
431 Rates Different) model was minimal (ER 168.46 vs. ARD 169.68). The Akaike weight for the ER
432 model (0.65) was higher than for the ARD model (0.32). Therefore, we reconstructed the
433 ancestral state of the lever mechanism based on the ER model. The ancestral state of the
434 lever mechanism for *Salvia* was equivocal (**Fig. 5**). In clade I, the ancestral state of the lever
435 mechanism was also equivocal, but the ancestral state of subg. *Salvia*, *Sclarea*, and
436 *Heterosphace* is an active lever mechanism. In clade II, the ancestral state is equivocal with
437 several shifts in subg. *Calosphace* from an active lever to a non-active lever. In clade III, *Salvia*
438 species lack an active lever mechanism, and the ancestral state for the clade is equivocal.

439 The ARD model was moderately suggested as the best model (Delta AIC = 3.345) for inferring
440 the ancestral state of habit across the *Salvia* phylogeny. The ancestral state of habit for all of
441 *Salvia*, as well as major subclades, was found here to be equivocal (**Fig. 6**). In clade I, species
442 of subgen. *Sclarea* are mostly herbs with a few shifts to shrub forms, but subgen. *Salvia* and

443 *Heterosphace* are mostly shrubs with several shifts to herbaceousness. In clade II, especially
444 in subgen. *Calosphace*, shifting from herb to shrub was more frequent than in other clades.

445

446 **3.4. Tempo and mode of corolla length evolution**

447 The analysis of disparity through time showed that the rates of diversification in corolla length
448 among subclades of *Salvia* are higher than expected under a null hypothesis of Brownian
449 motion (MDI = +0.21). Therefore, *Salvia* subclades have diversified greatly in corolla length.
450 The corolla length decreased during the Miocene between approximately 17-15 Ma (within
451 the 95% CI calculated from simulations of corolla length disparity), but showed a remarkable
452 increase during the last ~10 Ma, during which the relative disparity of corolla length is higher
453 than the 95% DTT range of simulated data (**Fig. 7**).

454 The model-based analysis of corolla length diversification determined "OU" as the best
455 approximation model of this trait across *Salvia* phylogeny. Hence, our results suggest that
456 corolla length evolution underwent stabilizing selection towards a median value (**Table 2**).

457 **3.4.1. Corolla length evolutionary rates**

458 To assess whether the MCMC output of the BAMM analysis for corolla length has converged,
459 we checked the effective sample sizes of the log-likelihood and the number of shift events.
460 Based on $ESS_{\text{Number of shifts}} = 1139.461$ and $ESS_{\text{Loglike}} = 1458.028$, the MCMC simulation
461 converged. The phylorate plot confirmed heterogeneous rates of evolution of corolla length
462 in *Salvia*. The best distinct shift configuration with the highest posterior probability was
463 detected at the MRCA of core *Calosphace* in clade II (**Fig. 8**).

464

465 **3.5. Diversity-dependent diversification**

466 The maximum likelihood analysis of lineage diversification showed that among four fitted
467 models, with two models dependent on diversity, the Yule model was selected as the best
468 model based on AIC values for explaining *Salvia* diversification through time. Hence, the
469 evolutionary pattern of *Salvia* diversification is independent of diversity (**Table 3**). The
470 estimated carrying capacity ($K > 3000$), which refers to the potential number of species that a

471 clade can sustain, is higher than the number of extant species of *Salvia* (~1000). Rejection of
472 the diversity-dependent diversification model implies that *Salvia* has not reached its
473 ecological limit in terms of number of species and that speciation has not yet started to
474 decline due to increased species competition or fewer ecological resources.

475

476 **3.6. Lever-mechanism-dependent diversification**

477 We used HiSSE (Beaulieu and O'Meara, 2016) and FiSSE (Rabosky and Goldbeg., 2017)
478 methods for analyzing the effect of the active lever mechanism on diversification. We found
479 that the HiSSE model with an equal irreversible transition rate among states ($q_{0B1B}=0$,
480 $q_{1B0B}=0$, all other q 's equal) is the best model for explaining the effect of the lever
481 mechanism on *Salvia* diversification. Better performance of the HiSSE model than the BiSSE
482 model indicates a signal of lever-mechanism-dependent diversification as well as a signal of
483 other unobserved or unmeasured traits. Therefore, we infer that the lever mechanism is
484 indirectly responsible for *Salvia* diversification (**Table 4**). Based on FiSSE two-tailed
485 parameters, the P-value = 0.69; therefore, the null hypothesis of a close association between
486 the lever mechanism and *Salvia* diversification is rejected. The average tip rate of
487 diversification for an active lever mechanism is $\lambda_1 = 0.26$ and for a non-active lever mechanism
488 is $\lambda_0 = 0.22$.

489

490 **4. Discussion**

491 **4.1. Phylogeny**

492 By including 50 species of *Salvia* from the Iran region, the limited taxon sampling for the
493 Eastern Hemisphere encountered in previous studies (Drew and Sytsma, 2012; Will and
494 Claßen-Bockhoff, 2014, 2017; Drew et al., 2017) was remedied to some extent. To reconstruct
495 the phylogenetic tree of *Salvia* as comprehensively as possible, our newly generated data
496 were combined with relevant sequences from previous studies (Walker and Sytsma, 2007;
497 Drew and Sytsma, 2012; Takano and Okado 2011; Will and Claßen-Bockhoff, 2014; Fragoso-
498 Martineze, 2017).

499 Our results for *Salvia* as a whole are similar to those reported in previous phylogenetic results
500 in recovering four major well-supported clades comprising six subgenera were recovered for
501 *Salvia* (Will and Claßen-Bockhoff 2017; Drew et al., 2017; Kriebel et al., 2019). The resultant
502 trees for all the data sets largely agree with each other. Nevertheless, some discrepancies in
503 phylogenetic relationships within subclades were observed. In the paragraphs that follow, we
504 summarize and discuss the major phylogenetic results of this study and also compare our
505 findings to other studies of *Salvia*.

506 Clade I

507 This clade includes species from three subgenera, *Heterosphace*, *Salvia*, and *Sclarea* (Drew et
508 al., 2017; Kriebel et al., 2019). *Salvia* species in this clade are distributed in small areas of
509 North America, southern Africa and Madagascar, western Asia, Europe, and the Canary
510 Islands. Although the phylogenetic relationships among most of the taxa in clade I are still not
511 well resolved, our use of more nuclear and plastid regions was helpful in recovering the
512 African clade with higher bootstrap support than previously reported (Will and Claßen-
513 Bockhoff, 2017).

514 Subgen. *Heterosphace*

515 This group comprises three supported subclades (supplementary 1). 1) Subclade I-A includes
516 species from both northern and southern Africa. *Salvia nilotica* and *S. somalensis*, two species
517 distributed in Tanzania and Ethiopia, respectively, were recovered as successive sisters to the
518 southern African clade. 2) Subclade I-B comprises several species of *Salvia* from North
519 America, formerly classified in section *Salviastrum* Scheele. Kriebel et al. (2019) argued that
520 dispersal to eastern North America (sect. *Salviastrum* of subgen. “*Heterosphace*”) from the
521 Eastern Hemisphere lineage occurred during the mid-Miocene. 3) The *S. verticillata* group:
522 *Salvia taraxacifolia* was recovered as sister to the *S. verticillata* group (BS = 81%) consisting of
523 *S. verticillata*, *S. judaica*, and *S. russellii*. The latter clade was sister (BS = 95%) to the southern
524 African clade. Previous studies (Will and Claßen-Bockhoff, 2014; Will and Claßen-Bockhoff,
525 2017) failed to resolve the phylogenetic position of *S. taraxacifolia* (Mediterranean element)
526 or with low support (Kriebel et al., 2019) within the *S. verticillata* group. Our results from the
527 combined nuclear and plastid data recovered *S. taraxacifolia* as sister to the *S. verticillata*
528 group with high support. *S. nilotica* placed as sister to the southern African clade species.

529 Most of the *Salvia* species in clade I (Europe, Madagascar, Central Asia), along with Iranian
530 species of *Salvia*, are placed in subclades I-C and I-D and are classified as subgen. *Sclarea* and
531 *Salvia* following recent treatments (Drew et al., 2017; Kriebel et al., 2019). Although
532 phylogenetic relationships among species of *Salvia* in these subclades are mostly unresolved,
533 our increased taxon sampling was helpful in determining the phylogenetic position of Iranian
534 *Salvia* species and provides evolutionary insights and rationale for improving the taxonomy
535 of *Salvia*.

536 Clade II

537 As noted above, clade II comprises species from North and South America, within which
538 approximately half of all *Salvia* species are distributed. Because relationships among species
539 from this geographic region were not the focus of this study, our sampling from this region is
540 more limited than from central and western Asia, Europe, and Africa. Relationships are
541 therefore largely unresolved. For more detail about relationships among species of *Salvia*
542 from the Americas, we refer the reader to (Walker et al., 2015; Fragoso-Martínez 2018; Kriebel
543 et al., 2019)

544 Clade III

545 Clade III encompasses species distributed in northern Africa and southwestern Asia. Within
546 this clade, species are mostly dwarf shrubs with smaller flowers than those of other *Salvia*
547 clades. In the Iran flora, most species are distributed in the southern region of Iran (25-27 N°).
548 We present here the best-resolved phylogeny obtained for clade III with the most
549 comprehensive taxon sampling to date; our nuclear data set fully resolved relationships with
550 BS = 100%. *Salvia majdae*, formerly classified as the monotypic genus *Zhumeria*, is an endemic
551 aromatic shrub in southern Iran. Based on a recent study (Soltanipour et al., 2020), *S. majdae*
552 is reported as an endangered species on the IUCN Red List based on Extent of Occurrence
553 (EO) and Area Of Occupancy (AOO). *Salvia aristata* is another endemic species of Iran in this
554 clade placed as the sister species of *S. majdae*. This species has a different habit (herbaceous
555 perennial) from the remaining species in clade III, as well as a larger distribution in Iran.

556 Clade IV

557 Clade IV is restricted to eastern Asia. Notably, *S. glutinosa*, which is distributed in northern
558 Iran and western Europe, forms a clade with species from eastern Asia. *Salvia glutinosa* also
559 shares similar traits with *S. nubicola* in corolla color (yellow with brown-purple spots on the
560 lower lip) and with a clade of *S. koyamae*, *S. glabrescense*, and *S. nipponica* in leaf form and
561 flower shape (Hu et al., 2018). Thus, *S. glutinosa* may have historically had a larger distribution
562 than currently displayed. It is likely that *S. glutinosa* is a relict Arcto-Tertiary element and
563 that the Euxine-Hyrcanian province (western Europe, northern Iran) was a refugium for this
564 species (Browicz 1987, Akhiani et al., 2010). Ecological niche modeling projecting into the past
565 may enable a more complete view of the past distribution of *S. glutinosa*. A more detailed
566 view of the phylogeny of *Salvia* from eastern Asia is found in (Hu et al., 2018; Hu et al., 2020xx).

567 **4.2. Divergence times**

568 Our estimate for the date of origin of *Salvia* (31 Ma, 95% HPD = 37.6-27.5 Ma) is consistent
569 with previous studies (Drew et al., 2012; Drew et al., 2017), which is not surprising given that
570 the calibration used here was based on Drew et al. (2012) from analysis on a larger taxonomic
571 scale of Nepethoideae based on a fossil fruit of *Melissa* from the Early-Middle Oligocene.

572 The Qinghai-Tibetan Plateau (QTP) underwent four periods of uplift: 25-17 Ma, 15-13 Ma, 8-
573 7 Ma, and 3.5-1.6 Ma. The major radiation for *Salvia* in eastern Asia in clade IV is estimated
574 at 8-10 Ma, which coincides with the QTP uplift in the late Miocene. Our estimate for the
575 crown age of eastern Asian *Salvia* (~12 Ma) is consistent with that of Drew et al. (2017), but
576 is younger than that reported in another recent study (Hu et al., 2018) on eastern Asian *Salvia*
577 with an estimated date of ~17 Ma. This inconsistency might be because of different taxon
578 sampling, placement of calibrations, or prior distribution of the calibration node among the
579 studies. Our data suggest that the QTP uplift played an important role in local diversification
580 of *Salvia*, as it has for other plant genera in eastern Asia (Yao et al., 2016; Malik et al., 2017;
581 Hu et al., 2018).

582 The Arabia-Eurasian collision in the Oligocene-early Miocene led to the emergence of the
583 Alborz and Zagros Mountains in the Middle Miocene (15-12 Ma) in the Iranian plateau
584 (Manafzadeh et al., 2016). The main stage of crustal thickening from the collision was ~25 Ma,
585 and the uplift of the Iranian plateau took place ~15-12 Ma, with further uplift ~5 Ma (Djamali
586 et al., 2012; Manafzadeh et al., 2016). The emergence of these mountains coincides with the

587 age of the MRCA of Iranian *Salvia* species. Formation and uplift of mountains can play an
588 important role in evolutionary diversification through providing heterogeneous niches and
589 landscapes. Therefore, we postulate that the emergence and uplift of the Iranian Mountains
590 during the last ~12 Ma, along with subsequent aridification (Manafzadeh et al., 2016; Folk et
591 al., 2020), provided new ecological opportunities and habitat for *Salvia* diversification in Iran.

592

593 **4.3. Ancestral state reconstruction**

594 4.3.1. Corolla length

595 Across *Salvia* phylogeny, there were multiple shifts from a corolla length longer than 25 mm
596 to shorter corollas within and among clades. The MRCA of subg. *Calosphace* had a corolla
597 length less than 25 mm, but multiple shifts from short (~4 mm) to long (~45 mm) corollas
598 occurred in subclades of *Calosphace*. Based on the current study and previous reports (Wester
599 and Claßen-Bockhoff, 2011; Wester et al., 2020), most *Salvia* species with an average corolla
600 length of 22.3 ± 6.5 mm are visited by bees, while bird pollinators are more attracted to flowers
601 with an average corolla length of 31 ± 9.5 mm. Floral construction is associated with the type
602 of pollinators in *Salvia* (Wester et al., 2020), and an overall correlation between flower size
603 and pollinator is not expected across all *Salvia* lineages. For instance, *S. blepharochlaena*,
604 which is distributed in Turkey, is melittophilous, but has a long corolla. *Salvia purpurea* in
605 subgen. *Audibertia* has an intermediate flower (pollinated by bees and hummingbirds); *S.*
606 *purpurea* has a long corolla (19-36 mm) and long flower tube that is characteristic of
607 hummingbird-pollinated *Salvia* species, but the flower has the wide landing platform of a bee-
608 pollinated flower (Wester and Claßen-Bockhoff, 2011). Special flower traits like a short flower
609 tube cause a phenotypic trade-off and adaptation to birds and bees, but if a short tube is
610 combined with a narrow corolla opening, this combination of floral traits can generalize to
611 both pollinators (Ohashi et al., 2021). We do not imply that corolla length is the only trait
612 involved in *Salvia*–pollinator interactions; other factors, such as flower shape, tube length,
613 and color, may also be involved in pollinator attraction and adaptation (Landis et al., 2018;
614 Wessinger et al., 2019; Kriebel et al., 2020).

615 4.3.2. Lever mechanism

616 *Salvia* species with an active lever mechanism are characterized by modified stamens. The
617 lever is formed by elongation of the connective tissue that widens and separates the two
618 thecae from each other. Levers have evolved several times in parallel both within and
619 between clades I and II (Drew and Sytsma, 2012). In this study, we inferred the ancestral state
620 based on two models considering different rates of evolution. Based on the ER model (Equal
621 Rates), the ancestral state for *Salvia* is equivocal, and two alternative hypotheses may explain
622 the distribution of the lever mechanism across *Salvia*. First, the MRCA of *Salvia* may have had
623 a non-active lever mechanism, and a lever evolved independently multiple times in separate
624 lineages. Alternatively, the ancestor of *Salvia* may have had an active lever mechanism, and
625 several losses and reversals took place throughout the clade. Additionally, the HiSSE analysis,
626 with the preference of the irreversible model for lever mechanism diversification, suggests
627 that changes from non-active to active lever is not plausible or at the very least evolutionarily
628 difficult. Therefore, we argue that a *Salvia* ancestor with an active lever is more probable than
629 a non-active lever.

630 4.3.3. Habit

631 The ancestral habit in *Salvia* is reconstructed here as equivocal. Several shifts from woody to
632 herbaceous occurred within the main clades. This ambiguity might be due to diverse clades
633 that transition frequently between woody and herbaceous, making it difficult to infer the
634 state of the MRCA of *Salvia*.

635 **4.4. Corolla length evolution**

636 4.4.1. Disparity Through Time

637 The value obtained (MDI = 0.21) for the disparity of corolla length reflects a high rate of
638 diversification and morphological lability in related species. The positive MDI value for
639 disparity shows that most of the variation in corolla size is within subclades, while a negative
640 MDI indicates higher disparity among subclades, which is traditionally interpreted as adaptive
641 radiation (Harmon et al., 2010). Increasing disparity in corolla length during the last 10 M
642 years of *Salvia* evolution coincides with a number of geological events, including the Andean
643 uplift, Mexican vulcanization (clade II), the uplift of the QTP (clade IV), and the uplift of the
644 Zagros Mountains (occupied by species in clade I; Ferrari et al., 2012; Yao et al., 2016;

645 Manafzadeh et al., 2016), all major geological events that may have profoundly shaped *Salvia*
646 evolution worldwide.

647 Our positive value of MDI and support for the OU model contrast with traditional
648 interpretations of adaptive radiation in which MDI is negative through phenotypic
649 diversification with the Early Burst (EB) model of diversification (Harmon et al., 2010). In
650 addition, the DDD analyses do not support density-independent lineage diversification, and
651 the Yule model was selected as the best model with no apparent slowdown in *Salvia*
652 diversification. In the classic definition of adaptive radiation, the rate of diversification first
653 increases due to access to new niche space, followed by slow diversification as niche space
654 fills (Rabosky, 2013; Gillespie et al., 2020). However, Augilee et al. (2018) argued that
655 ecological niche filling as an explanation for negative-dependent diversity should be treated
656 with caution because biotic (competition) and abiotic factors (landscape dynamics) can
657 correspond to species diversity in different stages of a clade's history.

658 4.4.2. Corolla length diversification

659 Floral traits have played a key role in enhancing angiosperm diversification (e.g., Stebbins,
660 1970; Fenster et al., 2014; Armbruster, 2014; Van der Neit and Johnson, 2014), and some
661 floral characters (corolla length, corolla tube length, corolla shape, and flower color) are
662 associated with pollinator interactions. The positive effects of certain floral traits on the
663 effectiveness of one group of pollinators relative to others occurs most often in bilaterally
664 symmetrical flowers (Ollerton, 2009; Armbruster, 2014; Wester et al., 2020). The rate of
665 evolution of corolla length in one clade of *Calosphace* (clade II) was significantly higher than
666 in other clades. Detection of correlated rate shifts in this clade implies that changes in corolla
667 length may have enabled an adaptive radiation in this clade. Species in this clade are mostly
668 distributed in South and Central America, including Bolivia, Mexico, Peru, and Argentina, and
669 include hummingbird-pollinated species with several shifts to bee pollination (Fragoso-
670 Martinez et al., 2017; Kriebel et al., 2019). Therefore, corolla size may be a putatively adaptive
671 trait that facilitated pollinator-flower interactions in this clade.

672 **4.5. Lever-mechanism-dependent diversification**

673 The special lever-mechanism pollination system in *Salvia* has been hypothesized to have
674 played a major role in *Salvia* diversification (Claßen-Bockhoff et al., 2004; Drew and Sytsma,

675 2012). The functionality and structure of the lever mechanism were tested through field
676 investigation and biomechanical experiments (Claßen-Bockhoff et al., 2004; Wester and
677 Claßen-Bockhoff, 2004; Reith et al., 2007; Drew and Sytsma, 2012; Zheng et al., 2015).
678 However, the actual effect of the lever mechanism on diversification has not been previously
679 investigated. We examined this hypothesis across our phylogeny using a Hidden Markov
680 Model implemented in the HiSSE package. The best model fitted was the HiSSE model with
681 irreversible transitions among states. The lever mechanism likely has an important impact on
682 pollination success (Classen-Bockhoff et al., 2004; Zheng et al., 2015; Kriebel et al., 2019) and
683 may have influenced diversification, but we did not find any evidence for a direct association
684 of lever mechanism with *Salvia* diversification. Characters not measured here, including
685 flower shape features that are associated with the observed state, were likely influential as
686 well (Kriebel et al., 2020). Based on the HiSSE analysis, we suggest that emphasis on the lever
687 mechanism alone as the key promotor of diversification in *Salvia* may be misplaced and that
688 other phenotypic characters, especially other floral traits, should also be considered and
689 examined across the phylogeny. We should take into account that there might be
690 shortcomings and insufficient information in macroevolutionary models and that trees for
691 extant species may not permit the precise reconstruction of historical diversification (Louca
692 and Pennell, 2020). However, Helmsetter et al. (2021) argue that recent more complex
693 models can provide additional information and overcome the problems of relying on time
694 trees for extant species. An important issue for future studies in understanding *Salvia*
695 evolutionary history is assessing the effect of other floral traits on diversification via the
696 reconstruction of more robust phylogenetic trees using more genes and species.

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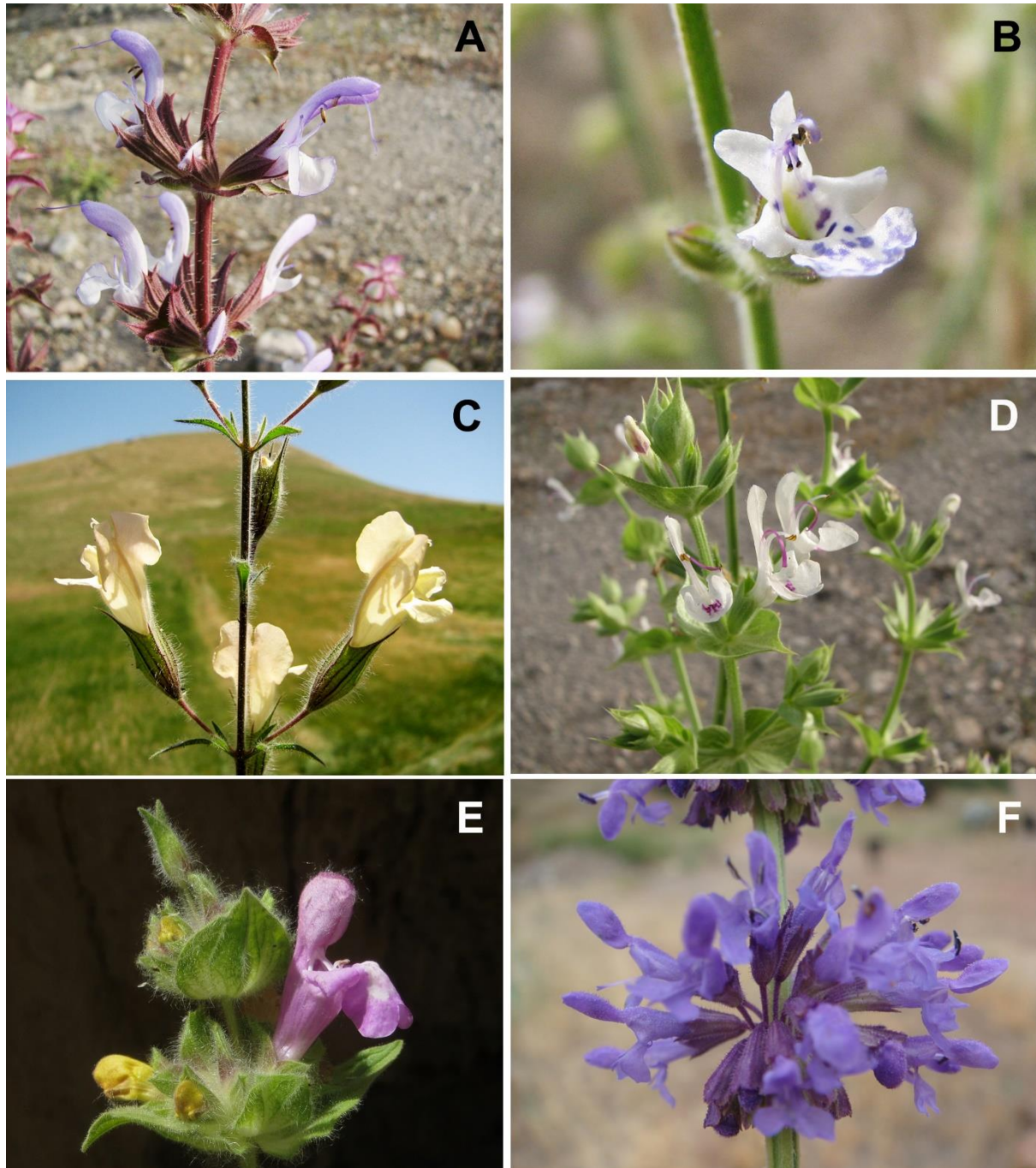
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1078 **Fig 1:** Phenotypic diversity in Iranian *Salvia*. A: *Salvia sclarea* (clade I), B: *Salvia aegyptiaca* (clade III)
1079 C: *Salvia aristata* (clade III), D: *Salvia macrosiphon* (clade I), E: *Salvia bracteata* (clade I), F: *Salvia*
1080 *verticillata* (clade I). A-E: Photos by M. Mirtajzadini, F: Photo by K. Safikhani.

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| | Walker and Sytsma (2007) | Will and Claßen -Bockhoff (2017) | Drew et al. (2017), Hu et al. (2018) |
|-----------|--------------------------|----------------------------------|--------------------------------------|
| Clade I | | | |
| Clade II | | | |
| Clade III | | | |
| Clade IV | Not determined | | |

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1086 **Fig 2.** Schematic trees provide a summary of changes in *Salvia* delimitation based on previous phylogenetic
1087 studies (Walker and Sytsma, 2007; Will and Bockhoff, 2017; Drew et al., 2017). Those species that are classified
1088 under *Salvia* infrageneric delimitations are shown in red. Distinct genera from *Salvia* are indicated in black.
1089 Walker and Systema (2007) recognized three distinct clades for *Salvia* phylogeny embedded within five genera
1090 (*Perovskia*, *Rosmarinus*, *Dorystaechas*, *Meriandra* and *Zhumeria*). Will and Bockhoff (2017) identified just part
1091 of clade I as *Salvia* sensu stricto and split *Salvia* into six genera. Drew et al. (2017) maintained *Salvia* in the broad
1092 sense and treated the five genera in Walker and Sytsma (2007) as subgenera of *Salvia*. Hu et al. (2018) treated
1093 clade IV (from eastern Asia) as subg. *Glutinaria*.

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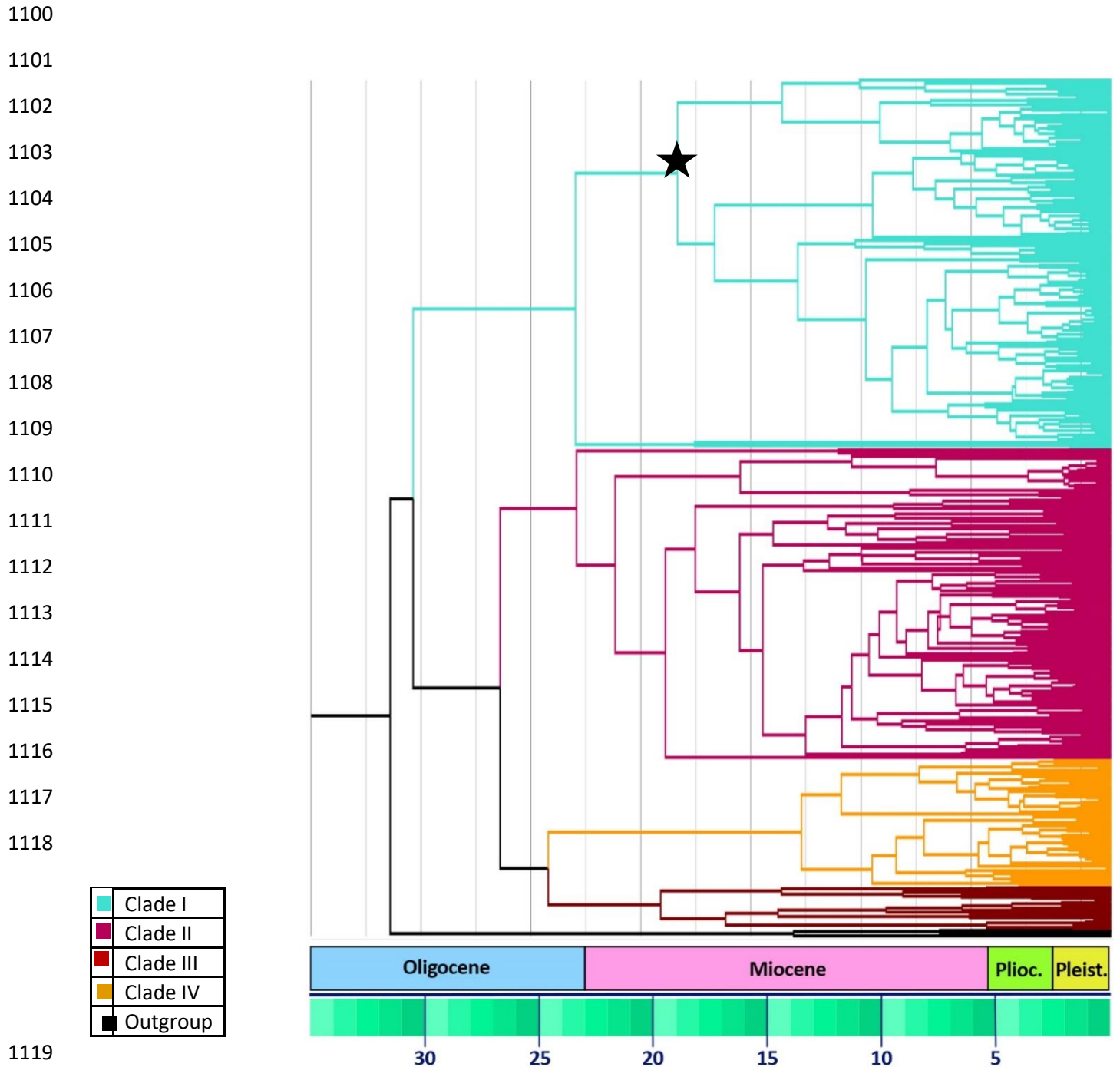
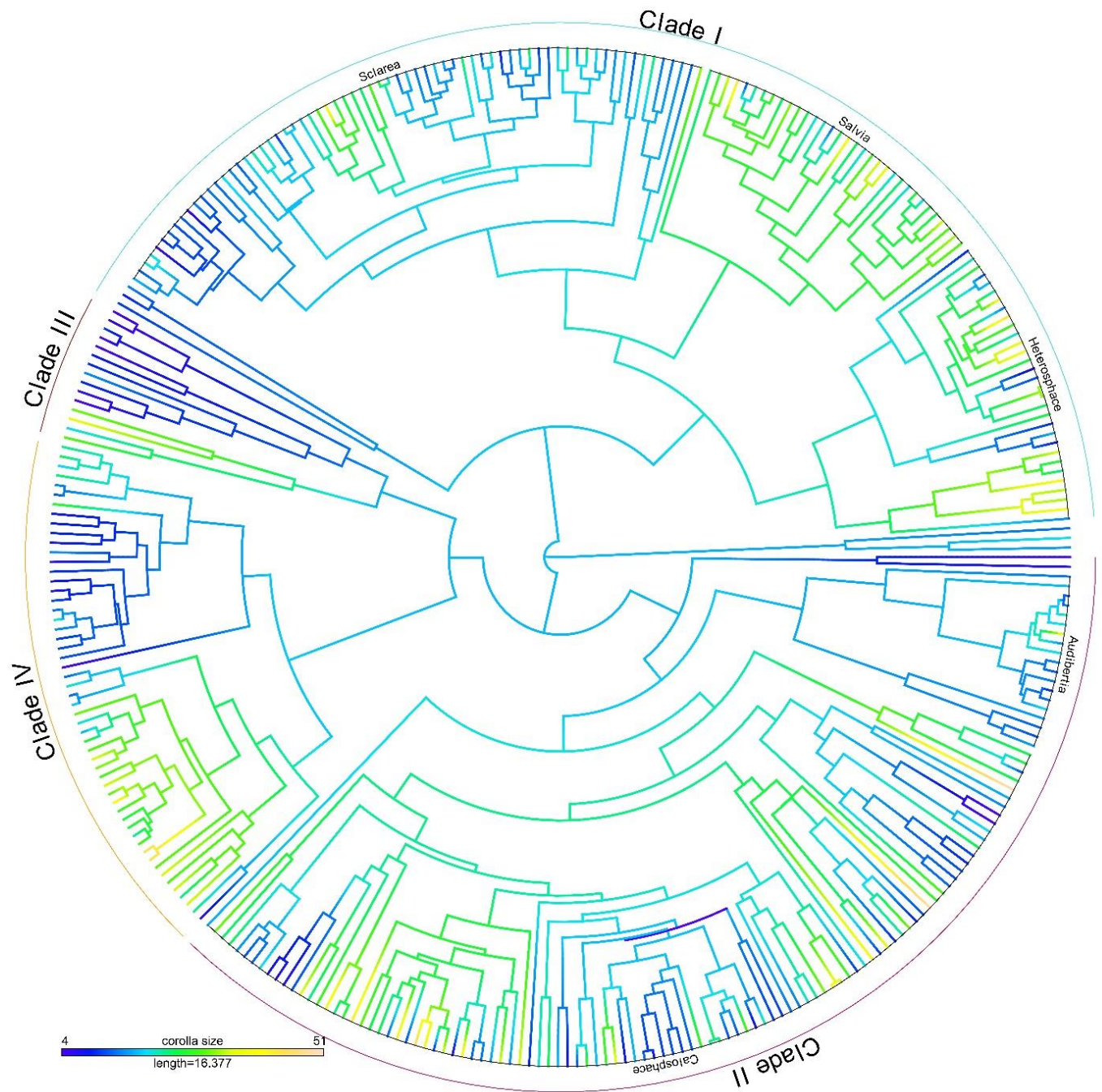


Fig. 3: Maximum Clade Credibility (MCC) obtained from BEAST analysis based on five combined nuclear and plastid spacer regions. The map is colored based on four identified clades in *Salvia*. The x-axis represents the age range of extant *Salvia* lineages. The star indicates divergence of the southwestern Asia clade I (Turkey and Iran) including subgenera *Sclarea* and *Salvia* from Subgenus *Heterosphaea*



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1131 **Fig. 4:** Ancestral reconstruction of corolla length in *Salvia* on a dated phylogeny using maximum
1132 likelihood in the phytools R package. The legend indicates the range of corolla length in mm by
1133 branch color in *Salvia*. Four distinct clades in *Salvia* are identified by relevant colors on the
1134 circumference of the tree.

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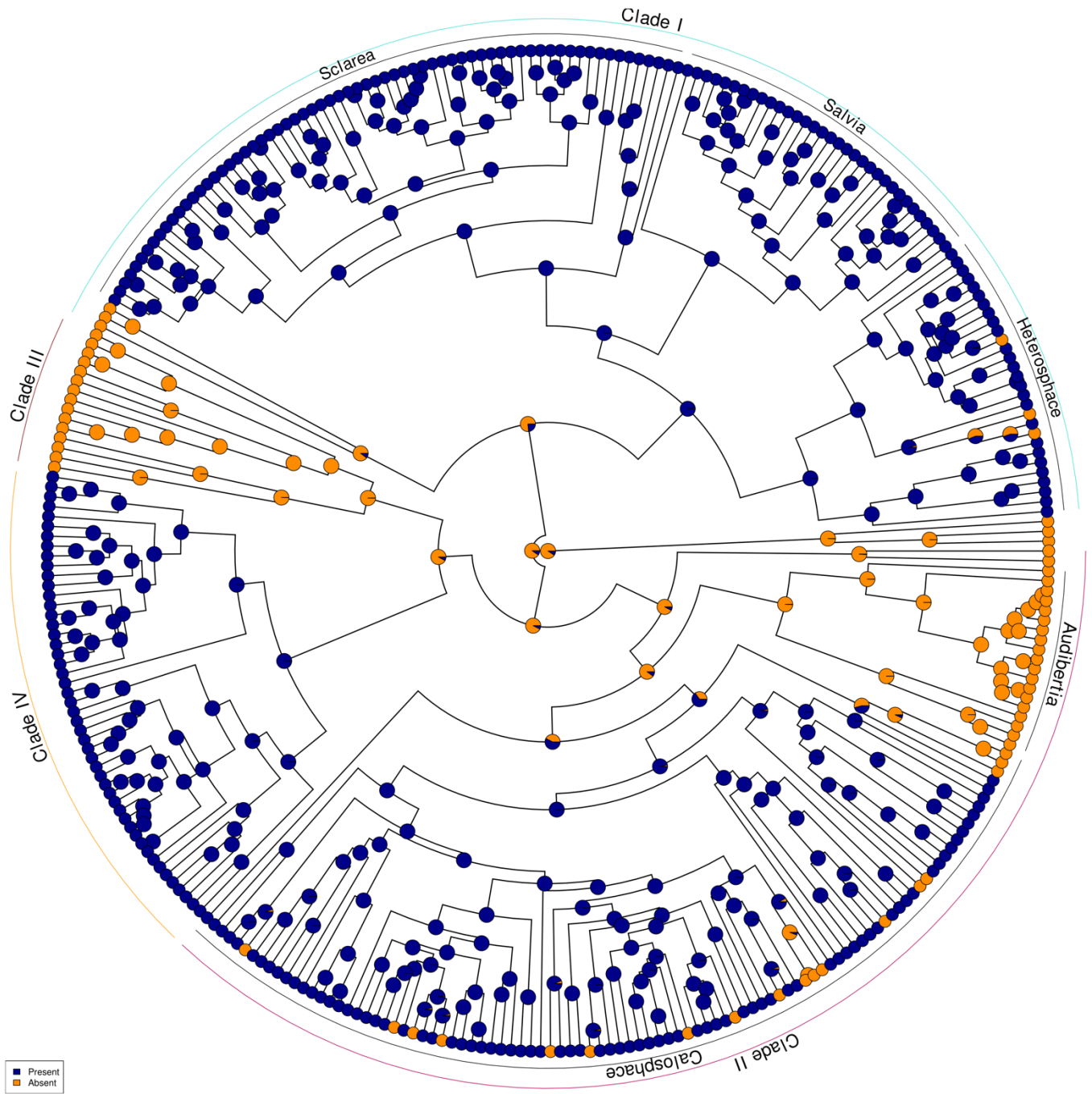
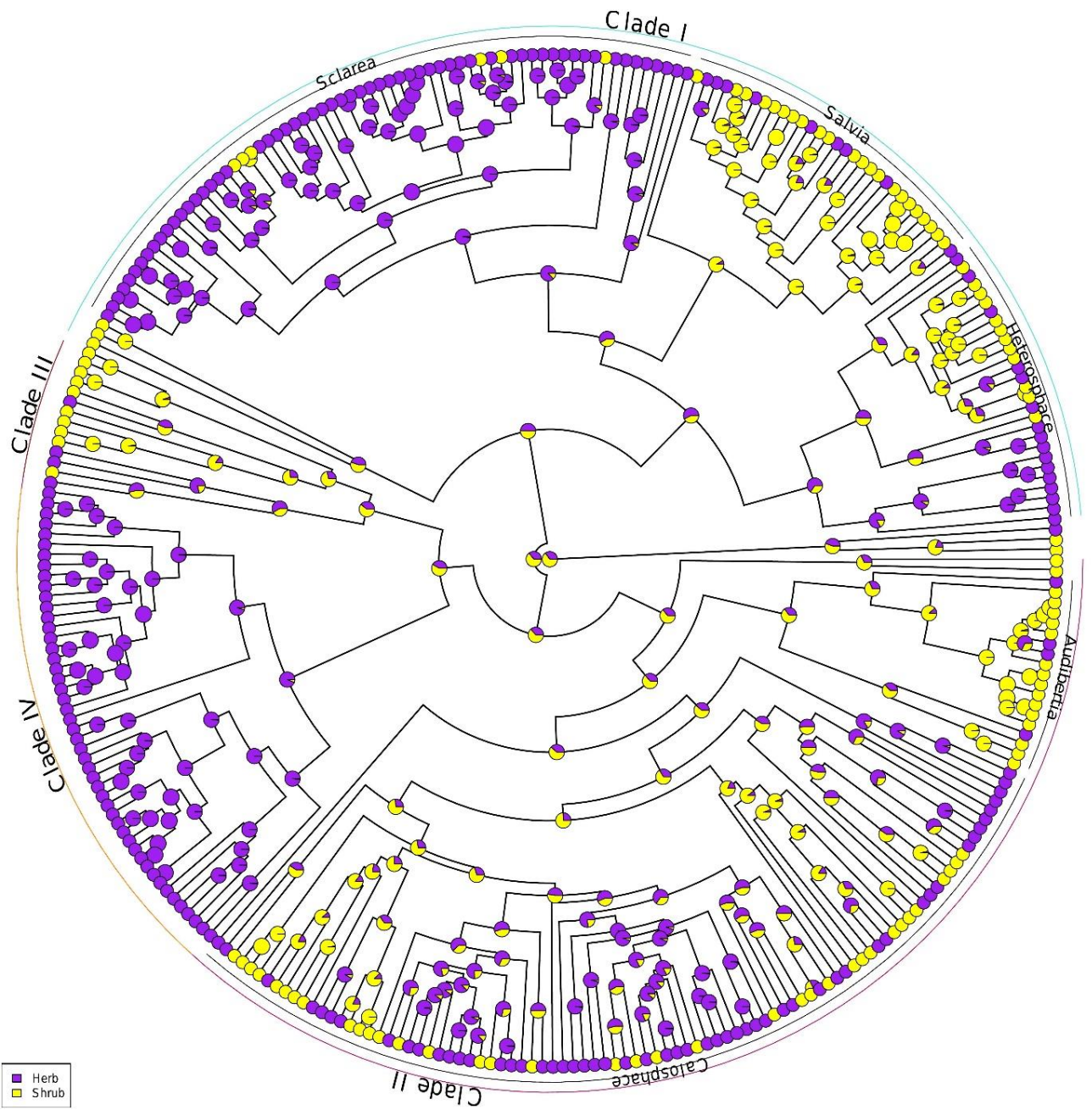


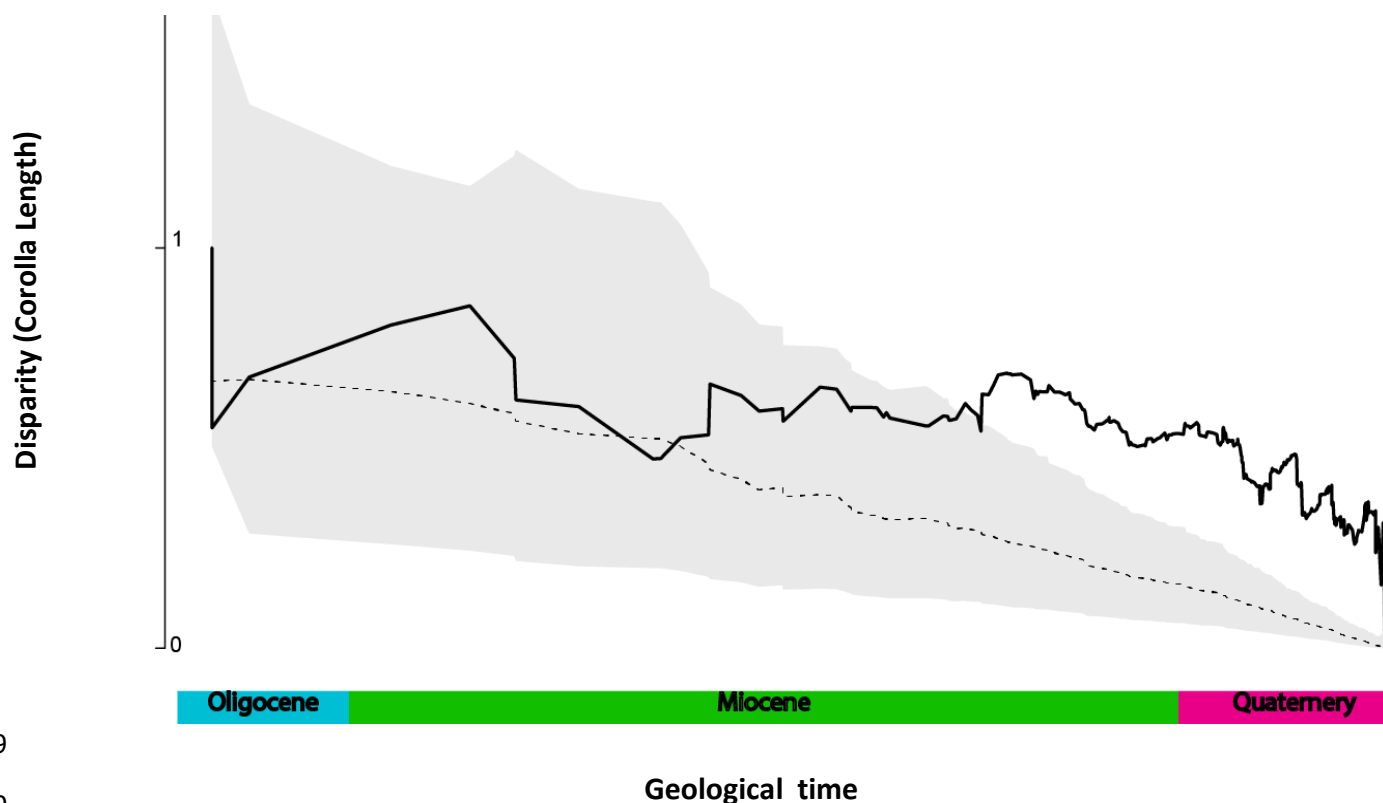
Fig. 5: Ancestral reconstruction of the lever mechanism trait (present/ absent) across *Salvia* phylogeny based on likelihood state with ARD model.

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1162 **Fig. 7:** The mean subclade Disparity Through Time (DTT) for corolla length compared with the
1163 median subclade disparity under a Brownian motion model. The solid line shows the observed
1164 disparity, and the dashed line is the mean disparity of 1000 simulations of corolla length disparity
1165 over the phylogenetic tree. The grey shade indicates the 95% confidence interval of DTT.

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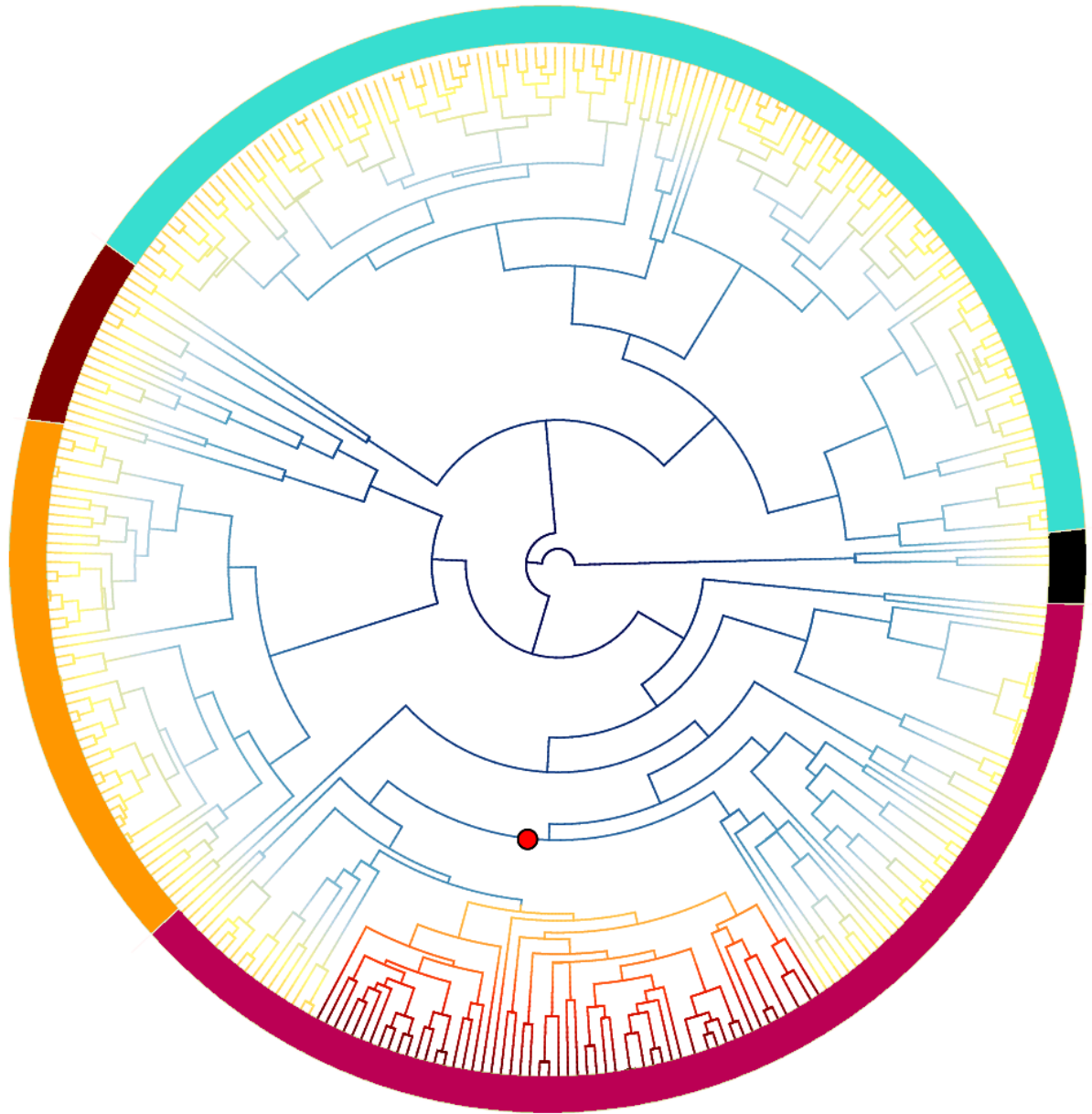
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|  | clade I |
|  | clade II |
|  | clade III |
|  | clade IV |
|  | Outgroup |

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1180 **Fig. 8:** Corolla length evolution across *Salvia* phylogeny based on a BAMM analysis. The best shift

1181 was detected in clade II in *Calosphace* clade

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Table 1: Plant materials used in this study with their accession numbers. Newly generated sequences are shown in bold. TARI (National Herbarium of Iran, Research Institute of Forests and Rangelands)

| | Voucher | ETS | ITS | Gen Bank rpl32-trnl | trnl-trnf | Ycf1 |
|--|--|------------|----------|------------------------|-----------|----------|
| <i>Lepechinia chamaedryoides</i> (Balb.) Epling (outgroup) | 1, 5) Drew and Sytsma 2011; 2) Walker and Sytsma 2007; 4) Walker et al., 2004. | JF301317 | DQ667231 | / | AY570459 | JF289031 |
| <i>Lepechinia leucopylloides</i> (Ramamoorthy, Hiriart & Medrano) B.T.Drew, Cacho & Sytsma, comb. nov. (outgroup) | 1, 2, 4, 5) Drew and Sytsma 2011; 3) Drew and Sytsma 2012. | JF301327.1 | JF301354 | JQ669348 | JF301390 | JF289047 |
| <i>Melissa officinalis</i> L. (outgroup) | 1, 2, 4, 5) Drew and Sytsma 2011; 3) Drew and Sytsma 2012. | JF301325 | JF301353 | JQ669335 | JF301386 | JF289042 |
| <i>S. africana-caerulea</i> L. | Will and Claßen-Bockhoff 2014. | | KJ584204 | Kj7472171 | / | / |
| <i>Salvia absconditiflora</i> Greuter & Burdet (syn. <i>S. cryptantha</i> Montbret & Aucher ex Benth.) | Will and Claßen-Bockhoff 2017 | / | KU563839 | KU578211 | / | // |
| <i>Salvia acerifolia</i> B.L.Turner. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664540 | / | MF663939 | / |
| <i>Salvia adenocaulon</i> H.P.Davis | Will and Claßen-Bockhoff 2017. | / | KU563828 | KU563828 | / | / |
| <i>Salvia adenophora</i> M.Martens & Galeotti | 2,4) Fragoso-Martinez et al., 2017. | / | MF622100 | / | MF663940 | / |
| <i>Salvia adenophylla</i> Hedge and Hub.-Mor. | Will and Claßen-Bockhoff 2017. | / | KU563789 | KU578218 | / | / |
| <i>Salvia aegyptiaca</i> L. | Iran: Bushehr, TARI (26835). | MK204892 | / | / | / | / |
| <i>Salvia aegyptiaca</i>. | Iran: Hormozgan, TARI (102853). | MK204891 | MK256969 | / | / | / |
| <i>Salvia aethiopsis</i> L. | Iran: TARI (6604). | MK204890 | / | / | | MK240102 |
| <i>Salvia agnes</i> | 2,4) Fragoso-Martinez et al., 2017. | | MF664541 | | MF663941 | |
| <i>Salvia akiensis</i> A.Takano, T.Sera et Kurosaki. | 1,2,4,5) Takano and Akiyama 2017. | LC060826 | LC060279 | / | LC124188 | LC060530 |

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|--|---|----------|----------|----------------|----------|----------|
| <i>Salvia albicaulis</i> Benth. | 1,2,3) Will and Claßen-Bockhoff 2014. | KJ584257 | KJ584206 | KJ747274 | / | / |
| <i>Salvia albimaculata</i> Hedge and Hub.-Mor. | Will and Claßen-Bockhoff 2017. | / | KU563790 | KU578219 | / | / |
| <i>Salvia amethystina</i> Sm. | 2) Fragoso-Martinez et al., 2017. | / | MF664545 | / | / | / |
| <i>Salvia amplexicaulis</i> Lam. | Will and Claßen-Bockhoff 2017. | / | KU563829 | KU578151 | / | / |
| <i>Salvia anatolica</i> Hamzaog̃lu and Duran | Will and Claßen-Bockhoff 2017. | / | / | KU563840 | KU578221 | / |
| <i>Salvia apiana</i> Jeps. | 1,4,5) Walker et al., 2015; 2) Walker et al., 2004; 3) Will and Claßen-Bockhoff 2014. | KP852935 | DQ667214 | KJ747321 | KP852890 | KP853066 |
| <i>Salvia aramiensis</i> Rech.f. | Will and Claßen-Bockhoff 2017 | / | KU563791 | KU578247 | / | / |
| <i>Salvia arbuscular</i> Fernald | 2,4) Jenks et al., 2010 | / | HQ418846 | / | HQ418949 | / |
| <i>Salvia argentea</i> L. | Will and Claßen-Bockhoff 2014. | / | KJ584164 | KJ747299 | / | / |
| <i>Salvia aristate</i> Aucher ex Benth. | 1) Drew and Sytsma 2011; 2,4) Walker and Sytsma 2007; 5) Drew and Sytsma 2011 | JF301336 | D667280 | / | DQ667465 | JF289059 |
| <i>Salvia aristata</i> | Iran: Isfahan, TARI (12495). | MK204889 | / | / | | MK240103 |
| <i>Salvia aspera</i> Fernald. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664547 | / | MF663948 | / |
| <i>Salvia atrocyanea</i> Epling. | 2,4) Walker and Sytsma 2007. | / | DQ667270 | / | DQ667456 | / |
| <i>Salvia atropatana</i> Bunge. | Iran, TARI (88803) | MK204887 | MK213193 | | | / |
| <i>Salvia atropatana.</i> | Iran, TARI (29283) | MK204888 | / | | | / |
| <i>Salvia aucheri</i> Benth. | 2,4) Walker and Sytsma 2007; Will and Claßen-Bockhoff 2017 | DQ667286 | KU578248 | DQ667471 | / | |
| <i>Salvia aurita</i> L. f. | Will and Claßen-Bockhoff 2014. | KJ584261 | KJ584218 | KJ747276 | / | / |
| <i>Salvia austriaca</i> Jacq. | 2,4) Walker and Sytsma 2007; 3) Will and Claßen-Bockhoff 2014. | / | DQ667323 | KJ747261 | DQ667512 | / |
| <i>Salvia axillaris</i> Moc. and Sessé ex Benth. | 1,3,5) Drew and Sytsma 2011. | JF301330 | MF664549 | JQ669366. 1 | MF663950 | JF301330 |
| <i>Salvia azurea</i> Michx. ex Vahl. | 2,4) Walker and Sytsma 2007. | / | DQ667317 | / | DQ667317 | / |
| <i>Salvia baimaensis</i> S.W.Su & Z.A.Shen | specimen_voucher="SBAI | / | JQ934103 | / | / | / |
| <i>Salvia ballotiflora</i> Benth. | 2,4) Jenks et al., 2010. | / | HQ418849 | / | HQ418952 | / |

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|--|---|------------|----------|----------|----------|----------|
| <i>Salvia bariensis</i> Thulin. | Will and Claßen-Bockhoff 2014. | KJ584262 | / | KJ747316 | / | / |
| <i>Salvia bazmanica</i> Rech.f. & Esfand. | Iran, TARI (43049). | MK204886 | / | / | / | |
| <i>Salvia blepharochlaena</i> Bedge and Hub.-Mor. | Will and Claßen-Bockhoff 2017. | / | KU578210 | KU578210 | / | / |
| <i>Salvia blepharophylla</i> Hedge & Hub.-Mor. | 2) Jenks et al., 2010. | / | HQ418850 | / | HQ418953 | / |
| <i>Salvia brachyantha</i> | Will and Claßen-Bockhoff 2017 | / | KU563844 | KU578154 | / | / |
| <i>Salvia brachysiphon</i> Stapf. | Iran, TARI (3162). | MK204885 | MK213194 | / | / | MK240104 |
| <i>Salvia brachysiphon</i> | Iran, TARI (1145). | MK204884 | MK213195 | / | / | MK240105 |
| <i>Salvia bracteata</i> Banks & Sol. | Iran, TARI (16642). | MK204883 | / | / | / | MK240107 |
| <i>Salvia brandegeei</i> Munz. | 1,2,4,5) Walker and Sytsma 2005. | KP852949.1 | KP852783 | / | KP852896 | KP853067 |
| <i>Salvia breviflora</i> Moc. & Sessé ex Benth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664551 | / | MF663952 | / |
| <i>Salvia brevipes</i> Benth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664552 | / | MF663953 | / |
| <i>Salvia broussonetii</i> Benth. | Will and Claßen-Bockhoff 2014. | KJ584263 | KJ584225 | KJ747293 | / | / |
| <i>Salvia bucharica</i> M.Popov. | Will and Claßen-Bockhoff 2017. | / | KU563794 | KU578222 | / | / |
| <i>Salvia bulleyana</i> Diels. | Will and Claßen-Bockhoff 2017 | / | / | KU578203 | / | / |
| <i>Salvia cabulica</i> Benth. | Walker and Sytsma 2007. | / | DQ667287 | / | DQ667472 | / |
| <i>Salvia cacaliifolia</i> Epling | 2) Jenks et al., 2010; 4) Walker and Sytsma 2007. | / | HQ418851 | / | DQ667259 | / |
| <i>Salvia cadmica</i> Boiss. | Will and Claßen-Bockhoff 2017. | / | KU563795 | KU578223 | / | / |
| <i>Salvia caespitosa</i> Montbret & Aucher. | Iran, TARI (85247). | MK204882 | MK213197 | / | / | / |
| <i>Salvia californica</i> Brandegee. | Drew and Sytsma 2015. | KP852951 | DQ667213 | / | DQ667424 | KP853068 |
| <i>Salvia candelabrum</i> Boiss. | Will and Claßen-Bockhoff 2014. | / | KJ584190 | KJ747255 | / | / |
| <i>Salvia candicans</i> M.Martens and Galeotti. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664557 | / | MF663958 | / |
| <i>Slavia candidissima</i> Vahl. | Walker and Sytsma 2007 | / | DQ667261 | / | DQ667447 | |
| <i>Salvia carduacea</i> Benth. | Walker et al., 2015. | / | KP852785 | / | KP852900 | KP853069 |
| <i>Salvia carnea</i> Kunth. | 2,4) Jenks et al., 2010. | / | HQ418854 | / | HQ418957 | / |

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|--|---|----------------|----------|----------|----------|----------|
| <i>Salvia cassia</i> Sam. ex Rech.f. | Will and Claßen-Bockhoff 2017. | / | KU563845 | KU578190 | / | / |
| <i>Salvia castanea</i> Diels | 2) Will and Claßen-Bockhoff 2017; 4) Wang et al., 2013. | / | KU563781 | / | KC414279 | / |
| <i>Salvia cavaleriei</i> H.Lév. | 1,4) Wang et al., 2013. | | KC473232 | | KC414280 | |
| <i>Salvia cedrosensis</i> Greene. | 1,5) Walker et al., 2015; 2) Walker and Sytsma 2007; 4) Murphy and Bola 2012. | KP852953 | DQ667228 | / | JQ888128 | KP853070 |
| <i>Salvia ceratophylla</i> L. | Iran, TARI, 17238B. | MK204881 | MK213198 | / | / | MK240107 |
| <i>Salvia chamaedryoides</i> Cav | 2) Jenks et al., 2010; 4) Walker et al., 2004 | / | HQ418855 | / | AY570471 | / |
| <i>Salvia chamelaeagnea</i> Berg. | Will and Claßen-Bockhoff 2014 | KJ584268 | KJ584210 | KJ747289 | / | / |
| <i>Salvia chienii</i> E. Peter. | Will and Claßen-Bockhoff 2014 | / | KJ584250 | KJ747322 | | |
| <i>Salvia chinensis</i> Benth. | PS0121MT04 | / | FJ883503 | / | / | / |
| <i>Salvia chionantha</i> Boiss. | Will and Claßen-Bockhoff 2017 | / | KU563846 | KU578155 | / | / |
| <i>Salvia chionoeplica</i> Epling. | 1,2,3) Will and Claßen-Bockhoff 2014; 4) Walker et al., 2004; 5) Walker et al., 2015. | KJ747318 | KJ584188 | KJ747318 | AY570472 | KP853071 |
| <i>Salvia chloroleuca</i> Rech.f. & Aellen. | Iran, TARI (36026). | MK204879 | MK212199 | / | / | MK240109 |
| <i>Salvia chloroleuca.</i> | Iran, TARI (12691). | MK204880 | / | / | / | MK240108 |
| <i>Salvia chorassanica</i> Bunge. | Iran, TARI (5354). | MK204878 | MK213200 | / | / | MK240110 |
| <i>Salvia chrysophylla</i> Stapf. | Will and Claßen-Bockhoff 2017. | / | KU563848 | KU578157 | / | / |
| <i>Salvia cinnabarina</i> M.Martens and Galeotti. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664559 | / | MF663960 | / |
| <i>Salvia clevelandii</i> (A. Gray). | 1) JBW 3079; 2,4) Fragoso-Martinez et al., 2017. | KP853032 | MF664560 | / | MF663961 | / |
| <i>Salvia clinopodioides</i> Kunth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664561 | / | MF663962 | / |
| <i>Slavia coccinea</i> Buc'hoz ex Etl. | 2) Trusty et al., 2004; 4) Wang et al., 2013. | / | AY506651 | / | KC414281 | / |
| <i>Salvia columbariae</i> Benth. | 4) Walker et al., 2015 | KP852960. 1 | KP852793 | / | KP852905 | KP853073 |
| <i>Salvia compressa</i> Vent. | Iran: Hormozgan, TARI (102856) | MK204877 | MK213201 | / | / | / |
| <i>Salvia concolor</i> Lamb. ex Benth. | 2,4) Jenks et al., 2010 | / | HQ418858 | / | HQ418961 | / |

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| <i>Salvia confertiflora</i> Pohl. | 2,4) Jenks et al., 2010. | / | HQ418859 | / | HQ418962 | / |
| <i>Salvia confertispicata</i> . | 2,4) Fragoso-Martinez et al., 2017 | / | MF664563 | / | MF663964 | / |
| <i>Slavia congestiflora</i> Epling. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664564 | / | MF663965 | / |
| <i>Salvia connivens</i> Epling. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664565 | / | MF663966 | / |
| <i>Salvia corrugata</i> Vahl. | 2) Fragoso-Martinez et al., 2017; 4) Walker et al., 2004. | | MF622122 | | AY570476 | |
| <i>Salvia cuspidata</i> (Benth.) J.R.I.Wood. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664568 | / | MF663970 | / |
| <i>Salvia cyanescens</i> Boiss. and Bal. | Will and Claßen-Bockhoff 2017. | / | KU563849 | KU578158 | / | / |
| <i>Salvia cyclostegia</i> E. Peter. | 2,4) Wang et al., 2013. | / | KC473274 | / | KC414282 | |
| <i>Salvia cynica</i> Dunn. | Walker and Sytsma 2007. | / | DQ667332 | / | DQ667521 | |
| <i>Salvia dabieshanesis</i> J.Q.He. | PS1723MT01 | | FJ883505 | / | / | / |
| <i>Salvia daghestanica</i> Sosn. | Walker and Sytsma 2007. | / | KJ584187 | KJ747308 | DQ667444 | / |
| <i>Salvia densiflora</i> Benth | 2,4) Fragoso-Martinez et al., 2017. | / | MF664570 | / | MF663972 | / |
| <i>Salvia deserta</i> omit. | Will and Claßen-Bockhoff 2017. | / | KJ584176 | KJ747263 | | |
| <i>Salvia deserti</i> Decne. | 2,3) Will and Claßen-Bockhoff 2014. | KJ584270 | / | KJ747312 | / | / |
| <i>Salvia dianthera</i> Roth ex Room, and Schult. | 2, 4) Walker and Sytsma 2007; 5) Drew and Sytsma 2011. | JF301326.1 | DQ667329 | / | DQ667518 | JF289044 |
| <i>Salvia dichroantha</i> Stapf. | Will and Claßen-Bockhoff 2017 | / | KU578159 | KU56830 | | |
| <i>Salvia digitaloides</i> Diels. | 2) Walker & Sytsma 2007; 4) Walker & Sytsma 2004. | / | / | DQ667255 | AY570477 | / |
| <i>Salvia discolor</i> Sessé & Moc. | 2,4) Jenks et al., 2010. | / | HQ418860 | / | HQ418963 | / |
| <i>Salvia disermas</i> L. | 1,2,3) Will and Claßen-Bockhoff 2014; 4) Walker et al., 2004. | KJ584271 | KJ584179 | KJ747296 | AY570478 | / |
| <i>Salvia disjuncta</i> Fernald. | 2,3) Will and Claßen-Bockhoff 2017; 4) Fragoso-Martinez et al., 2017. | / | KU563882 | KU578197 | MF663975 | / |
| <i>Salvia divaricata</i> Montbret & Auch. ex Benth. | Will and Claßen-Bockhoff 2017 | / | / | KU578226 | / | / |

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| <i>Salvia divinorum</i> Epling & Játiva. | 2,4) JBW 2330 | / | HQ418861 | / | DQ667440 | / |
| <i>Salvia dolomitica</i> Codd. | 1,3) Will and Claßen-Bockhoff 2014; 2,4) Walker and Sytsma 2007; | KJ584274 | DQ667322 | KJ747290 | DQ667511 | / |
| <i>Salvia dombeyi</i> Epling. | 2,4) Jenks et al., 2010 | / | HQ418862 | / | HQ418965 | / |
| <i>Salvia dorisiana</i> Standl. | 2,4) Jenks et al., 2010 | / | HQ418863 | / | HQ418966 | / |
| <i>Salvia dorrii</i> (Kellogg.) Abrams. | 1,4,5) Walker et al., 2015; 2) Walker and Sytsma 2007 | KP853037 | DQ667229 | / | KP852907 | KP853074 |
| <i>Salvia dorystaechas</i> B. T. Drew | 2) Will and Claßen-Bockhoff 2014; 3) Drew and Sytsma 2012; 4) Walker et al., 2004; 5) Drew and Sytsma 2011 | KJ584257 | KJ584284 | JQ669302 | AY570454 | JF289014 |
| <i>Salvia dracocephaloides</i> Boiss. | Iran, TARI (30192). | MK204876 | Mk213202 | / | / | MK240111 |
| <i>Salvia elegans</i> Vahl. | 2,4) Fragoso-Martinez et al., 2017. | / | MF622127 | / | MF663978 | / |
| <i>Salvia engelmannii</i> A. Grey. | Will and Claßen-Bockhoff 2017 | / | KU563870 | Ku578163 | / | / |
| <i>Salvia eremophila</i> Boiss. | Iran, TARI (41741). | MK204875 | / | / | / | MK240112 |
| <i>Salvia eremostachya</i> Jeps. | 1,4,5) Walker et al., 2015; 2) Walker and Sytsma 2007. | KP853039 | DQ667232 | / | KP852910 | KP853075 |
| <i>Salvia eriophora</i> Boiss. and Kotschy. | Will and Claßen-Bockhoff 2017 | / | KU563850 | KU578167 | | |
| <i>Salvia erythrostoma</i> Rusby. | Jenks et al., 2010. | / | HQ418864 | / | HQ418967 | / |
| <i>Salvia euphratica</i> Montbret and Aucher ex Benth. | Dizkirici et al., (2015). | / | KM519756 | KU578227 | KM519770 | / |
| <i>Salvia evansiana</i> Hand.-Mazz. | 2,3) Will and Claßen-Bockhoff 2014; 3) Zhong et al., 2010. | / | KJ584251 | KJ747323 | FJ593462.1 | / |
| <i>Salvia exserta</i> Grieseb. | 2,4) Fragoso-Martinez et al., 2017 | / | MF622128 | / | MF663979 | / |
| <i>Salvia farinacea</i> Benth. | 2) Chen et al., 2010; 4) Walker et al., 2004. | / | FJ546871 | / | AY570479 | / |
| <i>Salvia filifolia</i> Ramamoorthy. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664576 | / | MF663980 | / |
| <i>Salvia flocculosa</i> Benth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664578 | / | MF663982 | / |
| <i>Salvia formosa</i> L'Hér. | 2) Fragazo –Martinez et al., 2017. | / | MF622131 | / | / | / |
| <i>Salvia frigida</i> Boiss. | Will and Claßen-Bockhoff 2017. | / | KU563851 | KU578168 | / | / |
| <i>Salvia fruticosa</i> Miller. | Will and Claßen-Bockhoff 2014. | / | KJ584195 | KJ747256 | / | |

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| <i>Salvia fulgens</i> Cav. | 2) Walker and Sytsma 2007; 4) Benitez-Vieyra et al., 2014. | / | MF622133 | / | KJ473988 | / |
| <i>Salvia funerea</i> M. E. Jones. | Walker et al., 2015. | KP853041 | KP852812 | / | KP852911 | KP853076 |
| <i>Salvia galloana</i> B.L.Turner. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664581 | / | MF663985 | / |
| <i>Salvia garipensis</i> E.Meyer ex Benth | Walker and Sytsma 2007. | / | DQ667281 | / | DQ667466 | / |
| <i>Salvia geminata</i> Thulin. | 1) Will and Claßen-Bockhoff 2014. | KJ584276 | / | / | / | / |
| <i>Salvia gesneriiflora</i> Lindl. & Paxton. | 2,4) Fragoso-Martinez et al., 2017. | / | MF622133 | / | MF663986 | / |
| <i>Salvia glabrescens</i> var. <i>repens</i> (Koidz.) Kurosaki. | Sudarmono and Okada 2007. | LC060829.1 | AB295104 | / | AB295089 | LC060533 |
| <i>Salvia glutinosa</i> L. | Iran, TARI (21565). | MK204873 | MK213203 | / | / | Mk240113 |
| <i>Salvia glutinosa</i> . | 2) Will and Claßen-Bockhoff 2014; 4) Walker et al., 2004; 5) Drew and Sytsma 2011. | / | KU563774 | / | AY570480 | JF289061 |
| <i>Salvia gracilliramulosa</i> Epling & Játiva. | 2.4) Walker and Sytsma 2007. | / | DQ667276 | / | DQ667461 | / |
| <i>Salvia gravida</i> A.Gray. | 2,4) Jenks et al., 2010. | / | HQ418868 | / | HQ418971 | / |
| <i>Salvia greatae</i> Brandegee. | 1,5) Drew and Sytsma 2011; 2) Walker and Sytsma 2007; 3) Drew and Sytsma 2012; 4) Walker et al., 2004. | JF301331 | DQ667215 | JF289062 | AY570481 | JF289062 |
| <i>Salvia greggii</i> A.Gray. | 2,4) Jenks et al., 2010. | / | HQ418870 | / | HQ418972 | / |
| <i>Salvia grewiifolia</i> S. Moore. | 2,4) Jenks et al., 2010. | / | HQ418871 | / | HQ418973 | / |
| <i>Salvia grossheimii</i> Sosn. | Iran, TARI (84031). | MK204832 | MK213204 | / | / | / |
| <i>Salvia guadalajarensis</i> Briq. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664584 | / | MF663989 | / |
| <i>Salvia guaranitica</i> Briq. | 2,4) Wang et al., 2013. | / | KC473237 | / | KC414285 | |
| <i>Salvia handelii</i> E.Peter. | SHAN | | JQ934124 | / | / | / |
| <i>Salvia hayatana</i> Makino ex Hayata. | 2,4) Sudarmono and Okada 2007; 5) Takano 2017. | / | AB295099 | / | AB295084 | / |
| <i>Salvia heerii</i> Regel. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664587 | / | | / |
| <i>Salvia heldreichiana</i> Boiss. ex Benth | Will and Claßen-Bockhoff 2017. | / | KU563799 | KU578246 | / | / |

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| <i>Salvia henryi</i> Gray. | Will and Claßen-Bockhoff 2017. | / | KU563875 | KU578165 | / | / |
| <i>Salvia herbacea</i> Benth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664589 | / | MF663994 | / |
| <i>Salvia herbanica</i> A.Santos and M.Ferna´ndez. | Will and Claßen-Bockhoff 2014. | KJ584278 | KJ584246 | KJ747313 | / | / |
| <i>Salvia heterochroa</i> E. Peter. | 2,3) Will and Claßen-Bockhoff 2014. | / | KJ584252 | KJ747324 | / | / |
| <i>Salvia heterochroa</i> E.Peter. | Will and Claßen-Bockhoff 2017 | / | KJ584252 | KJ747324 | / | / |
| <i>Salvia heterofolia</i> Epling & Mathias. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664590 | / | MF663995 | / |
| <i>Salvia hians</i> Royle ex Benth. | 4) Walker et al., 2004. | / | DQ763239 | / | AY570483 | / |
| <i>Salvia hidalgensis</i> Miranda. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664591 | / | MF663996 | / |
| <i>Salvia hintonii</i> Epling. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664592 | / | MF663997 | / |
| <i>Salvia hirtella</i> Vahl | 2,4) Walker and Sytsma 2007. | / | DQ667326 | / | DQ667515 | / |
| <i>Salvia hispanica</i> L. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664593 | / | MF663998 | / |
| <i>Salvia honania</i> L.H.Bailey. | PS1722MT01 | / | FJ883513 | / | / | / |
| <i>Salvia huberi</i> Hedge. | Will and Claßen-Bockhoff 2017. | / | KU563800 | KU578228 | / | / |
| <i>Salvia hylocharis</i> Diels | Wang et al., 2013. | / | KC414286 | / | KC473238 | / |
| <i>Salvia hypargeia</i> Fisch. and Mey. | Will and Claßen-Bockhoff 2017. | / | KU563876 | KU578196 | / | / |
| <i>Salvia hypochionaea</i> Boiss. | Iran, TARI (30437). | MK204870 | MK213206 | / | / | / |
| <i>Salvia hypoleuca</i> Benth. | Iran, TARI (54151). | MK204869 | MK213207 | / | / | MK240115 |
| <i>Salvia indica</i> L. | Iran, TARI (90002). | MK204868 | MK213208 | / | / | MK240116 |
| <i>Salvia interrupta</i> Schousb. | Will and Claßen-Bockhoff 2014. | / | KJ584191 | KJ747265 | / | |
| <i>Salvia isensis</i> Nakai ex Hara. | Takano and Akiyama 2017. | LC060831.1 | LC060730 | / | LC124190 | LC060535 |
| <i>Salvia jamzadii</i> Mozaff. | Iran, TARI (61992). | MK204867 | MK213209 | | | MK240117 |
| <i>Salvia japonica</i> f. longipes (Nakai) Sugimoto. | 1,4,5) Sudarmono and Okada (2007); 2) Takano and Akiyama 2017. | LC060835.1 | AB266239 | / | LC124191 | LC060537 |
| <i>Salvia judaica</i> Boiss. | Will and Claßen-Bockhoff 2017. | / | KJ584241 | KU578160 | / | / |
| <i>Salvia jurisicii</i> Kořanin. | Will and Claßen-Bockhoff 2017 | / | KU563831 | KU578173 | / | / |
| <i>Salvia karwinskii</i> Benth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF622144 | / | MF664003 | / |
| <i>Salvia kiaometiensis</i> H. Lév. | 2,4) Wang et al., 2013 | / | KC473239 | / | KC414287 | / |

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| <i>Salvia Koyamae</i> Makino. | 2,4) Takano and Okada 2011 | | AB541114 | AB541142 | / | LC060540 |
| <i>Salvia kronenburgii</i> Rech. f. | Will and Claßen-Bockhoff 2017 | / | KM519759 | KU578245 | KM519773 | / |
| <i>Salvia kurdica</i> Boiss. and Hohen ex Benth. S. | Will and Claßen-Bockhoff 2017 | / | KU563821 | KU578212 | / | / |
| <i>Slavia lasiantha</i> Benth. | 2,4) Walker and Sytsma 2007. | / | DQ667300 | / | DQ667486 | / |
| <i>Salvia lachnocalyx</i> Hedge. | Iran, TARI (83023). | MK204866 | MK213210 | | | MK240118 |
| <i>Salvia lachnostachys</i> Benth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664598 | / | MF664005 | / |
| <i>Salvia lanceolata</i> Lam. | 2,3) Will and Claßen-Bockhoff 2014 | / | KJ584201 | KJ747277 | / | / |
| <i>Salvia leptostachys</i> Benth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664603 | / | MF664010 | / |
| <i>Salvia leriifolia</i> Benth. | Iran, TARI (35583). | MK204865 | MK213211 | | | / |
| <i>Salvia leucantha</i> Cav. | 2,4) Jenks et al., 2010. | / | HQ418875 | / | HQ418977 | / |
| <i>Salvia leucodermis</i> Baker. | Will and Claßen-Bockhoff 2014. | KJ747280 | KJ584220 | KJ747280 | / | / |
| <i>Salvia leucophylla</i> Greene. | 2) Walker and Sytsma 2007; 4) Walker et al., 2004 | / | DQ667210 | / | KP852913 | KP853077 |
| <i>Salvia limbata</i> C.A.Mey. | Iran, TARI (27761). | MK204862 | MK213212 | / | / | MK240120 |
| <i>Salvia limbata</i> | Iran, TARI (30364). | MK204864 | MK213213 | | | Mk24011 |
| <i>Salvia limbata</i> | Iran, TARI (85267). | MK204863 | / | / | / | / |
| <i>Salvia littae</i> Vis. | 2,4) Fragoso-Martinez et al., 2017. | / | MF622150 | / | MF664014 | / |
| <i>Salvia longispicata</i> M.Martens & Galeotti. | 2,4) Jenks et al., 2010. | / | HQ418876 | / | HQ418978 | / |
| <i>Salvia lophanthoides</i> Fernald. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664607 | / | MF664017 | / |
| <i>Salvia lutea</i> L. | Will and Claßen-Bockhoff 2014. | KJ747273 | KJ584205 | KJ747273 | / | / |
| <i>Salvia lutescens</i> var. <i>lutescens</i> Koidz. | Takano and Akiyam 2017; 2,4) Sudarmono and Okada 2007. | LC060845.1 | AB266232 | / | AB266232 | / |
| <i>Salvia lyrata</i> L. | Will and Claßen-Bockhoff 2017. | / | KU563873.1 | KU578166 | / | / |
| <i>Salvia macilenta</i> Boiss. | Iran, TARI (102851). | MK204861 | MK213214 | / | / | MK240122 |
| <i>Salvia macrochlamys</i> Boiss. & Kotschy | Iran, TARI (102852) | MK204860 | MK213215 | / | / | MK240123 |
| <i>Salvia macrophylla</i> Bent. | 2,4) Jenks et al., 2010. | / | HQ418877 | / | HQ418979 | |

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| <i>Salvia macrosiphon</i> Boiss. | Iran, TARI (58399). | MK204859 | MK213216 | / | / | MK240124 |
| <i>Salvia madrensis</i> Seem. | 2,4) Jenks et al., 2010. | / | HQ418878 | / | HQ418980 | / |
| <i>Salvia majdae</i> (Rech.f. & Wendelbo) Sytsma. | Iran: Hormozgan, Geno mountain, Mirtajzadin 201. | MK204858 | MK256967 | / | / | 1/ |
| <i>Salvia marashica</i> Ilçim, Celep and Dogan. | Will and Claßen-Bockhoff 2017. | / | KU563802 | KU578230 | / | / |
| <i>Salvia margaritae</i> Botsch. | 2,3) Will and Claßen-Bockhoff 2017. | KU563880 | / | KU578201 | / | / |
| <i>Salvia maximowicziana</i> Hemsl. | 1,3,4) Deng et al., 2015. | KM886617 | PS1730MT01 | KM886851 | KM886650 | |
| <i>Salvia maymanica</i> Hedge. | Will and Claßen-Bockhoff 2017. | / | KU563805 | KU578231 | / | / |
| <i>Salvia meilienis</i> S.W.Su. | PS1719MT01 | / | FJ546867 | / | / | / |
| <i>Salvia mellifera</i> E. Greene. | 1,4) Walker et al., 2015; 2) Jenks et al., 2011; 3) Drew and Sytsma 2012; 5) Drew et al., 2011 | KP852989 | HQ418879 | JQ669368 | KP852916 | JF289064 |
| <i>Salvia merjamie</i> Forsk. | Will and Claßen-Bockhoff 2014. | KJ584286 | KJ584184 | KJ747297 | / | / |
| <i>Salvia mexicana</i> L. | 2,4) I. Fragoso-Martinez 79 (FCME). | / | MF664611 | / | MF664021 | / |
| <i>Salvia microphylla</i> Kunth | 2,4) Fragoso-Martinez et al., 2017. | / | MF664022 | / | MF663986 | / |
| <i>Salvia microstegia</i> Boiss. & Balansa | Iran, TARI (5397). | MK204857 | MK213216 | / | / | / |
| <i>Salvia minarum</i> Briq. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664613 | / | MF664023 | / |
| <i>Salvia mirzayanii</i> Rech.f. & Esfand. | Iran, TARI (41724). | MK204856 | MK213217 | / | / | / |
| <i>Salvia misella</i> Kunth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664614 | / | / | / |
| <i>Salvia mocinoi</i> Benth. | 2) Fragoso-Martinez et al., 2017; 4) Walker and Sytsma 2007 | / | MF664615 | / | DQ667459 | / |
| <i>Salvia modesta</i> Boiss. | Will and Claßen-Bockhoff 2017 | / | KU563856 | KU578175 | / | / |
| <i>Salvia mohavensis</i> E. Greene. | 2) Walker and Sytsma 2007; 1,4,5) Walker et al., 2015 | KP852997 | DQ667212 | / | KP852920 | KP853078 |
| <i>Salvia moniliformis</i> Fernald. | 2,3) Will and Claßen-Bockhoff 2017 | / | KU563884 | KU578198 | / | / |
| <i>Salvia montbretii</i> Benth. | Will and Claßen-Bockhoff 2017 | / | KU563869 | KU578195 | / | / |

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| <i>Salvia muirii</i> L.Bolus. | Will and Claßen-Bockhoff 2014. | KJ584287 | KL584208 | KJ747283 | / | / |
| <i>Salvia multicaulis</i> Vahl. | Iran, TARI (102845) | / | MK213218 | / | / | / |
| <i>Salvia munzii</i> Epling. | 2) Walker and Sytsma 2007; 1,5) Walker et al., 2015; 4) Fragoso-Martinez et al., 2017. | KP853000 | DQ667224 | / | MF664026 | KP853079 |
| <i>Salvia namaensis</i> Schinz. | Will and Claßen-Bockhoff 2014. | KJ584289 | KJ584200 | KJ747284 | / | / |
| <i>Salvia nana</i> Kunth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664618 | / | MF664029 | / |
| <i>Salvia nemorosa</i> L. | Iran, TARI (43572) | MK204855 | MK213219 | / | / | MK240125 |
| <i>Salvia nervosa</i> Benth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664619 | / | MF664031 | / |
| <i>Salvia nilotica</i> Juss. ex Jacq. | 1,2,3) Will and Claßen-Bockhoff 2014; 4) Walker and Sytsma 2004 | KJ747281 | KJ584229 | KJ747258 | AY570487 | / |
| <i>Salvia nipponica</i> Miq. var. <i>kisoensis</i> | 1,5) Takano and Akiyam 2017; 2) Takano and Okada 2011 | LC060848 | AB295101 | / | / | LC060552 |
| <i>Salvia nitida</i> (M.Martens & Galeotti) Benth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664620 | / | MF664032 | / |
| <i>Salvia nubicola</i> Wall. ex Sweet | 2,4) Will and Claßen-Bockhoff 2017 | | KU563786 | KU578205 | / | / |
| <i>Salvia nutans</i> L. | Will and Claßen-Bockhoff 2017 | / | KU563832 | KU578176 | / | / |
| <i>Salvia nydeggeri</i> Hub.-Mor. | Will and Claßen-Bockhoff 2017 | / | KU563803 | KU578233 | / | / |
| <i>Salvia oaxacana</i> Fernald. | 3) Will and Bockhoff 2017. | / | / | KU578199 | HQ418983 | / |
| <i>Salvia occidentalis</i> Sw. | 2,4) Jenks et al., 2010. | / | HQ418882 | / | HQ418984 | / |
| <i>Salvia officinalis</i> L. | 1, 4, 5) Drew and Sytsma 2011; 2) Walker and Sytsma 2007 | JF301332 | DQ667225 | | JF301398 | JF289065 |
| <i>Salvia oligophylla</i> Aucher ex Benth. | Iran: Zanjan, Mirtajzadini | MK204853 | MK256968 | | | MK240126 |
| <i>Salvia omeiana</i> E. Peter. | Voucher: SOME | / | JQ934139 | EU200176 | / | / |
| <i>Salvia omerocalyx</i> Hayata var <i>omerocalyx</i> | 1,5) Takano 2017; 2,4) Takano and Okada 2011 | LC060852.1 | AB353205 | / | AB353195 | LC060557 |
| <i>Salvia oppositiflora</i> Ruiz & Pav. | 2,4) Jenks et al., 2010 | / | HQ418883 | / | HQ418985 | / |

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|---|---|------------|----------|----------|----------|----------|
| <i>Salvia orbignaei</i> Benth. | 2) Fragoso-Martinez et al., 2017; 4) Walker and Sytsma 2007 | / | DQ667279 | / | MF664033 | / |
| <i>Salvia ovalifolia</i> A.St.-Hil. ex Benth. | 4) Walker and Sytsma 2007 | / | DQ667315 | / | DQ667502 | / |
| <i>Salvia oxyphora</i> Briq. | 2,4) Jenks et al., 2010 | / | HQ418884 | / | HQ418986 | / |
| <i>Salvia pachyphylla</i> Munz. | 1,5) Walker et al., 2015; 2) Walker and Sytsma 2007 | KP853004 | / | / | DQ667431 | KP853080 |
| <i>Salvia palaestina</i> Benth. | Will and Claßen-Bockhoff 2014 | / | KJ584175 | KJ74304 | / | / |
| <i>Salvia pallida</i> Benth. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664623 | / | MF664035 | / |
| <i>Salvia paohsingensis</i> C.Y.Wu. | 2,4) Wang et al., 2013 | / | KC473252 | / | KC414297 | / |
| <i>Salvia patens</i> Cav. | 1,5) Drew and Sytsma 2011; 2) Jenks et al. 2010; 3) Drew and Sytsma 2012; 4) Walker and Sytsma 2007 | JF301333 | HQ418885 | JQ669370 | DQ667442 | JF289066 |
| <i>Salvia pauciflora</i> Kunth. | 2,4) Wang et al., 2013. | / | KC473254 | / | KC414299 | / |
| <i>Salviapentstemenoides</i> K.Koch and C.D.Bouché. | 3) Will and Claßen-Bockhoff 2014; 2,4) Walker and Sytsma 2007. | / | DQ667221 | KU578162 | AY570489 | / |
| <i>Salvia perlonga</i> Fernald. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664627 | / | MF664040 | / |
| <i>Salvia personata</i> Epling. | 2,4) Walker and Sytsma 2007. | / | DQ667269 | / | DQ667455 | / |
| <i>Salvia persopolitana</i> Boiss. | Iran, TARI (102854). | MK204852 | MK213220 | | | MK240127 |
| <i>Salvia phlomoides</i> Asso. | Will and Bockhof 2014. | / | KJ584186 | KJ747309 | / | / |
| <i>Salvia pinnata</i> L. | Will and Claßen-Bockhoff 2017. | / | KU563798 | KU578217 | / | / |
| <i>Salvia platystoma</i> | 2,4) Walker and Sytsma 2007. | / | DQ667277 | / | DQ667462 | / |
| <i>Salvia plebeia</i> R.Br. | 1,5) Takano 2017; 2) Will and Claßen-Bockhoff 2017; 3) Wang et al., 2013. | LC060859.1 | KU563788 | / | KC414300 | LC060563 |
| <i>Salvia plectranthoides</i> Griff. | 2,3) Will and Claßen-Bockhoff 2017. | / | KU563787 | KU578207 | / | / |
| <i>Salvia poculata</i> Nábelek. | Iran, TARI (102848). | MK204851 | MK213221 | / | / | / |
| <i>Salvia polystachya</i> Cav. | 1,5) Drew and Sytsma 2011; 2,4) Fragoso-Martinez et al., 2017; 3) Drew and Sytsma 2012. | JF301334 | MF664631 | JQ669371 | MF664044 | JF289067 |
| <i>Salvia potentillifolia</i> Boiss. and Heldr. ex Benth. | Will and Claßen-Bockhoff 2017. | / | KU563807 | KU578235 | / | / |
| <i>Salvia pratensis</i> L. | Will and Claßen-Bockhoff 2017. | / | KU563835 | KU578180 | / | / |

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|---|---|------------|----------|----------|----------|----------|
| <i>Salvia prattii</i> Hemsl. | 2,3) Will and Claßen-Bockhoff 2017. | / | KU578206 | / | KU563784 | / |
| <i>Salvia priontis</i> Hance. | specimen_voucher="PS1711MT01 | / | FJ883527 | / | / | / |
| <i>Salvia procurrens</i> Benth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664633 | / | MF664046 | / |
| <i>Salvia prunelloides</i> Kunth. | 2) Walker and Sytsma 2007; 4) Fragoso-Martinez et al., 2017. | / | DQ667275 | / | MF664048 | / |
| <i>Salvia przewalskii</i> Maxim. | 1,5) Drew and Sytsma 2011; 2,4) Walker and Sytsma 2007; 3) Drew and Sytsma 2012. | JF301339.1 | DQ667254 | JQ669372 | DQ667443 | JF289068 |
| <i>Salvia pterocalyx</i> Hedge. | 3) Will and Claßen-Bockhoff 2017. | / | / | KU578200 | / | / |
| <i>Salvia pubescens</i> Benth. | 2,4) Walker and Sytsma 2007. | / | DQ667296 | / | DQ667482 | / |
| <i>Salvia purpurea</i> Sessé & Moc. | 2,4) Benitez-Vieyra et al., 2014. | / | MF664636 | / | KJ473981 | / |
| <i>Salvia pygmaea</i> Matsum. | 1, 5) Takano and Akiyama 2017; 2) Takano and Okada 2011; 4) Sudarmono and Okada 2007. | LC060854.1 | AB541126 | / | AB295083 | LC060558 |
| <i>Salvia qimenensis</i> S.W.Su & J.Q.He. | specimen_voucher="SQIM" | / | JQ934155 | / | / | / |
| <i>Salvia quezelii</i> Hedge and Afzal-Rafi | Will and Claßen-Bockhoff 2017. | / | KU563808 | KU578249 | / | / |
| <i>Salvia radula</i> Benth. | 1,2) Will and Claßen-Bockhoff 2014. | KJ584293 | KJ584180 | / | / | / |
| <i>Salvia ranzianiana</i> Makino. | 2,4) Sudarmono and Okada (2007); 5) Takano 2017. | / | AB287375 | / | AB287374 | LC060560 |
| <i>Salvia repens</i> Burch. ex Benth. | Will and Claßen-Bockhoff 2014. | KJ584295 | KJ584231 | KJ747282 | / | / |
| <i>Salvia retinervia</i> Briq. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664058 | / | MF664058 | / |
| <i>Salvia reuterana</i> Boiss. | Iran, TARI (102849). | MK204850 | MK213222 | / | / | |
| <i>Salvia reuterana</i>. | Iran, TARI (102842). | MK204849 | / | / | / | / |
| <i>Salvia rhytidea</i> Benth. | Iran, TARI, (102850). | MK204848 | MK213223 | / | / | MK240129 |
| <i>Salvia rhytidea</i>. | Iran, Bahonar University (16297). | MK204847 | / | / | / | MK240128 |
| <i>Salvia ringens</i> Sm. | Will and Claßen-Bockhoff 2017. | / | KU563810 | KU578213 | / | / |
| <i>Salvia roborowskii</i> Maxim. | 2)Walker and Sytsma 2007. | / | DQ667289 | / | DQ667474 | / |
| <i>Salvia roemeriana</i> Scheele. | 1,5) Drew and Sytsma 2011; 2) walker and Sytsma 2007. | JF301340 | DQ667211 | / | / | / |

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|--|---|----------|---------------|----------|----------|------------|
| <i>Salvia rosifolia</i> Sm. | Will and Claßen-Bockhoff 2017 | / | KU578209 | / | / | / |
| <i>Salvia rosmarinus</i> (L.) Schield., Handb. Med.-Pharm | 1,5) Drew and Sytsma 2011; 2) Trusty et al. 2004; 3) Drew and Sytsma 2012 4) Walker et al., 2004. | JF30328 | AY506649 | JQ669364 | AY570465 | JF289058.1 |
| <i>Salvia rufula</i> Kunth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF622179 | / | MF664063 | / |
| <i>Salvia rugosa</i> | 2,5) Walker & Sytsma 2007 | / | DQ667290 | / | DQ667475 | / |
| <i>Salvia rusbyi</i> Britton ex Rusby. | 2,4) Walker and Sytsma 2007. | / | DQ667266 | / | DQ667452 | / |
| <i>Salvia russellii</i> Benth. | Iran, TARI (86040). | MK204846 | MK213224 | / | / | MK240130 |
| <i>Salvia rypara</i> Briq. | 2,4) Walker and Sytsma 2007. | / | DQ667266 | / | DQ667452 | / |
| <i>Salvia rzedowskii</i> Ramamoorthy | 2,4) Fragoso-Martinez et al., 2017. | / | MF664650 | / | MF664067 | / |
| <i>Salvia sagittata</i> Ruiz & Pav. | 2,4) Walker and Sytsma 2007. | / | DQ667446 | / | DQ667260 | / |
| <i>Salvia sahendica</i> Boiss. & Buhse | Iran, TARI (73990). | MK204845 | MK213225 | / | / | / |
| <i>Salvia santalonifolia</i> Boiss. | Iran, TARI (102846). | MK204844 | MK213226 | / | / | / |
| <i>Salvia scabiosifolia</i> Lam. | Will and Claßen-Bockhoff 2017 | / | KU563811 | KU578237 | / | / |
| <i>Salvia scabra</i> L. | Will and Claßen-Bockhoff (2014) | KJ584297 | KJ584233 | KJ747285 | / | / |
| <i>Salvia scapiformis</i> Hance | 2,4) Deng et al., 2015 | | KM886675 1 | | KM886852 | |
| <i>Salvia schimperi</i> Benth. | Will and Claßen-Bockhoff 2014 | KJ584298 | KJ584174 | / | / | / |
| <i>Salvia schlechteri</i> Briq, | Will and Claßen-Bockhoff 2014 | KJ584299 | KJ584235 | KJ747286 | / | / |
| <i>Salvia sclarea</i> L. | 2) Walker and Sytsma 2007; 3,5) Drew and Sytsma 2012 | / | DQ667222 | JQ669373 | / | JQ669265 |
| <i>Salvia sclarea</i>. | Iran, TARI (69493). | MK204843 | MK213227 | / | / | MK240131 |
| <i>Salvia sclareopsis</i> Bornm. ex Hedge | Iran, TARI (3533). | MK204842 | MK213228 | / | / | MK240131 |
| <i>Salvia scrophularifolia</i> (Bunge) B. T. Drew | 2,4) Walker and Sytsma 2007; 3) Drew and Sytsma 2012; 5) Drew and Sytsma 2011 | / | DQ667330 | JQ669352 | DQ667519 | JF289051 |
| <i>Salvia scutellaroides</i> Kunth. | 2,4) Walker and Sytsma 2007 | / | DQ667327 | | DQ667516 | |

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|---|---|----------|----------|----------|----------|----------|
| <i>Salvia sericeo-tomentosa</i> Rech. F. | Will and Claßen-Bockhoff 2017 | / | KU563822 | KU578238 | / | / |
| <i>Salvia sessei</i> Benth. | 2,4) Jenks et al., 2010 | / | HQ418889 | / | HQ418991 | / |
| <i>Salvia sessilifolia</i> Baker. | 3) Walker and Sytsma 2007; | KJ584303 | DQ667282 | DQ667467 | / | / |
| <i>Salvia sinica</i> Migo. | SS201301 | / | KJ397257 | / | / | / |
| <i>Salvia somalensis</i> Vatke. | Will and Claßen-Bockhoff 2014 | KJ584304 | KJ584240 | KJ747311 | / | / |
| <i>Salvia sonomensis</i> E. Greene. | 1,4) Walker and Sytsma 2007; 2,5) Walker et al., 2015 | KP853008 | DQ667218 | / | DQ667426 | KP853081 |
| <i>Salvia sophrona</i> Briq. | 2,4) Fragoso-Martinez et al., 2017 | / | MF664655 | / | MF664073 | / |
| <i>Salvia spinosa</i> L. | Iran, TARI (102844) | MK204841 | MK213229 | / | / | MK240132 |
| <i>Salvia spiraeifolia</i> Boiss. & Hohen. | Iran, TARI (1506) | MK204872 | MK21204 | | | / |
| <i>Salvia splendens</i> Sellow ex Schult. | 2,4) Fragoso-Martinez et al., 2017 | / | MF622186 | / | MF664076 | / |
| <i>Salvia stachydifolia</i> Benth. | 2,4) Walker and Sytsma 2007 | / | DQ667267 | / | DQ667453 | / |
| <i>Salvia staminea</i> Montbret & Aucher ex Benth. | Iran, TARI (51624) | MK204840 | MK213230 | / | / | / |
| <i>Salvia stenophylla</i> Burch. ex Benth. | Will and Claßen-Bockhoff 2014 | KJ584305 | KJ584237 | KJ747260 | / | / |
| <i>Salvia styphelus</i> Epling | 4) Jenks et al., 2010 | / | HQ418891 | / | HQ418993 | / |
| <i>Salvia suffruticosa</i> Montbret & Aucher ex Benth. | Iran, TARI (86522) | | MK213223 | | | |
| <i>Salvia summa</i> A.Nelson. | 1) Will and Claßen-Bockhoff 2014; 2,3) Will and Claßen-Bockhoff 2017. | KJ584307 | KU563874 | KU578164 | / | / |
| <i>Salvia superba</i> | voucher="PS0134MT01 | / | FJ546849 | / | / | |
| <i>Salvia syriaca</i> L. | Iran, TARI (16699). | MK204839 | MK213232 | / | / | / |
| <i>Salvia</i> × <i>sylvestris</i> L. | 2) Will and Claßen-Bockhoff 2017; 3,4) Wang et al., 2013. | / | KJ584177 | KJ747292 | KC414323 | / |
| <i>Salvia taraxacifolia</i> Hook.f. | 1,2,3) Will and Claßen-Bockhoff 2014; Walker et al., 2004. | KJ584308 | KJ584228 | KJ747270 | AY570497 | / |
| <i>Salvia tebesana</i> Bunge. | Iran, TARI (84759). | MK204838 | MK213233 | / | / | / |
| <i>Salvia texana</i> (Scheele) Torr. | Will and Claßen-Bockhoff 2017. | / | KJ584199 | KJ747267 | DQ667510 | / |

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|---|---|----------|----------|----------|------------|----------|
| <i>Salvia thermarum</i> Van Jaarsv. | P. Wester and R. Claßen-Bockhoff 336 (MJG 041398). | KJ584309 | / | KJ747288 | / | / |
| <i>Salvia thymoides</i> Benth | 2,4) Walker and Sytsma 2007. | / | DQ667273 | / | DQ667458 | / |
| <i>Salvia thyriflora</i> Benth. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664668 | / | MF664088 | / |
| <i>Salvia tiliifolia</i> Vahl. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664669 | / | MF664089 | / |
| <i>Salvia tobeyi</i> Hedge. | Will and Claßen-Bockhoff 2017. | / | KU563865 | KU578188 | / | / |
| <i>Salvia tomentosa</i> Mill. | Will and Claßen-Bockhoff 2017. | / | KU563816 | KU578214 | / | / |
| <i>Salvia tonaticensis</i> Ramamoorthy ex Lara, Bedolla et Zamudio. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664670 | / | MF664090 | / |
| <i>Salvia tortuosa</i> Urb. | 2,4) Jenks et al., 2010. | / | HQ418893 | / | HQ418995 | / |
| <i>Salvia trichocalycina</i> Benth. | Walker & Sytsma 2007 | / | DQ667283 | / | DQ667468 | / |
| <i>Salvia trichoclada</i> Benth. | Will and Claßen-Bockhoff 2017. | / | / | KU578243 | / | / |
| <i>Salvia trichostephna</i> Epling. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664671 | / | MF664091 | / |
| <i>Salvia tricuspis</i> Franch. | China: Sichuan | / | EF373633 | / | EU220730 | / |
| <i>Salvia trijuga</i> Diels. | 2) Will and Claßen-Bockhoff 2017; 4) Wang et al 2013 | / | KU563779 | / | KC414322.1 | / |
| <i>Salvia tubifera</i> Cav. | 2,4) Fragoso-Martinez et al., 2017. | / | HQ418894 | / | HQ418996 | / |
| <i>Salvia tubiflora</i> Sm. | 2,4) Fragoso-Martinez et al., 2017. | / | MF664672 | / | MF664092 | / |
| <i>Salvia uliginosa</i> Benth. | 2,4) Jenks et al., 2010. | / | HQ418895 | / | HQ418997 | / |
| Salvia urmiensis Bunge. | Iran, TARI (19586). | MK204837 | MK213234 | / | / | / |
| <i>Salvia vaseyi</i> (Porter) Parish. | 4)Walker et al., 2015. | KP853013 | / | / | KP852932 | KP853083 |
| <i>Salvia veneris</i> Hedge | Will and Claßen-Bockhoff 2017. | / | KJ584170 | KJ747306 | / | / |
| <i>Salvia venulosa</i> Epling | 2,4) Jenks et al., 2010. | / | HQ418896 | / | HQ418998 | / |
| Salvia verbascifolia M.Bieb. | Iran, TARI (88803). | MK204831 | MK213235 | / | / | / |
| <i>Salvia verbenaca</i> L. | Will and Claßen-Bockhoff 2014. | / | KJ584183 | KJ747298 | / | / |
| <i>Salvia vermifolia</i> Bedge and Huber-Morath. | Will and Claßen-Bockhoff 2017. | / | Ku563866 | KU578192 | / | / |
| Salvia verticillata L. | Iran, TARI (2765). | MK204836 | MK213236 | / | / | / |
| Salvia virgata Jacq. | Iran, TARI (3772). | MK204835 | MK213237 | / | / | / |

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|---|---|----------|----------|----------|----------|-----------|
| <i>Salvia viridis</i> L. | Iran, TARI (13283). | MK204834 | MK213238 | / | / | MK240135 |
| <i>Salvia viscosa</i> Jacq. | Will and Claßen-Bockhoff 2017. | / | KU563838 | KU578186 | / | / |
| <i>Salvia vvedenskii</i> Nikitina . | 2,3) Will and Claßen-Bockhoff 2017. | / | KU563879 | KU578202 | / | / |
| <i>Salvia whitehousei</i> Alziar | 1,2,3) Will and Claßen-Bockhoff 2014; 4) Walker and Sytsma 2007. | KJ584311 | KJ584198 | KJ747268 | DQ667509 | / |
| <i>Salvia xanthocheila</i> Boiss. ex Benth. | Iran, TARI (69728). | MK204833 | MK213239 | / | / | MK240136 |
| <i>Salvia yangii</i> B. T. Drew | 1,5) Drew and Sytsma 2011; 2) Will and Claßen-Bockhoff (2014); 3) Drew and Sytsma 2011. | JF301328 | KJ584242 | JQ669352 | | JF289051` |
| <i>Salvia yunnanensis</i> C.H.Wright. | 2) YunN0309-2; 3) G.X. Hu & al., QT001, 4) H.F. Guo 2017257(PE) | / | DQ132866 | KT210283 | EF014356 | |

Table 2: Rate and modes of *Salvia* corolla length diversification. Fitted models are Brownian motion (BM), Ornstein-Uhlenbeck (OU) and Early Burst (EB). The best-fit model is estimated based on the lowest bias-corrected Akaike Information Criterion.

| Model | Model Parameters | LogL | AICc | ΔAIC |
|--------------|-------------------------|--------------|-------------|-------------------------------|
| BM | $\alpha = 0$ | -1233 | 2470 | 68 |
| OU | $\alpha = 0.15$ | -1198.020364 | 2402 | 0 |
| EB | $\alpha = -0.00001$ | -1233.21 | 2472 | 70 |

Table 3: Rates of *Salvia* diversification examining multiple evolutionary models. Models fitted include diversity-dependent linear speciation and extinction (DDL + E), diversity-dependent exponential speciation and extinction (DDE+E) and two constant-rate diversification models: a pure-birth (Yule) model and birth-death (crBD) model. λ = speciation rate (Ma/lineage); μ = extinction rate (Ma/lineage); K = carrying capacity; AIC = Akaike Information Criterion (AIC) for testing model fit. The capacity for the potential number of *Salvia* species is higher than the number of extant species (~1000 spp.), suggesting that current *Salvia* diversification is independent of diversity.

| Model | lambda | mu | K | loglik | AIC |
|-------|--------|---------|---------|-----------|----------|
| Yule | 0.246 | 0 | ----- | -989.739 | 1977.782 |
| CrBD | 0.290 | 0.079 | ----- | -987.888 | 1979.768 |
| DDE+E | 0.6682 | 0.2331 | 36504.2 | -993.5864 | 1993.169 |
| DDS+E | 0.3579 | 0.14616 | 3315.75 | -988.042 | 1982.86 |

Table 4: HiSSE model subsets that were fitted for study of the effect of the lever mechanism on diversification across *Salvia* phylogeny. The best-fit model shown in bold was selected based on a bias-corrected Akaike Information Criterion (AICc).

| Active lever mechanism | | | |
|---|----------------|-----------------|--------------|
| Model | lnLik | AIC | Δ AIC |
| CID-4: q's equal | -948.8211 | 1915.642 | 77.136 |
| HiSSE: $\tau_{0A}=\tau_{1A}$, $\epsilon_{0A}=\epsilon_{1A}$, $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -909.27 | 1828.541 | 16.943 |
| HiSSE: ϵ 's equal, $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -907.778 | 1825.556 | 18.575 |
| HiSSE: $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -899.79 | 1811.598 | 0 |
| HiSSE: $\tau_{0A}=\tau_{1A}$, ϵ 's equal, $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -906.91 | 1827.827 | 16.229 |
| HiSSE full model | -895.706 | 1823.521 | 11.923 |
| HiSSE: $\tau_{0A}=\tau_{0B}$, $\epsilon_{0A}=\epsilon_{0B}$, $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -899.44 | 1812.896 | 1.3 |
| HiSSE: $\tau_{0A}=\tau_{0B}$, ϵ 's equal, $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -897.76 | 1813.521 | 1.923 |
| HiSSE: q's and ϵ 's equal | -908.375 | 1828.751 | 16.377 |
| HiSSE: q's equal | -905.77 | 1829.55 | 17.152 |
| CID-2: q's equal and ϵ 's equal | -906.591 | 1821.312 | 9.714 |
| HiSSE: $\tau_{0A}=\tau_{0B}$, $\epsilon_{0A}=\epsilon_{0B}$ | -904.426 | 1822.853 | 11.255 |
| HiSSE: $\tau_{0A}=\tau_{1A}$, $\epsilon_{0A}=\epsilon_{1A}$, q's equal | -905.968 | 1825.937 | 14.339 |
| HiSSE: $\tau_{0A}=\tau_{1A}=\tau_{0B}$, ϵ 's and q's equal | -909.93 | 1827.878 | 16.28 |
| HiSSE: $\tau_{0A}=\tau_{0B}$, ϵ 's and q's equal | -907.96 | 1825.93 | 14.332 |
| HiSSE: $\tau_{0A}=\tau_{1A}$, ϵ 's and q's equal | -908.76 | 1826.255 | 14.657 |
| CID-2: q's equal | 906.591- | 1823.183 | 11.585 |
| HiSSE: $\tau_{0A}=\tau_{1A}=\tau_{0B}$, $\epsilon_{0A}=\epsilon_{1A}=\epsilon_{1B}$, q's equal | -907.552 | 1825.044 | 13.446 |
| HiSSE: 25 $\tau_{0A}=\tau_{1A}=\tau_{0B}$, $\epsilon_{0A}=\epsilon_{1A}=\epsilon_{0B}$, $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -907.778 | 1825.556 | 13.958 |
| BiSSE model: q's equal | -914.4616 | 1838.923 | 27.325 |
| CID-4: ϵ 's and q's equal | -927.820 | 1867.641 | 56.043 |
| BiSSE model: q's equal, $\epsilon_0=\epsilon_1$ | -906.786 | 1841.536 | 29.938 |
| BiSSE model: All free | -913.091 | 1834.183 | 22.585 |
| HiSSE $\tau_{0A}=\tau_{1A}=\tau_{0B}$, ϵ 's equal, $q_{0B1B}=0$, $q_{1B0B}=0$, All other q's equal | -910.34 | 1828.69 | 17.092 |
| BiSSE model: $\epsilon_0=\epsilon_1$ | -916.701 | 1843.409 | 11.255 |