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

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Abstract

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

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

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

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

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

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

1. Introduction

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

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

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

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

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

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

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

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

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

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

2. Materials & Methods

2.1. Taxon Sampling

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

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

2.2. DNA extraction, amplification, and sequencing

Total DNA was extracted from herbarium and silica-dried material using a modified CTAB method (Doyle & Doyle 1987) in which, to break down secondary metabolites, the mixture of ground leaf tissue and CTAB solution was kept at room temperature for 24 hours. ITS, ETS, and *ycf1* regions were amplified using the polymerase chain reaction (PCR) with each sample prepared in 25- μ l volumes with the following components: 1 μ l of DNA solution (20 ng), 2.5 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 $MgCl_2$, and 1.5 μ l of *Taq* DNA polymerase. The PCR conditions for the nuclear regions for most species were: 95°C for 2 minutes, 32 cycles of denaturation for 20 seconds at 94°C, primer annealing for 20 seconds at 50°C, and 2 minutes extension at 72°C, with a final extension of 7 minutes at 72°C. For the *ycf1* region, we modified the annealing temperature to 52°C for 1 minute (PCR optimization was set based on personal communication with B. Drew). High-quality PCR products were sequenced on an ABI 3730 DNA Analyzer (Applied Biosystems, Inc.) at the University of Florida Interdisciplinary Center for Biotechnology Research (ICBR).

2.3. Alignment and phylogenetic analysis

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

2.4. BEAST analysis (divergence time estimation)

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

2.5. Ancestral state reconstruction

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

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

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

2.6. Macroevolutionary patterns within corolla length

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

2.6.1. Diversification model

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

2.6.2. Disparity Through Time

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

2.6.3. Diversification rate

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

2.8. Lever-mechanism-dependent diversification

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

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

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

2.9. Diversity-dependent diversification

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

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

3. Results

3.1. Characteristics of the phylogenetic data matrix and phylogenetic analysis

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

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

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

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

Clade I

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

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

Clade II

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

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

Clade III

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

Clade IV

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

3.2. Divergence times

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

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

3.3. Ancestral character reconstruction

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

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

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

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

3.4. Tempo and mode of corolla length evolution

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

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

3.4.1. Corolla length evolutionary rates

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

3.5. Diversity-dependent diversification

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

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

3.6. Lever-mechanism-dependent diversification

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

4. Discussion

4.1. Phylogeny

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

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

Clade I

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

Subgen. *Heterosphaece*

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

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

Clade II

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

Clade III

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

Clade IV

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

4.2. Divergence times

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

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

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

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

4.3. Ancestral state reconstruction

4.3.1. Corolla length

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

4.3.2. Lever mechanism

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

4.3.3. Habit

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

4.4. Corolla length evolution

4.4.1. Disparity Through Time

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

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

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

4.4.2. Corolla length diversification

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

4.5. Lever-mechanism-dependent diversification

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

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

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

	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		

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

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*

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

■ Present
■ Absent

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

Fig. 6: Ancestral reconstruction of habit (herb/shrub) across *Salvia* phylogeny using stochastic mapping in phyttools.

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

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

Fig. 8: Corolla length evolution across *Salvia* phylogeny based on a BAMM analysis. The best shift was detected in clade II in *Calosphace* clade

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

<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	/

<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	/

<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	/

<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	/	/

<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	/	

<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> Brandegees.	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 grewiaefolia</i> S. Moore.	2,4) Jenks et al., 2010.	/	HQ418871	/	HQ418973	/
<i>Salvia grossheimii</i> Sosn.	Iran, TARI (84031).	MK204832	MK213204	/	/	/
<i>Salvia guadalupensis</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	/	/

<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> Košanin.	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	/

<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	

<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	/	/	/
<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	PS1730MT 01	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	/	/

<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. kisoensis	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 omerocalyx	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	/

<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>Salviapentstemonoides</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 perspolitana</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	/	/

<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 ranzaniana</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, Bamonar 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	/	/	/

<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	

<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 x 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	/

<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	/
<i>Salvia urmiensis</i> 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	/
<i>Salvia verbascifolia</i> 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	/	/
<i>Salvia verticillata</i> L.	Iran, TARI (2765).	MK204836	MK213236	/	/	/
<i>Salvia virgata</i> Jacq.	Iran, TARI (3772).	MK204835	MK213237	/	/	/

<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	Δ AIC
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