

Salvia united: The greatest good for the greatest number

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Abstract Previous molecular phylogenetic research, based on chloroplast and nuclear ribosomal DNA data, has demonstrated that the large genus *Salvia* (Lamiaceae) is paraphyletic as traditionally circumscribed. However, neither relationships within *Salvia* s.l. nor within subtribe Salviinae have been evaluated using low-copy nuclear gene regions. Here, we use two low-copy nuclear gene regions (*PPR-AT3G09060*, *GBSSI*) to further assess relationships of *Salvia* and related genera within Salviinae. Our results largely confirm results from previous studies based on chloroplast and nuclear ribosomal DNA. Based upon the phylogenetic results presented here, previous phylogenetic studies, and taxonomic, morphological, and practical considerations, we conclude that the botanical community would be best served by maintaining a broadly defined *Salvia*, including the five small embedded genera *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria* as *Salvia* species. We subsequently present an updated circumscription of *Salvia*.

Keywords *Dorystaechas*; Lamiaceae; *Meriandra*; *Perovskia*; *Rosmarinus*; *Zhumeria*

Supplementary Material The Electronic Supplement (Figs. S1–S4) is available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>; DNA sequence alignments are available in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19616>)

The beginning of wisdom is to call things by their right names.
Liberal translation of the original Chinese best translated as:

If names be not correct, language is not in accordance with the truth of things. — Confucius in *Analects* (~475 BC–221 BC)

■ INTRODUCTION

The field of molecular phylogenetics has fundamentally altered the basis of organizing and classifying organisms. Prior to DNA-based phylogenies, organisms were classified, by necessity, primarily or solely on the basis of morphological similarity. This morphocentric classification scheme allowed biologists to create order and structure in a heterogeneous natural world, and created a requisite platform for evolutionary thought, study, and discourse (Stevens, 1994, 2002; Knox, 1998). The downside to these more traditional, morphology-based classifications is that these classifications can be subjective, and emphasizing different morphological characters may retrieve different results and hence potentially

competing classifications (Stevens, 1985; Diggs & Lipscomb, 2002; Humphreys & Linder, 2009). In addition, similar morphological features can arise in convergent or parallel fashion among unrelated organisms that occur in similar environments or under similar ecological selection (Hapeman & Inoue, 1997; Patterson & Givnish, 2003). However, in many organismal disciplines, morphological features have been identified that are deemed “more evolutionarily important” and thus have been afforded added clout in classification schemes. Within flowering plants, not surprisingly, floral architecture has traditionally formed the backbone of hierarchical classifications.

While the use of flower morphology as a primary taxonomic classification trait has been useful in angiosperms and often reflected phylogenetic relationships at many taxonomic levels accurately (Endress & Matthews, 2012; Schönberger & Balthazar, 2012), the flower-based classification schemes of the past have created some taxonomic headaches vis-à-vis contemporary molecular phylogeny-based classification approaches (e.g., Stace, 2005; Endress & Matthews, 2012). This is especially apparent when broadly recognizable, iconic genera are revealed to be non-monophyletic (Frodin, 2004; Humphreys

& Linder, 2009). Perhaps the most spectacular example of this is in the ongoing *Acacia* Mill. controversy (Luckow & al., 2005; Smith & al., 2006; Moore, 2007; Moore & al., 2010, 2011; Carruthers & Robin, 2010; Smith & Figueiredo, 2011; Thiele & al., 2011; Miller & al., 2014). *Acacia* is a source of pride in both Australia and Africa (and in North America to a lesser extent), but unfortunately keeping the generic name *Acacia* for all taxa previously under that umbrella is intractable because numerous genera, some iconic in their own right, are interspersed within the various *Acacia* s.l. lineages (but see Hörandl & Stuessy, 2010; Miller & al., 2014). Similar and additional issues have arisen in the dismantling of *Aster* L. (Nesom, 1994; Noyes & Rieseberg, 1999; Dorn, 2003; Li & al., 2012), *Clerodendrum* L. (Steane & al., 1997, 1999, 2004; Yuan & al., 2010), *Senecio* L. (Pelser & al., 2007), and *Psychotria* L. (Nepokroeff & al., 1999; Razafimandimbison & al., 2014). Discussions are ongoing regarding the circumscription of other large genera, for example in *Lobelia* L. (Knox & al., 1993; Givnish & al., 1995, 2009; Buss & al., 2001; Antonelli, 2008; Lammers, 2011; Stuessy & al., 2014), *Metrosideros* Banks ex Gartn. (Dawson, 1976; Briggs & Johnson, 1979; Govaerts & al., 2016; Wilson, 2011; Buys & al., subm.), and in *Scirpus* L./*Eriophorum* L. (Gilmour & al., 2013; Jung & Choi, 2013; Lévillé-Bourret & al., 2014, 2015; Spalink, 2015).

Salvia L. (Lamiaceae: Nepetoideae: Mentheae: Salviinae), another iconic and widely recognized genus over much of its range, has also been shown to be non-monophyletic in molecular phylogenetic studies (Walker & al., 2004, 2015; Walker & Sytsma, 2007; Drew & Sytsma, 2011, 2012; Will & Claßen-Bockhoff, 2014; Will & al., 2015). Wagstaff & al. (1995), using chloroplast restriction site data, first demonstrated a close relationship between *Dorystaechas* Boiss. & Heldr., *Perovskia* Kar., *Rosmarinus* L., and *Salvia*. The focus of their study was Lamiaceae-wide, however, so only a single *Salvia* accession was included in their analyses. Walker & al. (2004), using the *rbcL* and *trnL-F* gene regions and broad sampling within *Salvia*, were the first to reveal that *Salvia* was non-monophyletic. They found *Dorystaechas*, *Perovskia*, and *Rosmarinus*, as well as *Mentha* L., *Origanum* L., and *Thymus* L., embedded within *Salvia*. A close relationship between *Mentha*, *Origanum*, *Thymus* and *Salvia* was previously suggested by Kaufmann & Wink (1994) using *rbcL* data. Since Walker & al. (2004), no other studies have found *Mentha*, *Origanum*, or *Thymus* embedded within *Salvia*. We investigated their results by comparing *rbcL* sequences from Kaufmann & Wink (1994) to recently produced *rbcL* sequences of common taxa, and found that spurious *rbcL* sequences shared between the Kaufmann & Wink (1994) and Walker & al. (2004) studies were responsible for these results. Walker & Sytsma (2007) went on to show that *Meriandra* Benth. and *Zhumeria* Rech.f. & Wendelbo, in addition to *Dorystaechas*, *Perovskia*, and *Rosmarinus*, are embedded within *Salvia*. Subsequent studies (Drew & Sytsma, 2011, 2012; Will & Claßen-Bockhoff, 2014; Walker & al., 2015; Will & al., 2015) have corroborated the findings of Walker & Sytsma (2007).

Salvia, as traditionally circumscribed (Linnaeus, 1753; Bentham, 1834, 1848, 1876; Harley & al., 2004), is a genus of

almost 1000 species with a virtually worldwide distribution, being notably absent from only Australia (1 species) and New Zealand. *Salvia* has long been recognized as a distinct lineage based on a suite of morphological features, with the single most prominent character being an elongate connective in the anther, which separates the thecae of the anthers in the two functional stamens. This connective often exceeds the filament and has apparently evolved multiple times into a lever-like apparatus that assists in pollination (Sprengel, 1793; Himmelbaur & Stibal, 1933–1935; Claßen-Bockhoff & al., 2003, 2004; Harley & al., 2004; Walker & Sytsma, 2007). Walker & Sytsma (2007) demonstrated that there have been either at least three separate origins of this “lever mechanism”, or a single origin followed by multiple losses. Five of these “losses” would correspond to the five genera embedded within *Salvia* (Walker & Sytsma, 2007): *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria*. Together, these five genera consist of 15 species, and are chiefly found in the Mediterranean region and adjacent SW and central Asia. These five genera have previously been considered closely related to *Salvia*, and based on morphology were treated together as part of the subtribe Salviinae in the most recent and comprehensive conspectus of Lamiaceae (Harley & al., 2004). *Salvia* and these five genera are distinctive within the subtribe Salviinae by virtue of having two fertile stamens (as opposed to four), bireticulate sexine ornamentation (as opposed to perforate; Moon & al., 2008), and the presence of “large crystals in the innermost cell layer of the mesocarp” (Ryding, 2010). This putative kinship is further endorsed by the fact that *Rosmarinus* and one species of *Meriandra* (*Meriandra dianthera* (Roth ex Roem. & Schult.) Briq.) previously have been treated as *Salvia*, and that taxa from *Perovskia* are often called “Russian sage”.

Recently, Will & al. (2015) argued that the five aforementioned genera embedded within *Salvia* should be retained as distinct genera, and that *Salvia* should be broken up into smaller, “more manageable” groups. This course of action would leave only the clade (ca. 250 species; Walker & Sytsma, 2007) containing the type of *Salvia* (*Salvia officinalis* L.) as taxa bearing the *Salvia* name (assuming no new genera are proposed within the “*Salvia officinalis*” clade). However, alternative approaches to deal with the classification of *Salvia* and related genera exist and have been suggested previously (e.g., El-Gazzar & al., 1968; Walker & al., 2004, 2015; Drew & al., 2015; González-Gallegos, 2015). Indeed, over a decade ago Walker & al. (2004) concluded: “any modifications to nomenclature at the generic level will take into account the significant broader impact of any changes.” Here, for the first time, we use low-copy nuclear markers to further assess the monophyly of *Salvia*. Based upon these results, previous phylogenetic findings (Walker & Sytsma, 2007; Drew & Sytsma, 2011, 2012; Walker & al., 2015), morphological similarities, and both practical and broader impact considerations, we conclude the botanical community would be better served by keeping the genus *Salvia* as traditionally circumscribed, but with the inclusion of the five small embedded genera. Subsequently, we provide updated nomenclatural combinations necessary to implement this approach.

■ MATERIALS AND METHODS

Sampling. — For this study we employed two separate data matrices. The first dataset contained two low-copy nuclear markers (*PPR-AT3G09060* and *GBSSI*; collectively referred to as LCN), and the second was a four-gene region supermatrix alignment that included four plastid markers (*psbA-trnH*, *trnL-trnF*, *ycf1*, *ycf1-rps15* spacer region; cpDNA).

In total, 28 taxa were included in our LCN analyses. This dataset comprised 21 species from *Salvia* sensu Walker & Sytsma (2007; i.e., *Salvia*+*Dorystaechas*, *Perovskia*, *Rosmarinus*, and *Zhumeria*), 5 species from *Lepechinia* Willd., 1 species of *Melissa* L. (*Melissa officinalis* L.), and *Hedeoma piperita* Benth. as an outgroup. This sampling represented 13 of the 14 staminal types identified by Walker & Sytsma (2007) and seven of the eight genera within the subtribe Salviinae (Harley & al., 2004; Drew & Sytsma, 2012; Drew & al., 2014). Due to only having degraded herbarium material as source material, we were unable to amplify *Meriandra* for the LCN gene regions. The *PPR-AT3G09060* dataset included all 28 species while the *GBSSI* dataset included 23 species. The five species missing from the *GBSSI* dataset were *Salvia dorrii* (Kellogg) Abrams, *S. henryi* A.Gray, *S. mohavensis* Greene, *S. pachyphylla* Epling ex Munz, and *S. spathacea* Greene. The combined two-gene alignment contained 28 taxa.

The cpDNA supermatrix alignment contained 351 accessions and 7723 characters. This sampling included 342 accessions of *Salvia*, seven species of *Lepechinia*, and two species of *Melissa*. *Lepechinia* and *Melissa* served as a monophyletic outgroup based on Drew & Sytsma (2012). In this dataset *Dorystaechas*, *Meriandra*, *Rosmarinus*, and *Zhumeria* were represented by single species while *Perovskia* had two species. This sampling encompassed all staminal types within Salviinae as identified by Walker & Sytsma (2007) and all Salviinae genera. The cpDNA supermatrix sequences were downloaded from GenBank and have been used in previous Lamiaceae and *Salvia* studies (Walker & al., 2004, 2015; Walker & Sytsma, 2007; Drew & Sytsma, 2011, 2012, 2013; Jenks & al., 2012; Li & al., 2013; Drew & al., 2014, 2015; Will & Claßen-Bockhoff, 2014).

DNA extraction and sequencing. — The DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.) was used to extract DNA from silica-dried leaves and herbarium specimens (Appendix 1). Polymerase chain reaction (PCR) primers, methodology, and thermal cycling conditions were as in Drew & Sytsma (2013). PCR products were diluted in water (30×), cycle sequenced, and then cleaned with magnetic beads (Agencourt, Beverly, Massachusetts, U.S.A.). The ABI PRISM BigDye Terminator cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, California, U.S.A.) was used for cycle sequencing reactions. Cycle Sequencing products were electrophoresed on an Applied Biosystems 3730xl automated DNA sequencer.

Seven *PPR-AT3G09060* sequences exhibited polymorphic nucleotide characters (chromatogram double peaks) at an elevated rate (from 0.5% to 2.0%; 21 others had less than 0.5% polymorphic characters). It was unclear whether these polymorphisms represented allelic variation or multiple copies,

so we cloned these seven accessions to assess the effect that these polymorphic characters had on phylogeny estimation. Cloning procedures followed the methods described in Drew & al. (2014). Six to eight clones were amplified from the following taxa: *Dorystaechas hastata*, *Salvia aristata* Aucher ex Benth., *S. carduacea* Benth., *S. greatae* Brandegee, *S. patens* Cav., *S. spathacea* Greene, and *Zhumeria majdae*.

Phylogenetic analyses. — Sequencher v.4.7 (Gene Codes, Ann Arbor, Michigan, U.S.A.) was used to assemble and edit the raw sequence data, and Mesquite v.3.02 (Maddison & Maddison, 2015) was employed for adjusting alignments in the LCN dataset. The *PPR-AT3G09060* (no clones) and *GBSSI* datasets were analyzed both individually and as a combined dataset. We also analyzed the *PPR-AT3G09060* dataset with all clones included. Phylogenetic analyses for each LCN dataset were performed with MrBayes v.3.2.3 using the XSEDE interface of CIPRES (Miller & al., 2010) and ML using Garli v.2.0 (Zwickl, 2006). The MrBayes analyses were run for 3 million generations with a tempval=0.1. We used the GTR+ Γ +I but otherwise used the CIPRES default settings. We assessed convergence and mixing of the two independent runs with Tracer v.1.6 (Rambaut & al., 2014), and the first 25% of trees were discarded as burn-in. We confirmed that our runs achieved convergence by checking that the standard deviation of split frequencies fell below 0.01. In GARLI, our analyses employed the TIM3+ Γ +I (*PPR-AT3G09060*; no clones), TIM3+ Γ (*PPR-AT3G09060*; with clones), and the GTR+ Γ +I (*GBSSI*) models of evolution as suggested by the Akaike information criterion (AIC) as implemented in jModelTest v.2 (Posada, 2008; Darriba & al., 2012), while the other settings in the program were kept at default values. Clade support was assessed by running 100 bootstrap repetitions with the same GARLI settings as the initial ML analyses with the exception that only one search per replicate was conducted. For the cpDNA supermatrix alignment sequences were downloaded from GenBank and aligned in Mesquite. In the *psbA-trnH* region a 21 base pair inversion was observed and separated prior to analyses. For the supermatrix phylogenetic analyses we employed RAXML v.8.2.8 (Stamatakis, 2014) as implemented on CIPRES, using the default settings. For divergence time estimation we used the RAXML ML tree as an input for treePL (Smith & O'Meara, 2012). In the treePL configuration file, the following nodes were constrained based on the 95% highest posterior density (HPD) intervals found in the cpDNA and nrDNA analyses of Drew & Sytsma (2012): The crown of *Salvia axillaris* Moc. & Sessé+*S. patens* Cav. = 8.8–17.3 million years ago (mya); crown of *S. mellifera* Greene+*S. funerea* = 6.6–19.5 mya; crown of *S. patens*+*Meriandra bengalensis* (J.Koenig ex Roxb.) Benth. = 13.2–24.3 mya; crown of *Salvia patens*+*S. aristata* Aucher ex Benth. = 19.3–32 mya; crown of *S. officinalis*+*Rosmarinus officinalis* L. = 13.2–35.5 mya; crown of *Salvia officinalis*+*S. patens* = 24.3–37.7 mya; crown of *Melissa officinalis* L.+*M. axillaris* (Benth.) Bakh.f. = 0.5–6.8 mya; crown of *Lepechinia calycina* (Benth.) Epling ex Munz+*L. chamaedryoides* (Balb.) Epling = 7.5–19.5 mya; crown of *L. calycina*+*Melissa officinalis* = 29.7–35 mya; crown of *Lepechinia calycina*+*Salvia officinalis* = 30.8–41.5 mya. In all analyses gaps were treated as missing data. Alignments and trees are available in TreeBASE as study S19616.

RESULTS

PPR-AT3G09060 (no clones) analyses. — The PPR-AT3G09060 alignment contained 1132 characters. Within the alignment there was a six-base pair insertion (*Salvia mohavensis*) and a three-base pair deletion (*S. dorrii*, *S. mohavensis*, *S. pachyphylla*, *S. spathacea*), so alignment was straightforward. In the PPR-AT3G09060 phylogeny a clade with *Dorystaechas*, *Perovskia*, *Rosmarinus*, and *Zhumeria* embedded within *Salvia* was recovered with posterior probability (PP) = 1.00 and ML bootstrap support (BS) = 100% (Fig. S1).

PPR-AT3G09060 (with clones) analyses. — The PPR-AT3G09060 alignment with clones included contained 1182 characters, and contained no additional insertions or deletions. All six clones of *Salvia spathacea* had the same three-base pair deletion as the directly sequenced accession. All seven taxa that were cloned clustered in clades with their directly sequenced analogs (Fig. S2). Since no evidence of non-monophyly was found in any of the cloned taxa, we used the PPR-AT3G09060 dataset with only directly sequenced taxa for our subsequent combined LCN analyses.

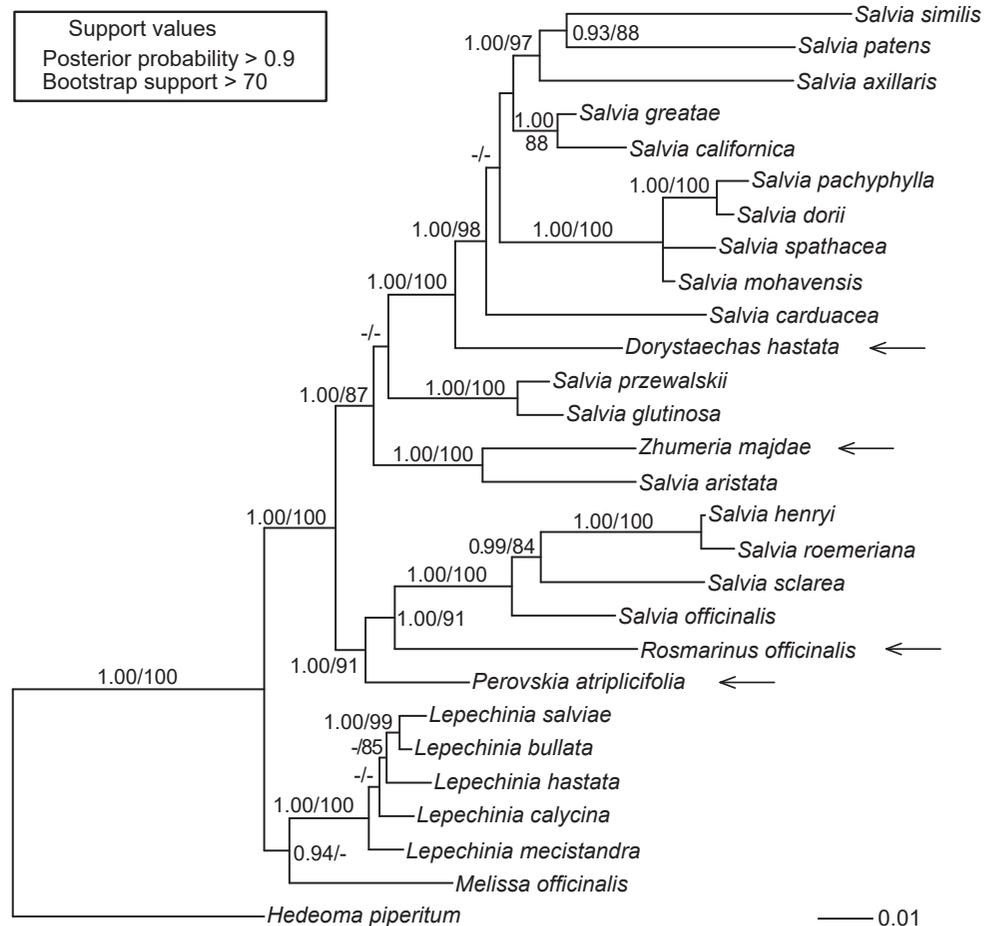
GBSSI analyses. — The GBSSI alignment consisted of 1624 characters. After excluding regions of ambiguous alignment and single-taxon insertions, the alignment used for analyses was comprised of 1285 characters. A single long insertion

in *Melissa officinalis* accounted for 139 of the 339 excluded characters. In our GBSSI analyses we recovered a clade with *Dorystaechas*, *Perovskia*, *Rosmarinus*, and *Zhumeria* embedded within *Salvia* with PP = 1.00 and BS = 100%. (Fig. S3).

Combined LCN analyses. — Our combined PPR-AT3G09060+GBSSI alignment contained 2417 characters. There were no supported incongruencies of relevance between the two separate datasets. In the combined dataset phylogeny we again recovered a clade with *Dorystaechas*, *Perovskia*, *Rosmarinus*, and *Zhumeria* embedded within *Salvia*, with posterior probability (PP) = 1.00 and ML bootstrap support (BS) = 100% (Fig. 1).

Supermatrix analyses. — After excluding 31 ambiguously aligned characters, the final cpDNA alignment had 6692 characters, and had 80.1% missing data. The supermatrix phylogeny (Figs. 2 & S4) is in general agreement with previous studies that have employed wide sampling across Salviinae (e.g., Walker & Sytsma, 2007; Drew & Sytsma, 2012). *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria* were embedded within *Salvia*, and together formed a clade sister to *Lepechinia* and *Melissa*, and the three largest clades within *Salvia* (*Salvia* subg. *Calosphace*, the “*Salvia glutinosa* clade”, and the “*Salvia officinalis* clade”) possess forms of the staminal lever mechanism. Virtually all cladogenesis within *Salvia* has apparently occurred within the past 15 million years, mostly since the onset of the Pliocene.

Fig. 1. Bayesian inference phylogram of subtribe Salviinae as inferred from analysis of PPR-AT3G09060 and GBSSI data. *Hedeoma piperitum* of subtribe Menthinae serves as an outgroup. Arrows indicate genera embedded within *Salvia*. Bayesian posterior probability/maximum likelihood bootstrap support values are shown near corresponding nodes (branch lengths in units of substitution).



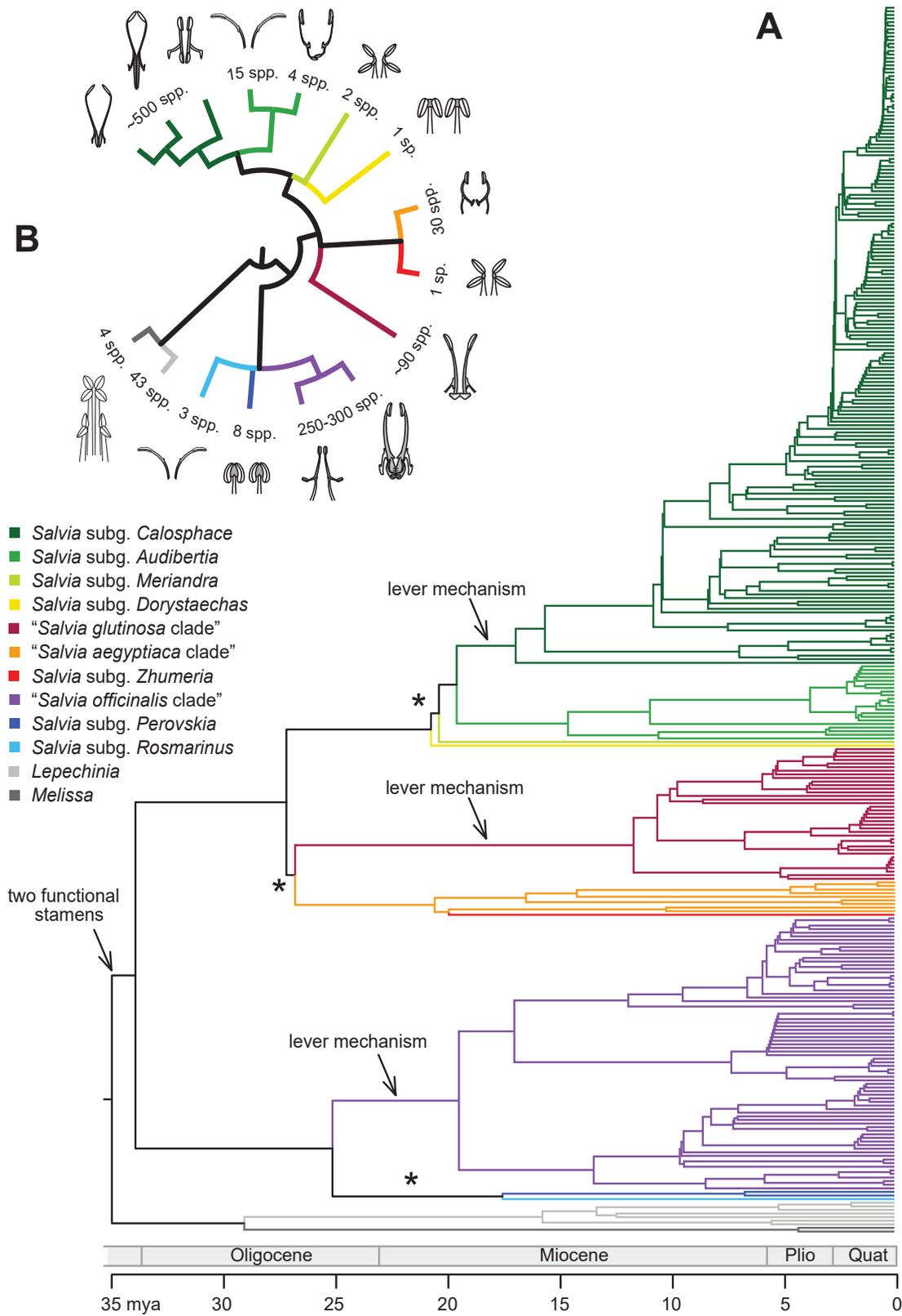


Fig. 2. A, Composite chronogram of subtribe Salviinae based on chloroplast DNA sequences from previous molecular phylogenetic analyses. Asterisks denote nodes with low support and/or conflicting resolution among previous analyses. *Salvia* nomenclature follows subgeneric clades described here, including three tentatively named clades that await proper circumscription. Calibrations based on Drew & Sytsma (2012) (see Fig. S4). **B**, Circle cladogram framed on larger chronogram with weakly supported nodes collapsed, depicting species diversity and generalized staminal types within each clade of *Salvia*; modified after Walker & Sytsma (2007) and Walker & al. (2015).

■ DISCUSSION

The phylogenetic argument for a broadly defined *Salvia*.

— This is the first published study to examine generic relationships within the Salviinae using low-copy nuclear genes. The results are clear: *Salvia*, *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria* form a clade within Salviinae. Although *Meriandra* was not represented in our low-copy nuclear gene analyses, the genus has been “deeply nested” within *Salvia* (often sister to *Dorystaechas*) in every molecular phylogenetic study in which it has been included, including the cpDNA supermatrix presented here (Figs. 2 & S4) (Walker & Sytsma, 2007; Drew & Sytsma, 2011, 2012; Will & Claßen-Bockhoff, 2014; Walker & al., 2015; Will & al., 2015). These findings confirm results from previous studies that have employed chloroplast and nuclear ribosomal DNA (e.g., Walker & Sytsma, 2007; Drew & Sytsma, 2011, 2012; Walker & al., 2015), as well as analyses that have used next-generation sequencing approaches (Drew & al., 2015; Drew & al., unpub. data). Additionally, these studies indicate that *Melissa* and *Lepechinia* are sister to a clade consisting of *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, *Salvia* and *Zhumeria* within Salviinae (see Fig. 2). Although some studies have failed to recover the above relationships, most of those studies had sparse gene and/or taxon sampling (e.g., Trusty, 2004; Takano & Okada, 2011; Will & Claßen-Bockhoff, 2014; Will & al., 2015), while others (e.g., Walker & al., 2004; Chen & al., 2014) produced relationships within the Salviinae that were in part compromised by erroneous *rbcL* sequences obtained from GenBank. Furthermore, no molecular phylogenetic study has demonstrated convincing support for relationships within the Salviinae that differ from what we present here.

As we have pointed out earlier (Walker & al., 2004, 2015; Drew & al., 2015; González-Gallegos, 2015), besides the “evolutionary taxonomic” (e.g., Brummitt, 2014) approach of maintaining a broadly paraphyletic *Salvia*—i.e., the status quo—two alternative approaches exist in classifying *Salvia* and relatives that preserve generic monophyly. The first is the lumping of the other five small genera (*Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria*; 15 species total) into *Salvia*, and the second is the splitting of *Salvia* into several genera—both approaches are phylogenetically defensible. Thus, unlike the often contentious dismantling of very broadly paraphyletic or polyphyletic genera (e.g., *Acacia*, *Aster*, *Psychotria*, *Senecio*) required for generic monophyly, the first approach precludes these drastic events for *Salvia*. However, recently Will & al. (2015) have initiated the second approach with their re-establishment of the genus *Pleudia* Raf., which matches *Salvia* sect. *Eremosphace* Bunge from northeast Africa and southwest Asia. As has been demonstrated in the context of a larger *Salvia*-wide framework (Walker & Sytsma, 2007; Drew & Sytsma, 2012; Walker & al., 2015), the small genera *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria* are either individually or in pairs sister to larger radiations of *Salvia*. This pattern of diversification is ostensibly because the latter have independently acquired the “staminal key innovation”, triggering speciation.

The morphological argument for a broadly defined *Salvia*.

— As a genus, *Salvia* has been recognized since Linnaeus (1753). Although *Salvia* exhibits at least three major species radiations (Meso-America/South America [~500 spp.], E Asia [~100 spp.], SW Asia and the Mediterranean region [~250 spp.]) and occurs on six continents, *Salvia* as traditionally circumscribed is clearly morphologically distinguishable as a genus throughout its range. While most Mentheae (including *Lepechinia* and *Melissa*) possess four fertile stamens (Harley & al., 2004; Drew & Sytsma, 2012), *Salvia* has only two anterior fertile stamens, with the two thecae of each stamen separated by an elongated connective tissue (Bentham, 1876; Claßen-Bockhoff & al., 2003; Walker & al., 2004, 2015). In several *Salvia* clades the expanded connective is positioned like a hinge, and pollinators push against the posterior (and usually non-fertile) thecae while accessing a nectar reward at the base of the corolla tube, causing the anterior thecae to deposit pollen on the pollinator via a lever mechanism (Sprengel, 1793; Himmelbaur & Stibal, 1933–1935; Claßen-Bockhoff & al., 2003; Walker & Sytsma, 2007). The elongated thecae connective tissue and the associated lever mechanism are found nowhere else in angiosperms. Somewhat elongated connectives can be seen in the Australian endemic mint genera, *Hemigenia* R.Br. and *Microcorys* R.Br. of subfamily Prostantheroideae (Guerin, 2005, 2008), and in some members of the justicioid clade of Acanthaceae (Keil & McDade, 2015).

The elongated connective tissue and lever mechanism within *Salvia* is a feature that is unique within Lamiaceae, and would serve as a “natural” character to delimit the vast majority of a broadly defined *Salvia* (Fig. 2). The five Salviinae genera embedded within *Salvia* also have only the two anterior fertile stamens. Furthermore, four of the embedded genera, *Dorystaechas*, *Meriandra*, *Perovskia*, and *Zhumeria*, have at least a swollen connective between the thecae (Bokhari & Hedge, 1976; Harley & al., 2004; Walker & Sytsma, 2007; Will & al., 2015). Importantly, *Rosmarinus* has a significantly elongated connective, only one fertile theca per anther, and a stamen morphology remarkably similar to some species of *Salvia* subg. *Audibertia* J.B.Walker & al. (Walker & al., 2015), leading Walker & Sytsma (2007) to remark: “independent of phylogeny, there is no morphological basis for why *Rosmarinus* should not be included in *Salvia*.” Harley & al. (2004) likewise noted that *Rosmarinus* “is scarcely separable from *Salvia*”. The other genera within Salviinae (*Lepechinia* and *Melissa*) have neither swollen nor elongated thecae connective tissue. Thus, the single feature “swollen or elongate thecae connective” would define all species of a broadly defined *Salvia* within the context of Salviinae. Furthermore, as noted by Ryding (2010), “the condition of having large crystals in the innermost cell layer of the mesocarp” can be considered a synapomorphy for the two-staminate Salviinae. This condition is unique in both Salviinae and Mentheae, as only one other taxon within Mentheae has these crystals (*Prunella* L.), and they are comparatively small (Ryding, 2010). Ryding (2010) went on to state that more homoplastic features such as “a particularly thick exocarp, many layers of mesocarp cells, and the absence of crystals in the sclerenchyma region” also lend support for this

(two-staminate *Salviinae*) group. Moreover, Moon & al. (2008) suggested that the two-staminate *Salviinae* were distinct based on “the number of layers in the sexine ornamentation”.

Thus, a number of diagnosable characters supports the inclusion of the five small genera into *Salvia* and exemplifies Frodin’s (2004) view that “in a few cases, a ‘good’ synapomorphy unites all members ... and that several of the ‘big’ genera are proving to be phylogenetically well-founded.” Indeed, we realize that trying to delimit morphologically “diagnosable” genera *within* a fragmented set of monophyletic clades arising out of *Salvia* is in fact the much greater difficulty. This latter endeavor is hampered by the lack of known phylogenetic relationships for many species, poor taxon sampling in most systematic studies, and the extensive morphological variation present often in a convergent or parallel fashion within and among clades (e.g., Wester & Claßen-Bockhoff, 2006, 2007, 2011; Walker & Sytsma, 2007; Jenks & al., 2012; Walker & al., 2015).

The practical argument for a broadly defined *Salvia*.

— The clear consensus from the broad participant base that formed “Systematics Agenda 2020” (Daly & al., 2012) was the articulation that three interlinked agendas remain central to the discipline of systematics: (1) to discover, describe, and inventory global species diversity; (2) to analyze and synthesize the information derived from this global discovery effort into a predictive classification system that reflects the history of life; and (3) to organize the information derived from this global program in an efficiently retrievable form that best meets the needs of science and society. The relevant goals of classification, especially at the generic level, that are at issue with respect to *Salvia* include names that are clear, universal, predictive, and stable (Stevens, 1985, 2002; Humphreys & Linder, 2009), and utility of the classification to both the systematic and larger public enterprises (Stevens, 1985; Sytsma & Pires, 2001; Frodin, 2004; Van Wyk, 2007; Humphreys & Linder, 2009). As the genus is integral to communicating biodiversity, even beyond the scientific community, it is imperative that we strive “to get it right” at the generic rank (Backlund & Bremer, 1998; Humphreys & Linder, 2009).

On the most practical level, retaining *Salvia* as the generic name for the nearly 1000 species already described and simply expanding it for 15 species now placed in five embedded genera is the most stable, practical approach (see “Taxonomic Combinations” below). For example, if *Salvia* is to be defined in a narrow sense and only encompasses *Salvia officinalis* and about 250 species of its clade, about three times that number would have to undergo name changes. Additionally, it would be necessary to reorganize tens of thousands of herbarium specimens around the world. Such monumental effort in both taxonomic name changes and herbarium management might be legitimate if no other reasonable course of action would ensure monophyly of named entities within *Salvia*. Retention of the generic name *Salvia* for all these species, however, is both legitimate, ensures monophyly, and thus preferred. If more manageable groups are desired, authors can simply name new subgenera, sections, etc., within the existing framework of a broadly circumscribed *Salvia*. For instance, the five embedded

genera (*Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, *Zhumeria*) can be afforded subgeneric ranks (as we have done here), other existing subgenera within *Salvia* could be retained, and newly recognized clades (e.g., *Pleudia* Raf.) could be designated as subgenera rather than genera, thereby obviating the need to rename hundreds of taxa. We have already implemented this approach with recognition of *Salvia* subg. *Audibertia* subg. nov. to encompass the two sections of western North American species (Walker & al., 2015), thereby retaining all previously used species names.

Finally, we argue that the dismantling of *Salvia* is unwise for another, important, and compelling reason—that is in the role that biological systematics serves in providing names for the world’s biological diversity to end-users of these names, a group far more numerous than the systematic community itself (Sytsma & Pires, 2001). Regions such as China, Meso-America, South America, and the southwestern United States would lose one of their most recognizable genera if this approach (dismantling *Salvia*) is endorsed. *Salvia* is extremely important in the horticultural trade and a large, worldwide following of *Salvia* enthusiasts have formed *Salvia* clubs, *Salvia* interest groups, and *Salvia* Summits. If *Salvia* were split into several or many new genera, it would be confusing and frustrating to this large, important, and vocal group within the botanical community, and ultimately damaging for our discipline. Systematic biologists have the opportunity and responsibility to engage other scientific disciplines and the general public and to communicate the wonder and excitement of systematics (Van Wyk, 2007; Humphreys & Linder, 2009; Daly & al., 2012). As a systematic community we indeed do have the freedom and ability to decide to rename over two-thirds of the world’s known *Salvia* species. However, as Stevens (2002) pointed out, “taxonomic freedom is not the issue, communication is.” We heartily agree. Both the systematic community and the wider general public are best served in this occasion by exercising constraint and communication, and by maintaining the generic integrity of *Salvia*, one of our most diverse, worldwide, and appreciated genera of flowering plants.

■ NOMENCLATURAL TREATMENT

Due to the phylogenetic, taxonomic, morphological, and practical factors discussed above in the context of *Salvia*, we offer these nomenclatural revisions and formally transfer the 15 species in the genera *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria* to *Salvia*. Additionally, we propose new subgeneric designations within *Salvia* for each of these former genera—these are presented graphically in Fig. 2 along with other recognized *Salvia* subgenera. Three additional lineages within *Salvia*, which require more thorough systematic work, are left with informal names in Fig 2: “*Salvia officinalis* clade”, “*Salvia glutinosa* clade”, and “*Salvia aegyptiaca* clade”.

Salvia L., Sp. Pl.: 23. 1753 – Type: *Salvia officinalis* L.

Annuals, perennials, or shrubs, usually aromatic; leaves simple, entire, toothed, less often pinnatifid to pinnate, rarely

spine-tipped; inflorescences axillary or terminal, spiciform to thyrsoid paniculate; calyx generally 2-lipped, 3–5-lobed, upper lip 1–3-lobed, lower lip 2- or 3-lobed; corolla generally strongly 2-lipped, upper lip 1- or 2(4)-lobed, lower lip 3(1)-lobed, middle lobe often expanded and emarginate; fertile stamens 2, posterior pair generally vestigial or absent, anterior pair inserted to exerted, thecae 1 or 2 (generally 1) per stamen, connective generally elongate (rarely swollen), posterior thecae fertile, often arched and included under upper corolla lip, anterior thecae generally sterile (rarely fertile), often flattened; style forked at tip, stigma lobes generally unequal; innermost cell layer of the mesocarp with large crystals. Mericarps often mucilaginous when wet.

Salvia subg. *Dorystaechas* (Boiss. & Heldr. ex Benth.) J.B.Walker, B.T.Drew & J.G.González, **comb. & stat. nov.** ≡ *Dorystaechas* Boiss. & Heldr. ex Benth. in Candolle, Prodr. 12: 261. 1848 – Type: *Salvia dorystaechas* B.T.Drew.

Salvia dorystaechas B.T.Drew, **nom. nov.** ≡ *Dorystaechas hastata* Boiss. & Heldr. ex Benth. in Candolle, Prodr. 12: 261. 1848 – **Lectotype (designated here):** TURKEY. Antalya, Kourmalu, May 1845, *T.H.H. Heldreich s.n.* (K barcode K000929627 [image!]; isolectotypes: BM [image!], E barcodes E00319680 [image!] & E00319681 [image!], GH [image!], K barcode K000929628 [image!], P barcodes P00714651 [image!], P00714652 [image!] & P00714653 [image!]).

Given that *Salvia hastata* Etl. is a name in current usage with priority against a new combination for *Dorystaechas hastata* into *Salvia*, a new epithet has been designated. This is the name of the former genus in apposition as a reminder of the taxonomic history of the species.

Salvia subg. *Meriandra* (Benth.) J.B.Walker, B.T.Drew & J.G.González, **comb. & stat. nov.** ≡ *Meriandra* Benth. in Edwards's Bot. Reg. 15: t. 1282. 1829 – Type: *Salvia dianthera* Roth ex Roem. & Schult., Syst. Veg. 1: 263. 1817.

Salvia dianthera Roth ex Roem. & Schult., Syst. Veg. 1: 263. 1817 ≡ *Meriandra dianthera* (Roth ex Roem. & Schult.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 288. 1896 – **Lectotype (designated here):** INDIA. *B. Heyne s.n.* (K barcode K000881724 [image!]).

= *Salvia abyssinica* R.Br. in Salt, Voy. Abyss.: lxiii [erroneously numbered lxii]. 1814, nom. nud.

= *Salvia bengalensis* J.Koenig ex Roxb., Fl. Ind. 1: 146. 1820 ≡ *Meriandra bengalensis* (J.Koenig ex Roxb.) Benth. in Edwards's Bot. Reg. 15: post pl. 1282. 1829.

= *Salvia stachydea* J.G.Klein ex Schult., Mant. 1: 216. 1822.

= *Meriandra abyssinica* F.Muell., Select Pl., ed. 2: 130. 1876.

Salvia strobilifera (Benth.) J.G.González, **comb. nov.** ≡ *Meriandra strobilifera* Benth. in Edwards's Bot. Reg. 15: post pl. 1282. 1829 – **Lectotype (designated here):** INDIA. 1829, *N. Wallich s.n.* (K barcode K000881723 [image!]).

Salvia subg. *Perovskia* (Kar.) J.B.Walker, B.T.Drew & J.G. González, **comb. & stat. nov.** ≡ *Perovskia* Kar. in Bull. Soc. Imp. Naturalistes Moscou 14: 15. 1841 – Type: *Salvia abrotanoides* Kar. in Bull. Soc. Imp. Naturalistes Moscou 14: 15. 1841.

= *Perovskia* Benth. in Candolle, Prodr. 12: 260. 1848.

Salvia abrotanoides (Kar.) Sytsma, **comb. nov.** ≡ *Perovskia abrotanoides* Kar. in Bull. Soc. Imp. Naturalistes Moscou 14: 15. 1841 – Holotype: TURKEMENISTAN: Balkan mountains, *G. Karelin s.n.* (LE).

= *Perovskia artemisioides* Boiss., Diagn. Pl. Orient., sér. 2, 4: 15. 1859.

Salvia bungei J.G.González, **nom. nov.** ≡ *Perovskia virgata* Kudrjasch. in Abh. Abt. Pfl.-Hilfsquellen Komitee Wiss. 2: 28. 1936 – Holotype: TAJIKISTAN. Darvoz, Kalai-Khum, 5000 ft [1524 m], Sep 1881, *A. Regel s.n.* (LE barcode LE 01009698 [image!]; isotypes: LE barcodes LE 01009699 [image!] & LE 01009701 [image!]).

The epithet honors Alexander A. Bunge (1803–1890), a German botanist working in Russia who described *P. scrophulariifolia* and almost 100 Lamiaceae species from Asia. The epithet *virgata* is not available for new combinations in *Salvia* (*S. virgata* Ait., *S. virgata* Jacq., *S. virgata* Ortega).

Salvia karelinii J.B.Walker, **nom. nov.** ≡ *Perovskia angustifolia* Kudr. in Abh. Abt. Pfl.-Hilfsquellen Komitee Wiss. 2: 23. 1936 – Holotype: KYRGYSTAN. Tian-schan occidentalis, Gandiga-sai 5 km septentrionem versus a Namangan, in decliviis lapidosis, in promontoris, 23 May 1912, *O.E. Knorring 13* (LE barcode LE 01009685 [image!]; isotypes: LE barcodes LE 01009686 [image!] & LE 01009687 [image!]).

The epithet *angustifolia* is not available in *Salvia* (*S. angustifolia* Benth., *S. angustifolia* (Benth.) Pugsley, *S. angustifolia* Bunge, *S. angustifolia* Cav., *S. angustifolia* Michx., *S. angustifolia* Salisb. and *S. angustifolia* Skan); hence, a new epithet is coined, this honors Grigorij S. Karelin (1801–1872), a Russian botanist who described the genus *Perovskia*.

Salvia klokovii J.B.Walker, **nom. nov.** ≡ *Perovskia linczevskii* Kudr. in Abh. Abt. Pfl.-Hilfsquellen Komitee Wiss. 2: 30. 1936 – Holotype: TAJIKISTAN: Dashti-Dzumsky, Montes Pamiro-Alaj, systema fl. Pjandsh. Fl. Sarbus in angustiis Vaschpuscht in lapidosis, 1200 m, 4 Oct 1935, *J.A. Linczevski & T.J. Maslennikova 1545* (LE barcode LE 01009693 [image!]).

The epithet honors Michail V. Klovov (1896–1981), Russian botanist who contributed with the description of more than 200 species of Lamiaceae, including several *Salvia*. The new epithet was designated since *linczevskii* is not available in *Salvia* (*S. linczevskii* Kudr.).

Salvia kudrjashevii (Gorsch. & Pjataeva) Sytsma, **comb. nov.** ≡ *Perovskia kudrjashevii* Gorsch. & Pjataeva in Bot. Mater. Gerb. Bot. Inst. Kovarova Akad. Nauk S.S.S.R.

16: 290. 1954 – Holotype: KAZAKHSTAN: Tjan-Schan occidentalis, districtus Bostandyk, in vicinitate pagi Britsh-Mulla, ad viam Chudaj-Dod, in glareosis ad ripam fluminis Tschatkal, 31 Jul 1950, *A. Pjataeva 98* (LE barcode LE 01009690 [image!]).

Salvia pobedimovae J.G.González, **nom. nov.** ≡ *Perovskia botschantzevii* Kovalevsk. & Kochk., Fl. Tadzhijskoi SSR 8: 483. 1986 – Holotype: UZBEKISTAN. Montes Aktau, ad orientem a urb. Nurata, vallis sicca Ingiczké, ad declivia lapidosa, 12 Jul 1970, *V. Botschantzev 123* (LE barcode LE 01009688 [image!]).

The epithet honors Eugenia G. Pobedimova (1898–1973), Russian botanist who made several contributions to the knowledge of the flora of her country, including the description of *Arischrada* Pobed., one of the current generic synonyms of *Salvia*. The new epithet was designated since *botschantzevii* is not available in *Salvia* (*Salvia botschantzevii* Czern.).

Salvia scrophulariifolia (Bunge) B.T.Drew, **comb. nov.** ≡ *Perovskia scrophulariifolia* Bunge in Mém. Acad. Imp. Sci. St.-Petersbourg Divers Savans 7: 433. 1851 – Holotype: KAZAKHSTAN. 6 Sep 1841, *A. Bunge s.n.* (LE barcode LE 01009696 [image!]; isotype: LE barcode LE 02009697 [image!]).

Salvia yangii B.T.Drew, **nom. nov.** ≡ *Perovskia atriplicifolia* Benth. in Candolle, Podr. 12: 261. 1848 – Holotype: AFGHANISTAN. Between Kabul and Ghazni, *W. Griffith 464* (K barcode K000929655 [image!]).

= *Perovskia pamirica* Chang Y. Yang & B. Wang in Bull. Bot. Res., Harbin 7: 95–96. 1987.

The epithet commemorates Chang Y. Yang (1928–), a Chinese botanist who described one of the synonyms of *Perovskia atriplicifolia*. *Salvia atriplicifolia* Fernald and *Salvia pamirica* Gand. are not available for a new combination.

Salvia* subg. *Rosmarinus (L.) J.B.Walker, B.T.Drew & J.G. González, **comb. & stat. nov.** ≡ *Rosmarinus* L., Sp. Pl.: 23. 1753 – Type: *Salvia rosmarinus* (L.) Schleid., Handb. Med.-Pharm. Bot. 1: 265. 1852.

Salvia granatensis B.T.Drew, **nom. nov.** ≡ *Rosmarinus tomentosus* Hub.-Mor. & Maire in Bull. Soc. Hist. Nat. Afrique N. 31: 79. 1940 ≡ *Rosmarinus eriocalyx* subsp. *tomentosus* (Hub.-Mor. & Maire) Fern.Casas in Cuad. Ci. Biol. 2: 40. 1973 – Holotype: SPAIN. Prov. Granada, Cabo Scratif rochers près de Motril, 16 May 1936, *A. Huber-Morath s.n.* (AL [image!]).

The epithet honors the Spanish province Granada, which embraces most populations of the species. The new name is proposed because *Salvia tomentosa* Mill. is already in use.

Salvia jordanii J.B.Walker, **nom. nov.** ≡ *Rosmarinus eriocalyx* Jord. & Fourr., Brev. Pl. Nov. 1: 44. 1866 – Holotype: ALGERIA. Pentes rocaïlleuses du Blockaus près de Boghar, 14 Mar 1856, *O. Debeaux 2124* (G barcode

G00169750 [image!]; isotypes: BM barcode BM000796984 [image!], P barcode P00076034 [image!]).

= *Rosmarinus officinalis* var. *tournefortii* Noë ex Jord. & Fourr., Brev. Pl. Nov. 1: 44. 1866.

= *Rosmarinus officinalis* var. *pubescens* Pamp., Pl. Tripol.: 216. 1914.

= *Rosmarinus eriocalyx* var. *pallescens* (Maire) Upson & Jury in Lagasalia 18: 296. 1996 ≡ *Rosmarinus tournefortii* f. *pallescens* Maire in Bull. Soc. Hist. Nat. Afrique N. 20: 34. 1929.

The epithet commemorates Claude T.A. Jordan (1814–1897), a French botanist who described *Rosmarinus eriocalyx* together with Jules P. Fourreau (1844–1871). The epithet *eriocalyx* is not available for a new combination in *Salvia* (*S. eriocalyx* Bertero ex Roem. & Schult.).

Salvia rosmarinus (L.) Schleid., Handb. Med.-Pharm. Bot. 1: 265. 1852 ≡ *Rosmarinus officinalis* L., Sp. Pl.: 23. 1753 – Lectotype (designated by Hedge in Regnum Veg. 127: 82. 1993): NETHERLANDS. Collected from cultivated material from the garden of George Clifford, *G. Clifford 14* (BM barcode BM000557615 [image!]; isotypes: BM barcodes BM000557614 [image!] & BM000557616 [image!]).

= *Rosmarinus officinalis* var. *angustifolius* (Mill.) DC., Fl. Franç. 3: 506. 1805.

= *Rosmarinus officinalis* var. *latifolius* (Mill.) DC., Fl. Franç. 3: 506. 1805.

= *Rosmarinus laxiflorus* Noë ex Lange in Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1863: 12. 1863.

= *Rosmarinus flexuosus* Jord. & Fourr., Brev. Pl. Nov. 1: 44. 1866.

= *Rosmarinus officinalis* var. *argentatus* Alef., Landw. Fl.: 120. 1866.

= *Rosmarinus officinalis* var. *auratus* Alef., Landw. Fl.: 120. 1866.

= *Rosmarinus officinalis* var. *vulgaris* Alef., Landw. Fl.: 120. 1866.

= *Rosmarinus rigidus* Jord. & Fourr., Brev. Pl. Nov. 1: 43. 1866.

= *Rosmarinus tenuifolius* Jord. & Fourr., Brev. Pl. Nov. 1: 43. 1866.

= *Rosmarinus officinalis* var. *prostratus* Pasq., Cat. Ort. Bot. Napoli: 91. 1867.

= *Rosmarinus serotinus* Loscos, Trat. Pl. Aragon 1: 71. 1876.

= *Rosmarinus officinalis* subsp. *laxiflorus* (Noë ex Lange) Nyman, Consp. Fl. Eur.: 571. 1881.

= *Rosmarinus officinalis* var. *rigidus* (Jord. & Fourr.) Cariot & St.-Lag., Étude Fl., ed. 8, 2: 657. 1889.

= *Rosmarinus officinalis* f. *laxiflorus* (Noë) Batt., Fl. Algérie 1, Dicot.: 690. 1890.

= *Rosmarinus officinalis* var. *angustissimus* Foucaud & E.Mandon in Bull. Soc. Bot. France 47: 95. 1900.

= *Rosmarinus officinalis* var. *nutans* Cout. in Bol. Soc. Brot. 23: 160. 1907.

= *Rosmarinus officinalis* var. *trogloditarum* Maire & Weiller in Bull. Soc. Hist. Nat. Afrique N. 30: 297. 1939.

= *Rosmarinus officinalis* var. *palaui* O.Bolòs & Ant.Molina in Collect. Bot. (Barcelona) 5: 757. 1959 ≡ *Rosmarinus*

- officinalis* subsp. *palau* (O.Bolòs & Ant.Molina) Malag., Subesp. Variac. Geogr.: 23. 1973 ≡ *Rosmarinus palau* (O.Bolòs & Ant.Molina) Rivas Mart. & M.J.Costa, Itinera Geobot. 15: 707. 2002.
- = *Rosmarinus officinalis* subvar. *macrocalyx* Font Quer ex O.Bolòs & Vigo in Collect. Bot. (Barcelona) 14: 95. 1983.
- = *Rosmarinus officinalis* var. *palau* O.Bolòs & Ant.Molina in Collect. Bot. (Barcelona) 5: 757. 1959.
- = *Rosmarinus officinalis* subsp. *valentinus* P.P.Ferrer, A.Guillén & Gómez Nav. in Phytotaxa 172(2): 62. 2014.

Salvia subg. *Zhumeria* (Rech.f. & Wendelbo) J.B.Walker, B.T.Drew & J.G.González, **comb. & stat. nov.** ≡ *Zhumeria* Rech.f. & Wendelbo in Nytt Mag. Bot. 14: 39. 1967 – Type: ≡ *Salvia majdae* (Rech.f. & Wendelbo) Sytsma.

Salvia majdae (Rech.f. & Wendelbo) Sytsma, **comb. nov.** ≡ *Zhumeria majdae* Rech.f. & Wendelbo in Nytt. Mag. Bot. 14. 39. 1967 – Holotype: IRAN. Prov. Laristán, Gotabad, ca. 100 km N of Bandar Abbas, ca. 800 m, 23 Mar 1966, *M. Žumer* 362 (BG barcode 2000174; isotype: E barcode E00319679 [image!]).

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Appendix 1. Voucher information and GenBank accession numbers for taxa used in this study. New sequences indicated by asterisk (*). Information is as follows: taxon name and authority, collecting locality, collector(s) name and collection number (herbarium), GenBank numbers are for *PPR-AT3G09060* and *GBBSI*, respectively. Taxa missing *GBBSI* sequences indicated with a dash-. Abbreviations: Royal Botanical Gardens at Edinburgh = RBGE, Rancho Santa Ana Botanical Garden = RSA, UC Berkeley Botanical Garden = UCBG.

Hedeoma piperitum Benth., Mexico, *B. Drew* 92 (WIS); KF307409, KF307565; *Lepechinia bullata* (Kunth) Epling, Ecuador, *B. Drew* 223 (WIS); KF307360, KF307500; *Lepechinia calycina* (Benth.) Epling ex Munz, U.S.A., *B. Drew* 20 (WIS); KF307361, KF307501; *Lepechinia hastata* (A.Gray) Epling, Mexico, *B. Drew* 44 (WIS); KF307370, KF307510; *Lepechinia mecistandra* Donn.Sm., El Salvador, *J.A. Monterrosa & R.A. Carballo* 213 (MO); KF307357, KF307497; *Lepechinia salviae* (Lindl.) Epling, Chile, *R. Jabaily s.n.* (WIS); KF307382, KF307522; *Melissa officinalis* L., cult. UW-Madison, *B. Drew* 70 (WIS); KF307390, KF307530; *Salvia aristata* Aucher ex Benth, Iran, *Wedelbo & Assadi s.n.* (E); KY067374*, KY067389*; *PPR-AT3G09060* clones 1–8: KY067331*, KY067332*, KY067333*, KY067334*, KY067335*, KY067336*, KY067337*, KY067338*; *Salvia axillaris* Moc. & Sessé, Mexico, *J. Walker* 3038 (WIS); KY067375*, KY067390*; *Salvia californica* Brandege, cultivated RSA, *J. Walker* 2520 (WIS); KY067376*, KY067391*; *Salvia carduacea* Benth., U.S.A., *J. Walker* 3091 (WIS); KY067377*, KY067392*; *PPR-AT3G09060* clones 1–7: KY067339*, KY067340*, KY067341*, KY067342*, KY067343*, KY067344*, KY067345*; *Salvia dorrii* (Kellogg) Abrams, cultivated RSA, *J. Walker* 2541 (WIS); KY067380*, –; *Salvia dorystaechas* B.T.Drew, cultivated RBGE 1972-0177D, *J. Walker s.n.* (WIS); KF307399, KF307555; *PPR-AT3G09060* clones 1–8: KY067323*, KY067324*, KY067325*, KY067326*, KY067327*, KY067328*, KY067329*, KY067330*; *Salvia glutinosa* L., cultivated, *J. Walker* 2568 (WIS); KF307402, KF307558; *Salvia greatae* Brandege, U.S.A., *J. Walker* 2511 (WIS); KY067381*, KY067393*; *PPR-AT3G09060* clones 1, 2, 4, 5, 7, 8: KY067346*, KY067347*, KY067348*, KY067349*, KY067350*, KY067351*; *Salvia henryi* A.Gray, U.S.A., *J. Walker* 2516 (WIS); KY067382, –; *Salvia majdae* (Rech.f. & Wendelbo) Sytsma, *Terme* 14573 (E); KF307408, KF307564. *PPR-AT3G09060* clones 1–7: KY067367*, KY067368*, KY067369*, KY067370*, KY067371*, KY067372*, KY067373*; *Salvia mohavensis* E.Greene, U.S.A., *J. Walker* 3119 (WIS); KY067384*, –; *Salvia officinalis* L., cultivated-UCBG 7.0083, *M. Palma s.n.* (UC); KF307404, KF307560; *Salvia pachyphylla* Munz, U.S.A., cultivated RSA, *J. Walker* 2535 (WIS); KY067385*, –; *Salvia patens* Cav., cultivated-RBGE 1973-9197, *J. Walker s.n.* (WIS); KF307405, KF307561; *PPR-AT3G09060* clones 1–5, 7–9: KY067352*, KY067353*, KY067354*, KY067355*, KY067356*, KY067357*, KY067358*, KY067359*; *Salvia przewalskii* Maxim., cultivated-RBGE 1993-2067A, *J. Walker s.n.* (WIS); KF307406, KF307562; *Salvia roemeriana* Scheele, U.S.A., *J. Walker* 2515 (WIS); KF307407, KF307563; *Salvia rosmarinus* (L.) Schleid., Handb., cultivated, *J. Walker* 2558 (WIS); KF307401, KF307557; *Salvia sclarea* L., cultivated, *J. Walker* 2527 (WIS); KY067386*, KY067394*; *Salvia similis* Brandege, Mexico, *B. Drew* 43 (WIS); KY067387*, KY067395*; *Salvia spathacea* E.Greene, U.S.A., *J. Walker* 2552 (WIS); KY067388*, –; *PPR-AT3G09060* clones 1–4, 6–8: KY067360*, KY067361*, KY067362*, KY067363*, KY067364*, KY067365*, KY067366*; *Salvia yangii* B.T.Drew, cultivated, *J. Walker* 2524 (WIS); KF307400, KF307556.