Int. J. Plant Sci. 181(8):000–000. 2020.

1058-5893/2020/18108-00XX$15.00 DOI: 10.1086/710711

SPECIAL ISSUE—EVOLUTION AND
POLLINATION OF *SALVIA*

EVOLUTION, POLLINATION BIOLOGY, AND SPECIES RICHNESS OF *SALVIA* (LAMIACEAE)

Bryan T. Drew[1],*

*Department of Biology, University of Nebraska–Kearney, Kearney, Nebraska 68849, USA

Salvia (Lamiaceae), or the sages, are one of the most species-rich and recognizable genera of flowering plants. *Salvia* contains about 1000 species, is native on six continents, and has more than 150 species in cultivation for ornamental, culinary, and/or medicinal purposes. While *Salvia* has been recognized as a genus since Linnaeus, it has had a tortuous taxonomic history. And although (and perhaps because) it has recently been circumscribed in a broad sense to include several other small genera, including the commonly cultivated *Rosmarinus* (rosemary) and *Perovskia* (Russian sage), the taxonomy of *Salvia* remains controversial (Walker and Sytsma 2007; Will et al. 2015; Drew et al. 2017; Will and Claßen-Bockhoff 2017; Kriebel et al. 2019). A major factor underlying the complicated taxonomic history of *Salvia* is the remarkable floral diversity within the genus. The long-standing putative synapomorphy of the genus, the "staminal lever mechanism" (Claßen-Bockhoff et al. 2004), not only has ostensibly evolved in parallel multiple times but also has numerous different forms (Walker and Sytsma 2007; Hu et al. 2018; Kriebel et al. 2020). While causing some headaches taxonomically, the myriad variations of the staminal lever mechanism have helped make *Salvia* a model genus for research in pollination biology.

In this special issue, we attempt both to elucidate some of the mechanisms underpinning the evolutionary success of *Salvia* and to clarify pollination biology, phylogenetic relationships, plastome evolution, and subgeneric classification within the genus. Three articles within this issue answer questions related to pollination biology within *Salvia*. Wester et al. (2020) use species of *Salvia* from several major clades to examine whether the "bee avoidance hypothesis" (Castellanos et al. 2004) holds with *Salvia*; Celep et al. (2020) investigate prezygotic isolation mechanisms and the pollination ecology of 12 species of *Salvia* growing in sympatry; and Cairampoma et al. (2020) look into the pollination biology of *S. rhombifolia*, an annual species endemic to the Atacama Desert of Peru and northern Chile. The other three articles in this issue reveal that two subgenera of *Salvia* are indeed native to East Asia (Hu et al. 2020), explore plastome evolution within the genus (Zhao et al. 2020), and provide some much-needed taxonomic clarity for *Salvia* subg. *Calosphace* (González-Gallegos et al. 2020). A brief description of each article is provided below.

Pollination Biology

It is not unusual to find multiple species of *Salvia* occurring in proximity, but the incidence of documented cases of hybridization between sympatric species is relatively low. One explanation for this low rate of hybridization is that the primary pollinators of *Salvia*, bees and hummingbirds (Wester and Claßen-Bockhoff 2007, 2011; Fragoso-Martínez et al. 2018; Kriebel et al. 2019; Celep et al. 2020), enforce reproductive isolation between sympatric species. Two of the studies in this issue consider the potential for pollinator-mediated reproductive isolation. Wester et al. (2020) report on how color and an absence of nectar guides can "discourage" bees from visiting bird-pollinated flowers, but they suggest that mechanical exclusion is the major factor that prevents bees from acting as pollen vectors in bird-pollinated *Salvia*. Celep et al. (2020) provide detailed information on flower and pollinator morphology and use this as a platform to describe how phenological and mechanical isolation inhibits hybridization among 12 sympatric species of *Salvia* in Turkey.

Although most species of *Salvia* seem to be pollinated primarily by either bees or birds, some species of *Salvia* are effectively pollinated by both (Wester and Claßen-Bockhoff 2011; Wester et al. 2020). Cairampoma et al. (2020), using the Atacama Desert–endemic *S. rhombifolia* as a case study, explore the adaptive value of more generalized pollination systems. They show that both bees and hummingbirds are effective pollinators of *S. rhombifolia*, and they suggest that this mixed pollination syndrome is a mechanism to help *S. rhombifolia* enhance reproductive success in the extreme Atacama Desert environment.

Phylogenetics and Genome Evolution

Although some subgenera of *Salvia* are geographically widespread, they are usually geographically contiguous (the outstanding exception being the informally named subg. "*Heterosphace*"). In keeping with the taxonomic complexity of the genus, until recently, East Asian *Salvia* was classified into three different subgenera, subg. *Salvia*, subg. *Sclarea*, and subg. *Allagospadonopsis*. However, Hu et al. (2018) demonstrated that all species of *Salvia* native to East Asia are monophyletic and formally placed them into the new subg. *Glutinaria*. In this issue, Hu et al. (2020) report on the rediscovery of the rare and enigmatic *S. grandifolia* from the provinces of Sichuan and Yunnan in southwestern China. Using molecular and morphological evidence, they demonstrate that *S. grandifolia* is in fact a member of subg. *Sclarea*, and thus *Salvia* has dispersed to East

---

[1] Email: bdrewfb@yahoo.com.

Manuscript received July 2020; electronically published September 1, 2020.

Asia at least twice. Notably, the dispersal of *S. grandifolia* into East Asia apparently occurred after the uplift of the Altay, Kunlun, and Tian Shan mountain ranges at the western edge of the Qinghai-Tibetan Plateau; they ostensibly present a major barrier to dispersal into or out of East Asia.

Other than putative convergent morphological evolution within *Salvia* (Walker et al. 2007; Will and Claßen-Bockhoff 2017), another factor that has hindered our ability to resolve relationships within the genus has been a lack of phylogenetically informative markers. In this issue, Zhao et al. (2020) present an analysis of 16 plastomes of *Salvia*. They use these plastomes to identify simple sequence repeats and hypervariable regions that should prove valuable for future phylogenetic analyses within *Salvia*. Zhao et al. (2020) then compare the efficacy of the identified hypervariable regions with that of whole plastomes for phylogenetic inference using *Salvia* subg. *Glutinaria* as a test study.

Species Richness

Because of the large number of species and wide geographic breadth of *Salvia*, it has proved challenging to provide an accurate estimate for the accepted number of species of *Salvia* that occur both worldwide and within most subgenera. Recent estimates of species numbers for the genus have ranged from about 700 to more than 1000. Much of this uncertainty is a product of both the broad geographic ranges of many species or species complexes of *Salvia* and researchers describing new species of *Salvia* in relative isolation (i.e., a lack of communication between researchers). In this issue, González-Gallegos et al. (2020) tackle the taxonomy of the most species-rich subgenus of *Salvia*, *Salvia* subg. *Calosphace*. This article brings together taxonomic experts from across the geographic breadth of the subgenus. This diverse group concluded that there are 580 species within the subgenus but that 30 of these species should not yet be considered “accepted.” Thus, there are currently 550–580 accepted species within *Salvia* subg. *Calosphace*. Additionally, González-Gallegos et al. (2020) provide a checklist of accepted species and synonyms of subg. *Calosphace*.

Future Directions

The articles in this special issue clarify aspects of pollination biology, biogeography, taxonomy, and evolution within *Salvia*. These articles, in concert with other ongoing research endeavors by these authors and others, will provide a springboard for better articulating the evolutionary history, pollination biology, and taxonomy of *Salvia*. Going forward, the synthesis of improved phylogenetic resolution via next-generation sequencing technologies, detailed and broad-scale morphometric analyses of both plants and pollinators, field-based pollinator observations, and taxonomic clarifications will provide unprecedented insights into *Salvia* evolution.

Acknowledgments

This special issue was inspired by a colloquium titled “Evolutionary History, Biogeography, and Floral Morphometrics of *Salvia* (Lamiaceae)” that took place at the Botanical Society of America conference in Rochester, Minnesota, in July 2018. We thank the organizers of the conference for hosting our colloquium and sparking this special issue. We gratefully acknowledge everyone who participated in the symposium as well as all the internal and external reviewers who helped improve the quality of the manuscripts within this issue. We are grateful to the editor in chief of the *International Journal of Plant Sciences*, Christina Caruso, for inviting us to produce this special issue as well as for editorial guidance. We also thank the *International Journal of Plant Sciences* managing editor at the University of Chicago Press, James Ellis, for providing invaluable assistance throughout. We acknowledge funding from NSF collaborative grants (DEB-1655606 and DEB-1655611).

Literature Cited

Cairampoma L, JA Tello, R Claßen-Bockhoff 2020 Pollination in the desert: adaptation to bees and birds in *Salvia rhombifolia*. Int J Plant Sci 181:XXX–XXX.

Castellanos MC, P Wilson, JD Thomson 2004 “Anti-bee” and “pro-bird” changes during the evolution of hummingbird pollination in Penstemon flowers. J Evol Biol 17:876–885.

Celep F, Z Atalay, F Dikmen, M Doğan, KJ Sytsma, R Claßen-Bockhoff 2020 Pollination ecology, specialization, and genetic isolation in sympatric bee-pollinated *Salvia* (Lamiaceae). Int J Plant Sci 181:XXX–XXX.

Claßen-Bockhoff R, T Speck, E Tweraser, P Wester, S Thimm, M Reith 2004 The staminal lever mechanism in *Salvia* L. (Lamiaceae): a key innovation for adaptive radiation? Org Divers Evol 4:189–205.

Drew BT, JG González-Gallegos, CL Xiang, R Kriebel, CP Drummond, JB Walker, KJ Sytsma 2017 *Salvia* united: the greatest good for the greatest number. Taxon 66:133–145.

Fragoso-Martínez I, M Martínez-Gordillo, GA Salazar, F Sazatornil, AA Jenks, MR García-Peña, G Barrera-Aveleida, et al 2018 Phylogeny of the Neotropical sages (*Salvia* subg. *Calosphace*; Lamiaceae) and insights into pollinator and area shifts. Plant Syst Evol 304:43–55.

González-Gallegos JG, BY Bedolla-García, G Cornejo-Tenorio, JL Fernández-Alonso, I Fragoso-Martínez, MR García-Peña, RM Harley, et al 2020 Richness and distribution of *Salvia* subgenus *Calosphace* (Lamiaceae). Int J Plant Sci 181:XXX–XXX.

Kriebel R, BT Drew, CP Drummond, JG González-Gallegos, F Celep, MM Mahdjoub, JP Rose, et al 2019 Tracking temporal shifts in area, biomes, and pollinators in the radiation of *Salvia* (sages) across continents: leveraging anchored hybrid enrichment and targeted sequence data. Am J Bot 106:573–597.

Kriebel R, BT Drew, JG González-Gallegos, F Celep, L Heeg, MM Mahdjoub, KJ Sytsma 2020 Pollinator shifts, contingent evolution, and evolutionary constraint drive floral disparity in *Salvia* (Lamiaceae): evidence from morphometrics and phylogenetic comparative methods. Evolution 74:1335–1355. https://doi.org/10.1111/evo.14030.

Hu GX, ED Liu, ZK Wu, KJ Sytsma, BT Drew, CL Xiang 2020 Integrating DNA sequences with morphological analysis clarifies phylogenetic position of *Salvia grandifolia* (Lamiaceae): an enigmatic species endemic to southwestern China. Int J Plant Sci 181:XXX–XXX.

Hu GX, A Takano, BT Drew, ED Liu, DE Soltis, PS Soltis, H Peng, CL Xiang 2018 Phylogeny and staminal evolution of *Salvia* (Lamiaceae, Nepetoideae) in East Asia. Ann Bot 122:649–668.

Walker JB, KJ Sytsma 2007 Staminal evolution in the genus *Salvia* (Lamiaceae): molecular phylogenetic evidence for multiple origins of the staminal lever. Ann Bot 100:375–391.

Wester P, L Cairampoma, S Haag, J Schramme, C Neumeyer, R Claßen-Bockhoff 2020 Bee exclusion in bird-pollinated *Salvia* flowers: the role of flower color versus flower construction. Int J Plant Sci 181:XXX–XXX.

Wester P, R Claßen-Bockhoff 2007 Floral diversity and pollen transfer mechanisms in bird-pollinated *Salvia* species. Ann Bot 100:401–421.

——— 2011 Pollination syndromes of New World *Salvia* species with special reference to bird pollination. Ann Mo Bot Gard 98:101–155.

Will M, R Claßen-Bockhoff 2017 Time to split *Salvia* s.l. (Lamiaceae): new insights from Old World *Salvia* phylogeny. Mol Phylogenet Evol 114:33–58.

Will M, N Schmalz, R Claßen-Bockhoff 2015 Towards a new classification of *Salvia* s.l.: (re)establishing the genus *Pleudia* Raf. Turk J Bot 39:693–707.

Zhao F, BT Drew, Y-P Chen, G-X Hu, B Li, C-L Xiang 2020 The chloroplast genome of *Salvia*: genomic characterization and phylogenetic analysis. Int J Plant Sci 181:XXX–XXX.