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RICHNESS AND DISTRIBUTION OF *SALVIA* SUBG. *CALOSPHACE* (LAMIACEAE)

Jesús G. González-Gallegos,[1,*] Brenda Y. Bedolla-García,† Guadalupe Cornejo-Tenorio,‡ José L. Fernández-Alonso,§ Itzi Fragoso-Martínez,†‖ María del Rosario García-Peña,‖ Raymond M. Harley,# Bente Klitgaard,# Martha J. Martínez-Gordillo,** John R. I. Wood,#,†† Sergio Zamudio,‡‡ Scott Zona,§§ and Cecilia C. Xifreda‖‖

*Cátedras Consejo Nacional de Ciencia y Tecnología, Instituto Politécnico Nacional, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Durango, Fraccionamiento 20 de Noviembre II, Sigma 119, Victoria de Durango 34234, Mexico; †Instituto de Ecología, A.C., Centro Regional del Bajío, Apartado Postal 386, Pátzcuaro 61600, Michoacán, Mexico; ‡Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia 58190, Mexico; §Real Jardín Botánico, Consejo Superior de Investigaciones Científicas, Claudio Moyano 1, Madrid 28104, Spain; ‖Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-367, 04510 Coyoacán, Mexico City, Mexico; #Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, United Kingdom; **Herbario de la Facultad de Ciencias, Universidad Nacional Autónoma de México, 04510 Coyoacán, Mexico City, Mexico; ††Department of Plant Sciences, Oxford University, Oxford OX1 3RB, United Kingdom; ‡‡Apartado Postal 392, Pátzcuaro 61600, Michoacán, Mexico; §§1807 Seminole Drive, Hillsborough, North Carolina 27278, USA; and ‖‖‖Instituto de Botánica Darwinion, Labardén 200, Casilla de Correo 22, San Isidro B1542HYD, Buenos Aires, Argentina

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Premise of research. *Salvia* is one of the most species-rich genera in the world. Its outstanding diversity and subcosmopolitan distribution have prevented the preparation of a modern comprehensive monograph and re-evaluation of its classification. As phylogenetic efforts advance to untangle the evolutionary relationships of *Salvia*, the need for a solid taxonomic footing is increasingly imperative. Accordingly, we present an updated checklist of the species richness and distribution of *Salvia* subg. *Calosphace*, which constitutes more than half of the diversity of the genus.

Methodology. A preliminary checklist of the species of *Salvia* subg. *Calosphace* was compiled through examination of the literature and online databases; this was revised and discussed by the authors in order to retrieve a consensus list. The distribution of each species by country or territory as well as by biome was also recorded from the sources consulted; affinities in composition were visualized with the unweighted pair group method with arithmetic mean based on a dissimilarity matrix (Sørensen's index).

Pivotal results. *Salvia* subg. *Calosphace* comprises 580 species; 30 were qualified as unresolved and require further analysis. The countries with the highest species richness are Mexico (295 spp.), Peru (77 spp.), Colombia (60 spp.), Brazil (58 spp.), Guatemala (49 spp.), and Ecuador (41 spp.). The affinity in species composition between countries and between biomes is explained mainly by geographical proximity.

Conclusions. The updated list of the species of *Salvia* subg. *Calosphace* will help to guide sampling for phylogenetic analyses, enabling the achievement of a more stable and solid phylogenetic hypothesis. At the same time, it is a potentially important tool for underpinning discussions toward a new sectional classification of the lineage.

Keywords: American *Salvia*, big plant genera, pollination syndromes, *Salvia* richness.

Online enhancements: supplemental PDF and Excel files.

Introduction

Big plant genera (those composed of more than 500 species) have been resistant to the efforts of systematists to establish robust classifications and phylogenetic frameworks that allow further research on broad patterns in the life sciences (Frodin 2004; Scotland and Wood 2012; Muñoz-Rodríguez et al. 2019). A large number of species in a genus is a major obstacle because of the great amount of time and resources that their study requires, especially if the taxon is amply distributed. The absence of modern updated checklists and monographs for most of these genera (Mabberly 2008) reflects these difficulties, so making accurate calculations of species numbers is difficult. However, as stated by Knapp et al. (2005), biodiversity lists are a synthesis of the products of scientific research, playing a role as the dynamic starting

[1] Author for correspondence; email: xanergo@hotmail.com.

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point for the efforts of the taxonomic community, and they are necessary for the generation of baseline data needed to achieve globally agreed targets such as international strategies for biological conservation. At the same time, checklists are essential tools for data cleansing when one is conducting biogeographical, ecological, and evolutionary studies; they also constitute a preliminary baseline guide that a monographer should consider.

The genus *Salvia* L. is one of these big genera, with about 1000 species (Li and Hedge 1994; Harley et al. 2004; Govaerts et al. 2019; http://www.catalogueoflife.org/col/browse/tree?60d25775f777cf667046e483e4c0c348) and a subcosmopolitan distribution (Hedge 1992). It suffers from the aforementioned problems in that it lacks both an updated checklist and a modern comprehensive monograph. Bentham (1832–1836, 1848) published the previous worldwide treatments of *Salvia* more than 150 years ago. Since Bentham's contributions, the number of recognized *Salvia* species has increased about sixfold, limiting the value of his publications today. Faced with the difficulty of dealing with such a big genus, subsequent taxonomists have concentrated their efforts on working with fragments of *Salvia* diversity that are geographically or taxonomically demarcated. *A Revision of* Salvia, *Subgenus* Calosphace (Epling 1939) has been the most significant taxonomic publication; it treats nearly half of the species in the genus, all from America. In a geographical context, the revisions of African (Hedge 1974), Argentinian (O'Leary and Moroni 2016), Bolivian (Wood 2007), Chinese (Li and Hedge 1994), Colombian (Wood and Harley 1989; Fernández-Alonso and Rivera-Díaz 2006), European (Hedge 1972), Iranian (Hedge 1982*b*), Mesoamerican (Klitgaard 2012), Peruvian (MacBride 1960), South American (Epling 1935–1937), and Turkish (Hedge 1982*a*) *Salvia* species stand out. There are also a multitude of less extensive publications, revisions, and synopses of sections as well as other studies that are more geographically restricted (e.g., Espejo-Serna and Ramamoorthy 1993; dos Santos 1996; Torke 2000; Ramamoorthy 2005; Turner 2009) and papers with descriptions of new species and taxonomic clarifications. A consequence of this specialized literature is that information provided is very dispersed, partial in its coverage, and without uniform taxonomic criteria. Additionally, most were published by only one or a few researchers, inevitably resulting in biased taxonomic circumscriptions. Alziar (1988–1993) has already highlighted the wide dispersal and heterogeneity of papers on *Salvia* and systematic treatments of the genus.

With regard to the checklists, the one compiled, updated, and maintained by the Royal Botanic Gardens, Kew (Govaerts et al. 2019), is the most accurate reference available. Nonetheless, it is not thoroughly revised; it is still classified as "not yet reviewed," and only a few taxonomists have been involved. It is worth noting that new names are automatically retrieved from the International Plant Names Index (http://www.ipni.org). Alziar's (1988–1993) list of *Salvia* synonyms is also a very useful tool, although it is currently outdated given the many new *Salvia* revisions and species that have been subsequently published.

The lack of a recent checklist and monograph for the genus has not prevented the development of different areas of research interest. Substantial advances have been made, especially in terms of the phylogenetic position of *Salvia* and its internal relationships. After the traditional *Salvia* circumscription was revealed to be paraphyletic (Walker et al. 2004; Walker and Sytsma 2007), expanded phylogenies and new molecular markers have helped to rearrange the genus into a monophyletic group with the inclusion of the genera *Dorystaechas* Boiss. & Hedlr., *Meriandra* Benth., *Perovskia* Kar., *Rosmarinus* L., and *Zhumeria* Rech.f. & Wendelbo (Drew et al. 2017). Even with limited sampling, it has also been possible to infer the evolution of some characters and their geographical distribution on phylogenetic trees (Fragoso-Martínez et al. 2018; Kriebel et al. 2019). A broad analysis of pollination syndromes within the genus (Wester and Claßen-Bockhoff 2011) has also been conducted. Nonetheless, as more phylogenetic information becomes available and more clarity regarding the evolutionary relationships among species is achieved, it is increasingly urgent to have a list of accepted taxa and their distributions that would serve as a starting point when developing a phylogenetic scheme to replace the current *Salvia* classification.

As working with the whole diversity of *Salvia* is still a very cumbersome task, the most efficient approach might be to break the genus into smaller and more manageable clades or species groups. Hence, we here present a thoroughly revised and updated checklist of *Salvia* L. subg. *Calosphace* (Benth.) Epling, hereafter referred to as *Calosphace*. The subgenus is traditionally recognized as having tridentate or entire upper calyx lips, internally exannulate corolla tubes, a substraight upper corolla lip, a patent or subdeflexed lower corolla lip, and posterior connective branches that are connate and that very rarely produce a sterile theca (Bentham 1832–1836; Bentham and Hooker 1876; Epling 1939). Nonetheless, these characters are not restricted to this subgenus; for example, fusion of the posterior connective is present in other subgenera, although in *Calosphace* it appears to be caused by the fusion of epidermal hairs in the inner faces of the posterior connective branches instead of by a postgenital fusion of epidermal papillae in the posterior thecae, as in other subgenera (Claßen-Bockhoff et al. 2004). *Calosphace* embraces about half of the species contained in the genus and almost 95% of all native American *Salvia* species; in fact, all species of *Calosphace* are restricted to the Americas, apart from a few that have been introduced to the Old World (Epling 1939; Ramamoorthy and Elliott 1993; Harley et al. 2004; Froissart 2008; Walker et al. 2015). Moreover, the species included in this group exhibit a wide array of habits, leaf morphologies, and inflorescence structures; flower morphology and coloration are particularly varied (fig. 1).

As stated, a revision of this subgenus with a series of subsequent supplementary notes in which a classification of 102 sections was proposed (Epling 1939, 1940, 1941, 1944, 1947, 1951, 1960; Epling and Mathias 1957; Epling and Játiva 1963, 1966, 1968) already exists. Most of Epling's sections have been revealed to be nonmonophyletic groups (Jenks et al. 2013; Fragoso-Martínez et al. 2018), and more than 100 species have been described since these publications; hence, the sectional classification is very outdated, and it will have to be recircumscribed. To contribute to and facilitate a rearranged classification of *Salvia* and to provide strong taxonomic support for research on the genus, we (1) present an updated checklist of *Calosphace*, (2) highlight the problematic taxa (those whose taxonomic status is unresolved and consequently will require specific analyses), and (3) summarize the distribution of the species by country and biome.

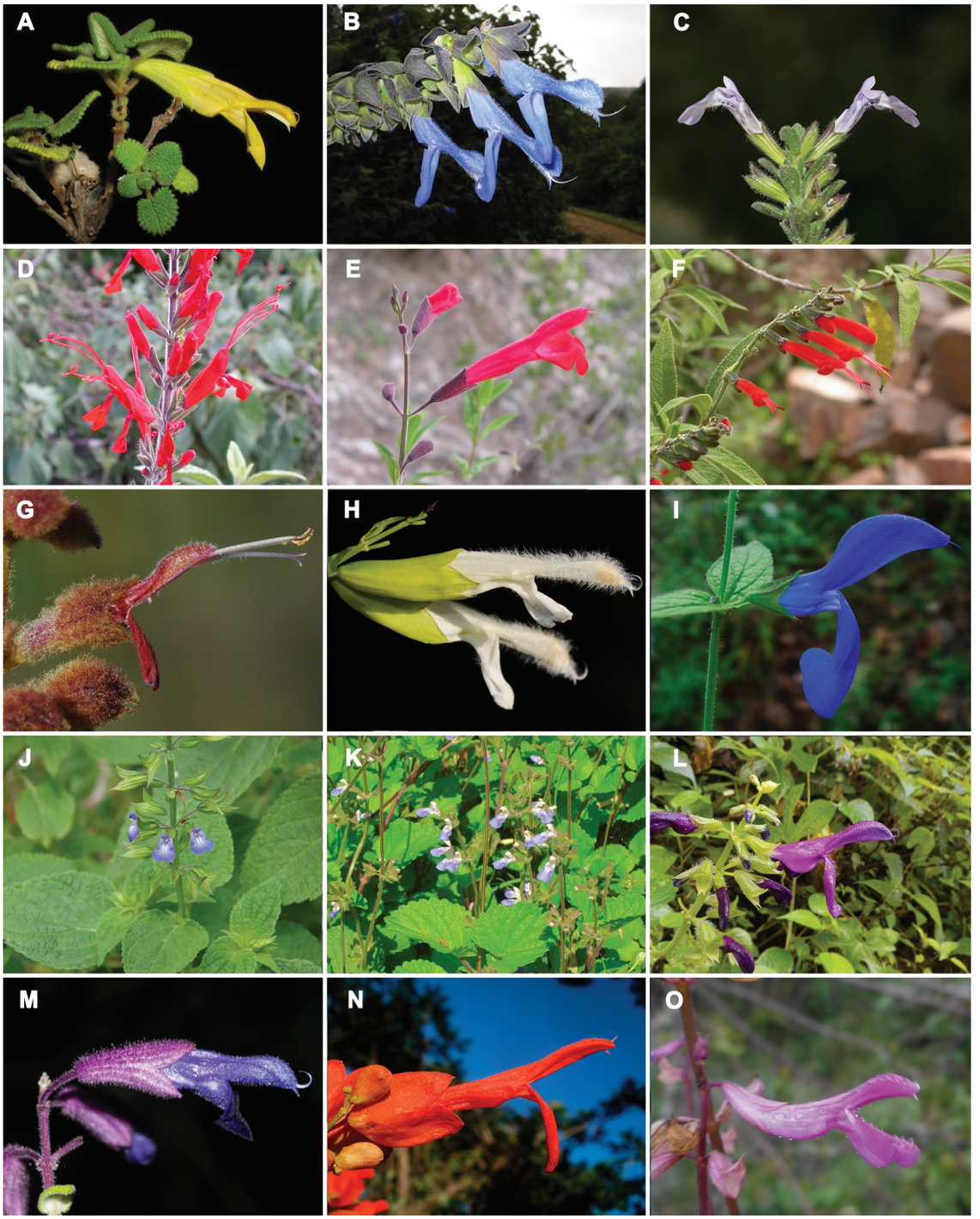

Fig. 1 Representation of the different corolla shapes and colors exhibited by the species of *Salvia* subg. *Calosphace*. *A*, *Salvia aspera*. *B*, *Salvia atrocyanea*. *C*, *Salvia axillaris*. *D*, *Salvia exserta*. *E*, *Salvia graciliramulosa*. *F*, *Salvia haenkei*. *G*, *Salvia lasiantha*. *H*, *Salvia madrigalii*. *I*, *Salvia patens*. *J*, *Salvia personata*. *K*, *Salvia procurrens*. *L*, *Salvia recurva*. *M*, *Salvia semiatrata*. *N*, *Salvia sessei*. *O*, *Salvia simulans*. *A* and *G* taken by P. Carrillo-Reyes. *B* and *D–F* were provided by Darwin Initiative project 16/11/010; *C* and *M* by H. Ávila-González; *H*, *I*, and *N* by G. Cornejo-Tenorio; *J* and *K* by R. Uría; and *L* and *O* by J. G. González-Gallegos.

Material and Methods

The process of preparing the final list consisted of three steps: (1) the compilation of a baseline checklist, (2) a first scrutiny to identify nonunanimously accepted species, and (3) a second scrutiny focused exclusively on the revision and categorization of those species identified in the previous step. The preliminary checklist of *Calosphace* species was compiled on the basis of a review of the specialized literature (supplemental materials 1, 2; supplemental materials 1–7 are available online) and online databases (dos Santos 2015; Fernández-Alonso 2018; Tropicos 2018; Govaerts et al. 2019; http://www.gbif.org; http://swbiodiversity.org/seinet/index.php). The taxonomic status of each taxon was carefully reviewed before it was added to the list. Epling's (1939) revision was taken as the starting point, so names already in synonymy in that publication (and not subsequently resurrected) were excluded. In contrast, some names accepted by Epling were placed in synonymy because of more recent evidence supporting such decisions. The list included the following columns: species name, author, taxonomic status (accepted taxa marked with 1, rejected taxa marked with 0), and accepted name (for those names in synonymy). Similarly, the distribution of each species was recorded by American country or territory and by biome on the basis of the available literature and databases. Accepted biomes follow the Olson et al. (2001) classification and map.

In the first scrutiny, the preliminary checklist and distribution data were distributed to all the authors for review. Each was asked to vote on the acceptance or rejection of each species. The votes were compiled in a single worksheet, and where results were not unanimous, the species were set apart for a more thorough examination; they were categorized as controversial species. It should be noted that when we were not confident in making a decision about a particular species, abstention was allowed.

During the second scrutiny, each author was asked to give succinct arguments to support the acceptance or rejection of the species classified as controversial. All of the observations generated were summarized and distributed to all participants, with a request to consider the different arguments, reevaluate, and decide whether each of the controversial species should be accepted, rejected, or kept as unresolved. On the basis of these statements, a final decision was made. The taxa were classified as accepted, rejected, or unresolved if any of these categories received more than 50% of the votes; otherwise, the species were treated as unresolved.

The strategy described above was carried out to unite all of the experience with and knowledge about *Calosphace* accumulated by all the authors during our research careers. Besides, there are no clear or universal criteria for species delimitation (Mayden 1999; de Queiroz 2005*a*, 2005*b*, 2007; Hey 2006; Naomi 2011); hence, the criteria applied by different taxonomists might be distinct, sometimes diverging considerably from those of their colleagues. The differences depend on the evidence that they have available and on the weight that they give to each kind of evidence, so they might favor a biological, ecological, evolutionary, genetic, phenetic, or phylogenetic species definition (de Queiroz 2005*a*, 2005*b*; Wheeler 2012). The consensus approach constrains taxonomists to a much more unified and consistent delimitation, thus diminishing subjective biases. Nonetheless, a morphological definition has prevailed.

The distributions of the species in each American country or territory (supplemental material 3) and biome (supplemental material 4) were also summarized. The similarities in *Salvia* composition among the different areas were assessed with unweighted pair group method with arithmetic mean (UPGMA) analysis based on Sørensen's dissimilarity index in R (R Core Team 2019) according to the procedures described in Borcard et al. (2018) and implementing the package stats 3.6.1 (R Core Team 2019). Multiscale bootstrap resampling with 10,000 repetitions was calculated with the package pvclust 2.2.0 (Suzuki and Shimodaira 2004, 2006). We considered only those species that are in at least two areas to avoid artifacts promoted by the heterogeneity of species richness among the different countries, territories, and biomes.

Results

The updated checklist of the species of *Calosphace* is presented in appendix A and the infraspecific taxa in appendix B. The species and infraspecific taxa are alphabetically arranged.

There are 702 legitimate species names in *Calosphace* that have been accepted at some point since Epling's (1939) revision and before this article (supplemental material 2). However, only 580 of these, including 30 names that are classified as unresolved (app. A), are accepted in this article. Hence, *Calosphace* is estimated to be composed of 550–580 species. Meanwhile, the infraspecific taxa consist of 63 taxa, including 47 subspecies and 16 varieties. In total, 613–643 taxa can be recognized within the subgenus.

The advancement in our knowledge of *Calosphace* is characterized by some periods of intense activity (contributions in terms of the description of new species) interspersed with others with little or no activity. The periods 1830–1850, 1900–1910, 1930–1940, and 2010–2019 were the most productive in terms of the addition of new species to the subgenus, with more than 40 per decade (fig. 2). The greatest increase, of about 25%, took place from 1930 to 1940. In total, 116 authors have contributed to the description of species within the subgenus *Calosphace*, but the major contributors to the naming of species were Carl Epling (participating in the description of 150 species that are still accepted), G. Bentham (77 spp.), and M. L. Fernald (50 spp.).

The sections *Angulatae* Epling (52 spp.), *Uliginosae* (Epling) Epling (33 spp.), *Flocculosae* (Epling) Epling (25 spp.), *Scorodonia* (Epling) Epling (22 spp.), and *Farinaceae* (Epling) Epling (20 spp.) are the sections with the highest numbers of species, but altogether, they constitute only about 26% of *Calosphace*. In contrast, 36 sections are monotypic, and 67 possess fewer than five species. However, the diversity of the different lineages of *Calosphace* cannot be truly evaluated until the phylogeny is resolved since most currently accepted sections are not monophyletic.

There are native species of *Calosphace* in 42 of the 55 American countries or territories. Mexico is outstanding, with 295 native species, followed by Peru (77 spp.), Colombia (60 spp.), Brazil (58 spp.), Guatemala (49 spp.), and Ecuador (41 spp.; figs. 3, 4). Among islands, Hispaniola (Haiti and the Dominican Republic), with 36 species, is home to the highest number of *Salvia* species, 31 of the 36 being endemic to the island; Haiti has 29 species, and the Dominican Republic has 21. The country endemism exhibited by the group is 77.72% (450 species are

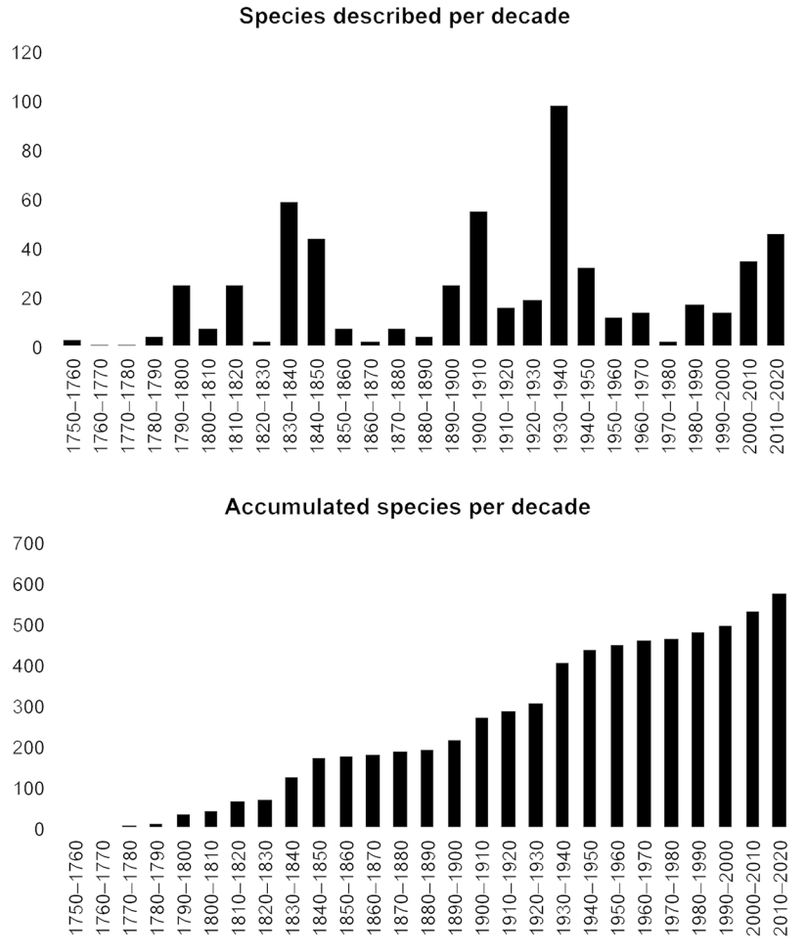

Fig. 2 Description of species of *Salvia* subg. *Calosphace* through time. Species described (*top*) and species accumulated (*bottom*) by decade. Only currently accepted species were considered.

restricted to one country). Mexico (243), Peru (49), Brazil (42), and Colombia (37) are the countries with the greatest number of endemic species (supplemental material 5). *Salvia misella* Kunth, *S. occidentalis* Sw., and *S. serotina* L. are the most widely distributed species; they are found in 28–30 countries (supplemental materials 3, 6). *Salvia coccinea* Buc'hoz ex Etl. is also recorded in 30 countries; however, it is considered to be a native species only in Mexico and the Mesoamerican region (see Klitgaard 2012 and references therein).

Three major geographical regions sharing a large number of species that are not shared with the other regions were identified according to the results of the UPGMA analysis: (1) eastern and southern South America; (2) North America, Central America, and northern South America; and (3) the Caribbean islands and Belize (fig. 5). The three groups are supported by bootstrap values higher than 80. Species similarity is highest between contiguous countries as long as they share habitats favoring *Salvia* colonization.

Of the 14 different biomes present in America, four do not host native species of *Calosphace* (supplemental material 4): (1) boreal forest/taiga; (2) Mediterranean forests, woodlands, and scrubs; (3) tundra; and (4) mangrove. In contrast, there are 241 species in the tropical and subtropical coniferous forests, 170 in the tropical and subtropical moist broad-leaved forests, 93 in the tropical and subtropical dry broad-leaved forests, and 81 in the montane grasslands and shrublands (supplemental material 4). About 74% of the species are restricted to a single biome; all the biomes present at least one species. Tropical and subtropical coniferous forests and tropical and subtropical moist broad-leaved forests have the highest number of restricted species, with 191 and 123, respectively.

In the dendrogram produced through the UPGMA analysis, three major groups are recovered; the first two have bootstrap values higher than 80 (fig. 6). The first is made up of the following biomes: tropical and subtropical forests; tropical, subtropical, and temperate grasslands; savannas and shrublands; and deserts and xeric shrublands. The second corresponds to the temperate forests. The last includes only the flooded grasslands and savannas.

Discussion

How many *Salvia* species are there? This is still a question in need of a precise answer. However, we have obtained a more

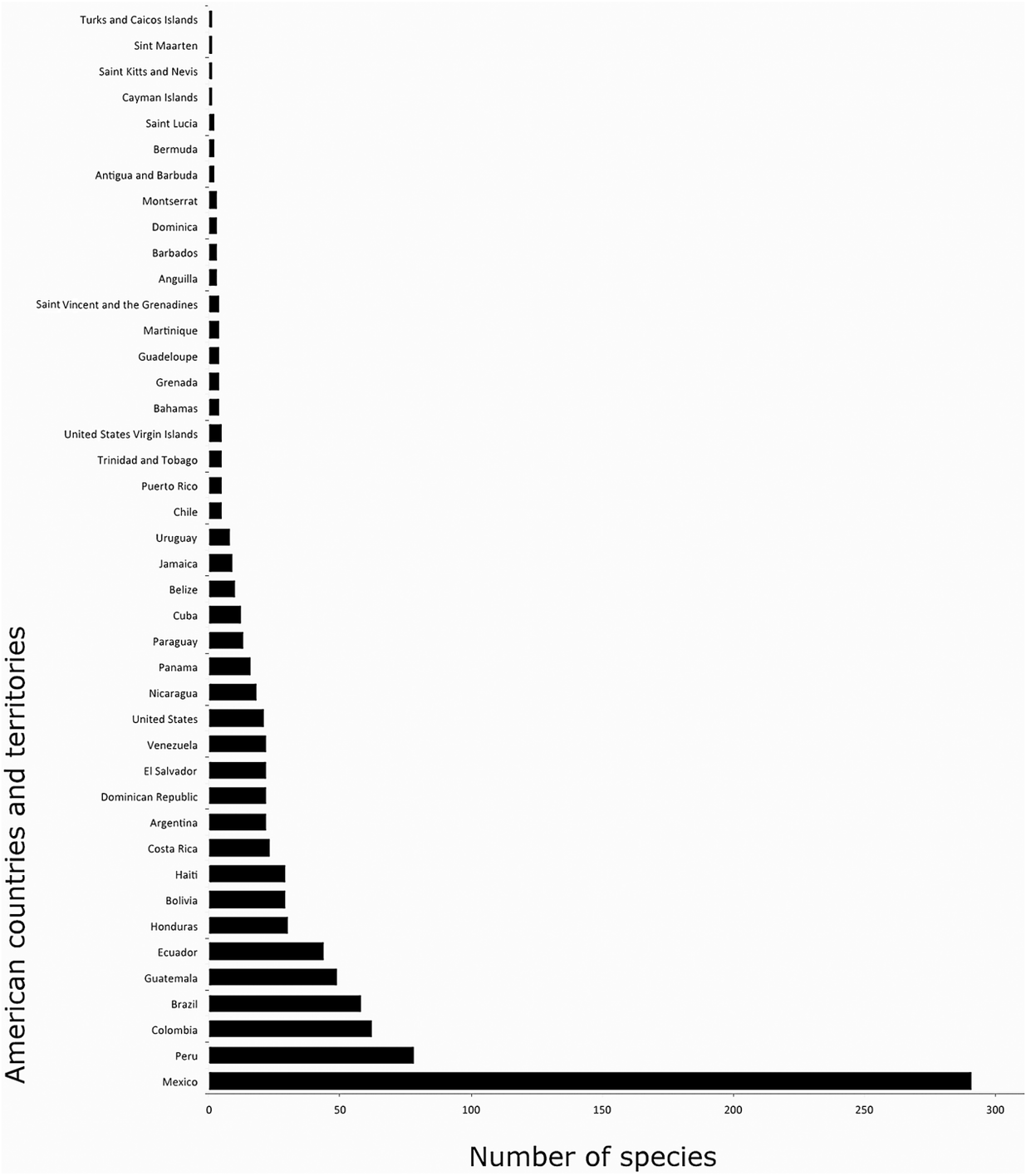

Fig. 3 Species richness of *Salvia* subg. *Calosphace* for each American country or territory.

concise number for *Calosphace*, which accounts for a little more than half of the diversity of the genus, and so we are getting closer to answering that question. Walker et al. (2004) estimated an approximate number of 510 species for *Calosphace* and 900 species for the whole genus. On the basis of that estimate and the numbers reported here, the global total should be in the range of 940–970 species. Nonetheless, parallel research efforts are needed to clarify *Salvia* diversity in the remaining subgenera, especially in Asia. As has happened with American *Salvia*, many new species and taxonomic realignments have been published for the other subgenera over recent decades (Dönmez 2001; Hamzaoğlu et al. 2005; İlçim et al. 2009; Celep and Doğan 2010; Kahraman et al. 2011; Zhu et al. 2011; Celep et al. 2015; Akhani et al. 2016; Drew et al. 2017; Hu et al. 2017), so an update of these geographically

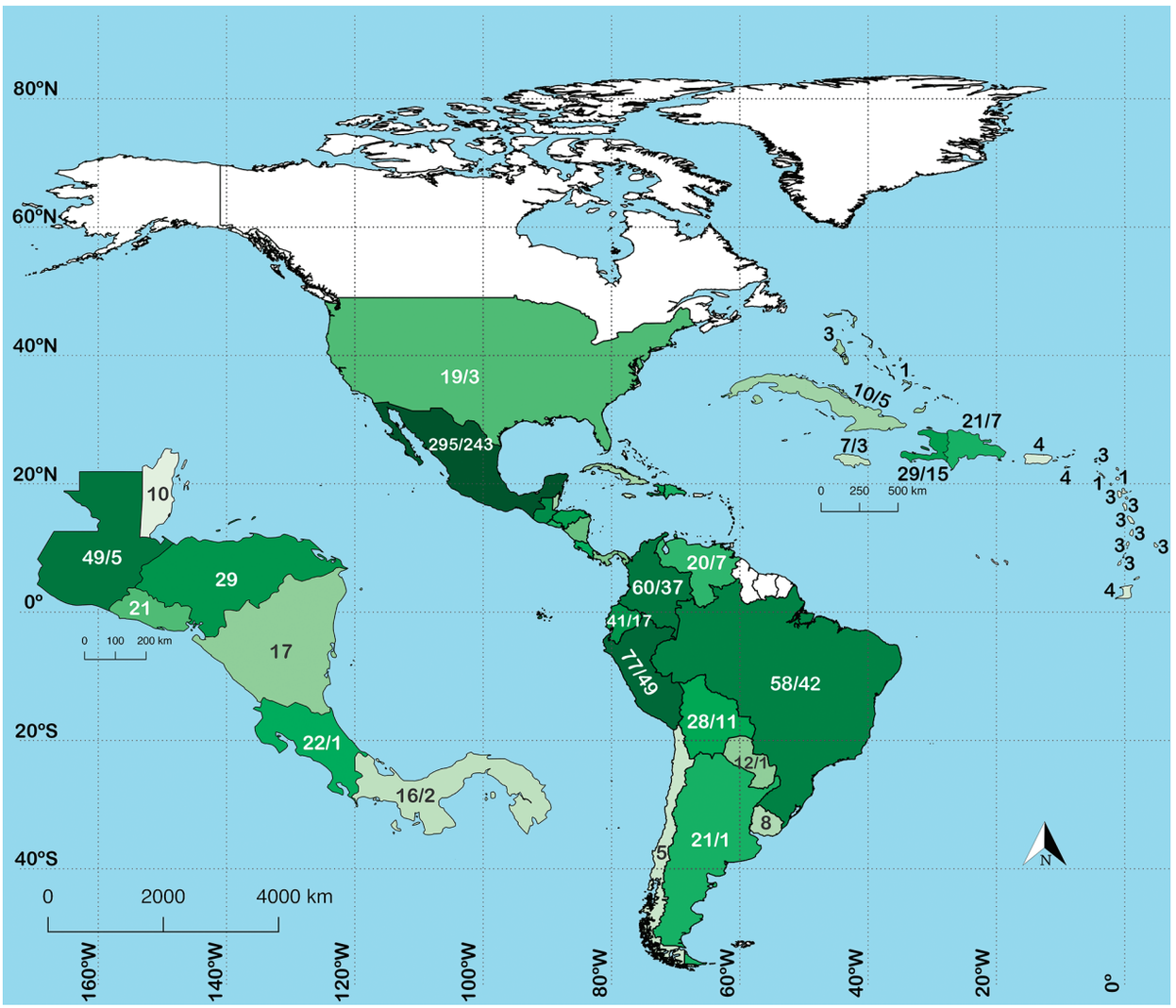

Fig. 4 Species richness of *Salvia* subg. *Calosphace* for each American country or territory. Richness is represented by a gradient green color: the more intense the color value, the higher the richness. Countries or territories in white lack any native species of *Calosphace*. The numbers per area are also given. If there are endemic species, these are indicated after a slash; values of zero are omitted. A close-up of Central American countries is given at the left and another for the Caribbean countries at the right.

circumscribed taxonomic treatments is necessary. It is worth noting that the estimated *Salvia* diversity, for either the subgenus or the entire genus, remains roughly within previously suggested ranges (Standley and Williams 1973; Ramamoorthy and Elliott 1993; Li and Hedge 1994; Frodin 2004; Harley et al. 2004; Walker et al. 2004; Jenks et al. 2013).

Our current checklist differs by 14.98% from the World Checklist of Selected Plant Families of the Royal Botanic Gardens (Govaerts et al. 2019). There are 63 species recorded in the Kew checklist that are lacking in ours and 29 in ours that are missing from the Kew checklist (supplemental material 7). This can be explained by our treatment of several species as synonyms and the additions corresponding to recently described species not yet added to Kew's checklist.

American native *Salvia* comprises 577–607 species. Of those, 550–580 belong to *Calosphace*; 19 to subg. *Audibertia* J.B. Walker, B.T. Drew & K.J. Sytsma (Walker et al. 2015); and eight, including three species formerly placed in the genus *Salviastrum* Scheele (Bentham and Hooker 1876; Correl and Johnston 1970), to the informal group "*Heterosphace*" (Walker and Elisens 2001; Kriebel et al. 2019). This great diversity in the Americas makes *Salvia* (and even *Calosphace* alone) one of the most species-rich genera on the continent, placing it just below *Epidendrum* L. (1500–2400 spp.; Hágsater et al. 2016) and *Miconia* Ruiz & Pav. (1060 spp.; Almeda 2007) and in a position similar to that of *Carex* L. (600–700 spp.; Chater 1994; Ball and Reznicek 2002; Wheeler 2002; González-Elizondo et al. 2018), *Pleurothallis* R. Br. (550–600 spp.; Chase et al. 2015), and *Astragalus* L. (ca. 500 spp.; Barneby 1964; Gómez-Sosa 2005).

The 30 species recovered as unresolved reflect the heterogeneity of the criteria used by each of us, which in turn is based on

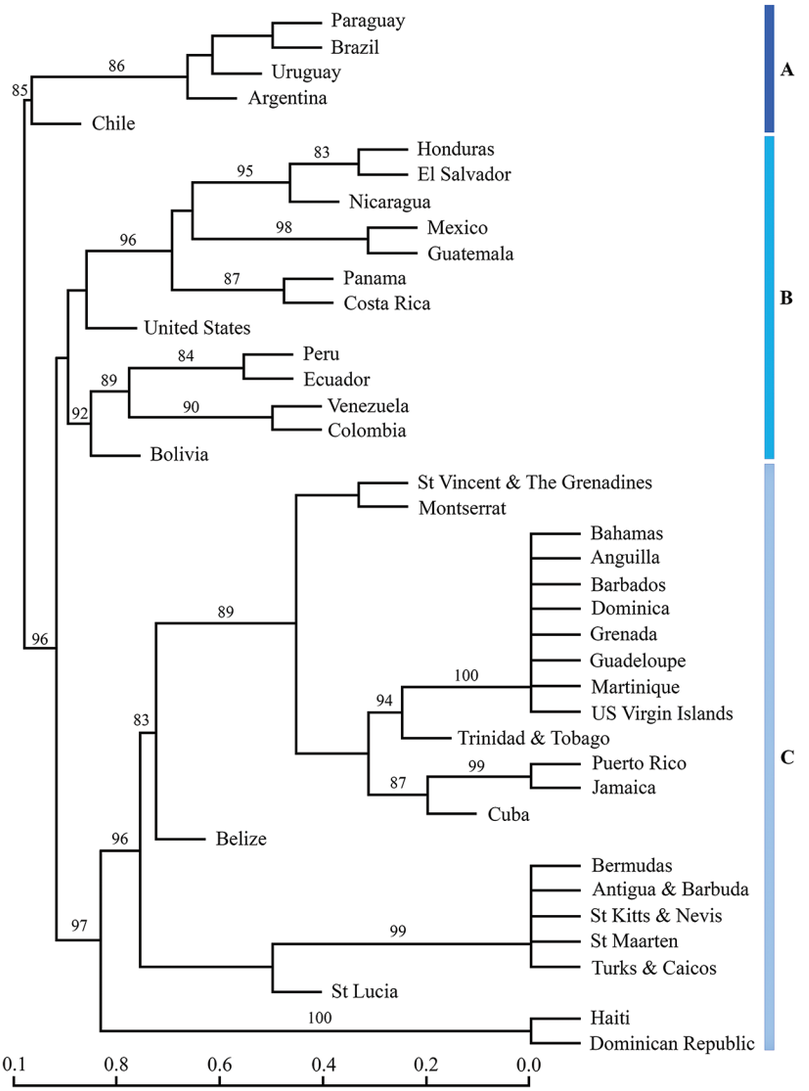

Fig. 5 Dendrogram of the American countries and territories based on an unweighted pair group method with arithmetic mean analysis based on a dissimilarity matrix of the composition of *Salvia* species with Sørensen's index. Group A, eastern and southern South America; group B, North America, Central America, and northern South America; group C, Caribbean islands and Belize. Bootstrap values higher than 80 are shown above branches. The scale bar at the bottom is a reference to similarity distances.

the evidence we have at hand, our own backgrounds and experience, and gaps in information. Nonetheless, an important explanation lies in the underlying inherent genetic or historical processes in some taxa that render species delimitation really difficult, for example, when there is strong phylogenetic incongruence derived from heterotachy, hidden paralogy, horizontal gene transference, hybridization, incomplete lineage sorting, or lack of variation in conventional markers resulting in unresolved phylogenies at shallow levels (Pamilo and Nei 1988; Templeton 2001; Machado and Hey 2002; Harris 2008; Maureira-Butler et al. 2008; Som 2014; Fragoso-Martínez et al. 2017). Specific studies analyzing these phenomena in *Calosphace* are lacking (Kriebel et al. 2019), and their role in the evolution of the group is considered only marginally; however, lineage sorting and reticulate evolution have been suggested as explanations for the heterogeneous distribution of indels in the *Uliginosae* clade of *Calosphace* (Jenks et al. 2013). Circumscribing species with a broad geographical/ecological distribution combined with continuous morphological variation is also hard. This is exemplified by controversial cases of delimiting species such as *S. mocinoi* Benth., which was circumscribed in seven different ways between 1973 and 2014, none of them widely accepted (Standley and Williams 1973; Alziar 1988–1993; Pool 2001; Fragoso-Martínez 2011; Klitgaard 2012; González-Gallegos 2014; Govaerts et al. 2019). *Salvia mocinoi* s.l. is distributed from western Mexico (21°N) to northern Nicaragua (13°N); it ranges from 30 to 2850 m in elevation and dwells in both temperate and tropical forests (González-Gallegos 2014). *Salvia carnea* Kunth, *S. languidula* Epling, *S. lavanduloides* Kunth, *S. longispicata* M.

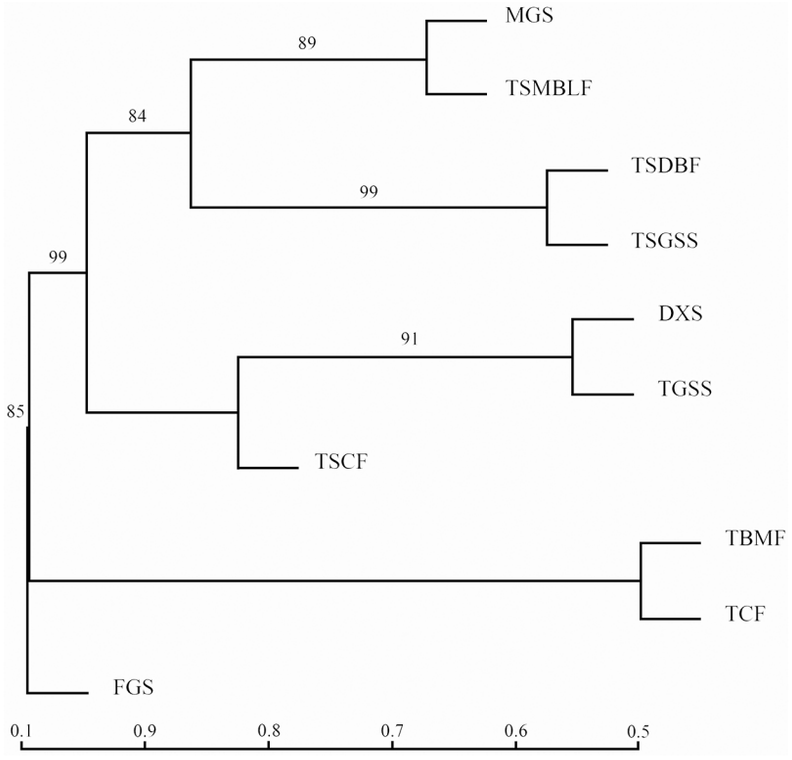

Fig. 6 Dendrogram of the biomes based on an unweighted pair group method with arithmetic mean analysis based on a dissimilarity matrix of the composition of *Salvia* species with Sørensen's index. DXS = deserts and xeric shrublands; FGS = flooded grasslands and savannas; MGS = montane grasslands and shrublands; TBMF = temperate broad-leaved and mixed forests; TCF = temperate coniferous forests; TGSS = temperate grasslands, savannas, and shrublands; TSCF = tropical and subtropical coniferous forests; TSDBF = tropical and subtropical dry broad-leaved forests; TSGSS = tropical and subtropical grasslands, savannas, and shrublands; TSMBLF = tropical and subtropical moist broad-leaved forests.

Martens & Galeotti, *S. melissodora* Lag., *S. microphylla* Kunth, *S. polystachya* Cav., *S. prunelloides* Kunth, *S. tiliifolia* Vahl, and their respective allies present similar issues.

The sections *Angulatae* and *Lavanduloideae* Epling have the most species classified as unresolved, each with six. Sect. *Angulatae* is clearly polyphyletic, with its species distributed in at least eight different clades across the core *Calosphace* (Fragoso-Martínez et al. 2018) and with only about 31% of its species phylogenetically analyzed. The unresolved species of this section can be accommodated in three groups: (1) those species fitting into a morphological gradient between *S. longispicata* and *S. roscida* Fernald (*S. fluviatilis* Fernald and *S. xalapensis* Benth.), (2) species differentiated from *S. languidula* with difficulty (*S. fusca* Epling and *S. prasiifolia* Benth.), and (3) those that are part of a morphological complex around *S. leptostachys* Benth. and *S. tiliifolia* Vahl (*S. rhyachophylla* Epling and *S. psylophylla* Epling). *Salvia* sect. *Angulatae* represents a major challenge, considering that it is the most diverse group and one of the most widely distributed, ranging from the southern United States to Argentina and the Caribbean islands. It is crucial to increase the representation of *Angulatae* species in phylogenetic analyses to clarify unresolved species.

Meanwhile, although the 14 species of sect. *Lavanduloideae* have already been phylogenetically analyzed (Fragoso-Martínez 2014; Fragoso-Martínez et al. 2018), the low support and resolution of several of the internal branches, the lack of variation due to the recent origin of the group, and the ambiguous or labile morphological delimitations of some of the species explain why several species are unresolved (Fragoso-Martínez 2014). It is hypothesized that the species in this section are undergoing an active or incipient diversification process in which several of the taxa could be receiving some level of gene transfer from *S. lavanduloides*, particularly because up to three species have been reported to coexist and bloom synchronously, and, considering that they are very similar in floral morphology, gene flow would not be prevented by physical constrictions; however, this putative hybridization needs to be tested (Fragoso-Martínez 2014). Gene exchange might be facilitated because of the similar corolla structure in species of this section; all of them conform to a melittophilous syndrome (Wester and Claßen-Bockhoff 2011). However, it is necessary to explore more informative markers, large-scale sequencing data (Fragoso-Martínez et al. 2017), and multifaceted integrative approaches, including morphometrics, niche modeling, phylogeographic analyses, and population genetics (Templeton 2001; Sites and Marshall 2003, 2004; Ruiz-Sánchez and Sosa 2010; Sistrom et al. 2013; Medrano et al. 2014; Li et al. 2019), to untangle species delimitation and either to support or to refute the hypothesis of incipient diversification.

The other outstanding case of species recognition controversy involves *S. carnea* and morphologically similar species. Wood and Harley (1989) treated seven names as synonyms and one as a variety of *S. carnea*. Fernández-Alonso (2003) erected one of the varieties of *S. carnea* to the specific level as *S. sciaphila* (J.R.I. Wood & Harley) Fern. Alonso. He suggested that it can be distinguished from *S. carnea* by its larger pendulous corollas and its lower lip, which is barely patent, corresponding to an ornithophilous pollination syndrome instead of to the melittophilous pattern observed in *S. carnea*. Klitgaard (2012) provisionally resurrected *S. gracilis* Benth. and *S. iodochroa* Briq., transferred some of the synonyms of *S. carnea* recognized by Wood and Harley (1989) to synonymy with *S. gracilis*, and synonymized *S. carnea* var. *punicans* (Epling) J.R.I. Wood & R. Harley with *S. carnea*. González-Gallegos and Gama-Villanueva (2013) resurrected *S. punicans* Epling and synonymized *S. gracilis* and *S. myriantha* Epling with *S. carnea*; *S. punicans* is supported at the specific level by several floral characters that fit an ornithophilous pollination pattern instead of a melittophilous one.

The constant changes in the taxonomic interpretation of the *S. carnea* group clearly indicate its great complexity and the difficulty of unambiguous differentiation of the species. Epling (1939) invoked differences mainly in the corolla tube length, while vegetative characters, in contrast, were very conserved among species. However, corolla length is quite variable in most of the taxa involved. Although the species in *Salvia* sect. *Carnea* can in general be grouped into three categories according to corolla size (short, intermediate, and long), this probably does not preclude genetic flow between them because the species in each group sometimes present flowers similar to those of the other species in size. Hence, it is possible that because of the occasional overlap in corolla length, there is also an overlap in pollinators, which in turn would maintain a level of gene transfer between the different taxa, slowing down any incipient process of diversification because of the homogenizing effects of genetic flow. In fact, there are no incompatibility mechanisms identified in *Salvia*. However, in some regions, for example, the Cordillera Oriental in Colombia, there are sympatric populations of several of the taxa involved in which potential hybridization has apparently not been detected (Fernández-Alonso 2003; J. L. Fernández-Alonso, personal observation). In addition, the ecological and geographical disjunction between morphologically analogous species, for example, *S. punicans* (Mexico) and *S. sciaphila* (Colombia), would suggest that these arose from different diversification processes. *Salvia* sect. *Carnea* could be an example of a syngameon (the more inclusive system of interbreeding populations in a hybrid swarm, i.e., a group of species or semispecies hybridizing; Lotsy 1925; Grant 1971), a hypothesis that should be evaluated with genetic analyses, and this would ultimately enable resolution of this group. A detailed study of the pollination and habitats of a wider representation of the populations of this complex over its complete geographical range is needed, but this implies a considerable amount of fieldwork.

Other controversial species that might be subject to an incipient speciation process, similar to that hypothesized for *S. carnea* and *S. lavanduloides*, are *S. assurgens* Kunth, *S. melissodora*, *S. microphylla*, *S. polystachya*, and *S. prunelloides*. The last three have a wide distribution in Mexico, ranging from the northwest (Chihuahua) and northeast (Tamaulipas) to the south (Chiapas or Oaxaca). *Salvia microphylla* is even present in the southern United States (Martínez-Gordillo et al. 2017), and it shows ample morphological variation. *Salvia assurgens* (including *S. prunifolia* Fernald) is known from two regions, the southern Sierra Madre Occidental (Durango, Jalisco, Nayarit, Sinaloa, and Zacatecas) and the western Trans-Mexican Volcanic Belt (Estado de México, Guanajuato, and Michoacán; González-Gallegos et al. 2016; Martínez-Gordillo et al. 2017). Although there is a subtle distinction in leaf and calyx shape between *S. assurgens* and *S. prunifolia*, the only strong and clear difference between them is the corolla color, white in the first and blue to sky blue with a white tube and nectar guides in the second. Additionally, *S. assurgens* belongs to the second geographical area mentioned above and *S. prunifolia* to the first. Corolla color alone is a very weak character, so it is unclear whether *S. prunifolia* should be treated as a variety of *S. assurgens*. Attempts have been made to distinguish *S. ramosa* Brandegee and *S. variana* Epling (even including *S. dugesii*) from *S. melissodora* on the basis of smaller leaves (Epling 1939) and different kinds of hair on the calyx (glandular-capitate and simple hairs in *S. melissodora* and dendritic [branched] hairs in the others; Olvera-Mendoza et al. 2017); however, such characters are variable in *S. melissodora*, which can present leaves as small as those characterizing the former species, and the indumentum variation in *S. melissodora* also overlaps with that of the other two species (González-Gallegos et al. 2016). *Salvia microphylla* and *S. prunelloides* are differentiated from *S. modica* Epling and *S. glechomifolia* Kunth, respectively, by leaf shape and the indumentum; nevertheless, these characters are not stable. Rather, they seem to vary under the influence of ecological conditions (González-Gallegos et al. 2016; J. G. González-Gallegos, personal observation). Clarifying the taxonomic situation of the taxa involved here would require detailed studies with thorough examination of morphological and genetic variation at the population level.

Moreover, it would be possible to clarify the taxonomic status of the other species treated as controversial if more specimens were available to better define their morphological variation and circumscription. This is the case for *S. darcyi* J. Compton, *S. erythrostephana* Epling, *S. festiva* Epling, *S. glandulifera* Cav., and *S. inornata* Epling, all of which are known only from the type specimens and a few additional collections. Hence, it is essential to encourage botanical exploration to secure additional herbarium collections of these species.

It is important to emphasize that species are not static entities but are subject to a multitude of ecological pressures, genetic phenomena, and historical processes, which means that not all the *Salvia* treated here are at the same evolutionary stage (Chambers 2012). Therefore, the exercise of identifying the unresolved species helps to make evident such differences and to define research priorities, contributing, at the same time, to the congruence between the classification of one taxon and its evolutionary history.

The periods with the greatest increases in our knowledge of the diversity of *Calosphace* are explained by the projects active at the time. Thus, 1830–1850 corresponds to the most active and productive period of G. Bentham, with the publication of *Labiatarum Genera et Species* and his contribution of the chapter "Labiatae" to De Candolle's *Prodromus* (Bentham 1832–1836, 1848). Then, 1900–1910 encompasses the contributions made by M. L. Fernald with "A Synopsis of the Mexican and Central American Species of *Salvia*" (Fernald 1900*a*, 1900*b*, 1904, 1907, 1910). The greatest increase comes from Epling's revision

of *Salvia* subg. *Calosphace* (Epling 1939). And finally, the current decade again exhibits a modest increase with the description of more than 40 new species as a result of collaborative efforts by several researchers as well as ongoing local flora projects. As shown in figure 2, the increase in the description of species of the subgenus has not yet stabilized. The rate of the addition of new species has ranged from 6.6%–8% in the previous two decades, so it is probable that some new species will eventually be added to the checklist of *Calosphace*.

The relatively high species richness of *Calosphace* in the floras of Brazil, Colombia, Ecuador, Mexico, and Peru (figs. 3, 4) is not surprising, as they have consistently been identified among the countries with the highest diversity of seed plants worldwide and with many endemic plants (Groombridge 1992; Brako and Zarucchi 1993; Govaerts 2003; Morawetz and Raedig 2007; Rangel-Churio 2015; Villaseñor 2016). Most of the territory of these countries lies within the Neotropics, which is the biogeographical region with more species of seed plants than any other (Gentry 1982; Antonelli and Sanmartín 2011). Several factors that are closely related to the global latitudinal pattern of species richness have been adduced to explain the greater richness of the Neotropics; these include a tropical conservatism hypothesis, the long continuous time available for diversification, higher productivity, higher spatial heterogeneity, larger area, and less hostile seasonality effects (McArthur 1975; Currie and Paquin 1987; Currie 1991; Gould and Walker 1997; Rosenzweig 2003; Stephens and Wiens 2003; Wiens and Donoghue 2004; Begon et al. 2006; Mittelbach et al. 2007; Antonelli and Sanmartín 2011; Hawkins et al. 2011). However, none of these factors alone can provide a satisfactory and convincing explanation, as the unique histories and geographical positions of each region, as well as biological interactions, play a major role in biota assemblages (Latham and Ricklefs 1993; Mittelbach et al. 2007). Interdisciplinary collaboration, improved sampling, and dated phylogenies are much needed for the proposal and corroboration of more integrative hypotheses (Antonelli and Sanmartín 2011). With regard to biological interactions, for example, the diversification of *Salvia* in Mexico and then in Central and South America can also be understood as a history of adaptation to pollinators and new habitats (Kriebel et al. 2019). For South American countries and Mexico, orogenic history probably has extensively contributed to the diversification of *Salvia*, particularly with the formation of the Andean Cordillera and the Mexican mountain ranges (Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, Trans-Mexican Volcanic Belt, and the higher lands of Chiapas). The uplift of these mountain systems undoubtedly increased spatial heterogeneity and favored dispersal of some lineages along a north-south corridor while isolating others, resulting in a series of linked events that led to speciation processes (Hoorn et al. 2010; Antonelli and Sanmartín 2011; Mastretta-Yanes et al. 2015). Particularly, the uplift of the Andean Cordillera has already been hypothesized as an explanation for the diversification of South American representatives of *Calosphace* by acting as a species pump and biotic corridor as well as a territory with increasing habitat heterogeneity (Fragoso-Martínez et al. 2018). The role of spatial heterogeneity in terms of orography and habitats, combined with hybridization events (Fernández-Alonso 2002, 2008), has also been postulated as the potential trigger for an adaptive radiation of the species of the sections *Angulatae*, *Purpurea* (Epling) Epling, and *Rubescentes* (Epling) Epling from the Colombian Andes (Fernández-Alonso 2003; Fernández-Alonso and Rivera 2006).

The diversity of Mexican *Salvia* far exceeds that of other countries. Thus, it is necessary to understand the peculiarities of Mexican orography that promote such diversity. Perhaps the main factor is that the territory of Mexico comprises several mountain ranges that form the largest part of the area in which the Nearctic and Neotropic biogeographic realms collide, forming a transitional zone where species of both realms can thrive together (Morrone 2005, 2010, 2014). Considering that Mexican *Salvia* species appear to display greater diversity in montane areas (Ramamoorthy and Elliott 1993) and that biotic transitional zones are subject to intense biological interactions (Ruggiero and Ezcurra 2003), this could have accelerated *Salvia* speciation. Another prime event is the Great American Biotic Interchange, during which the Mexican flora was enriched with the addition of immigrant plants from both the north (temperate elements) and the south (tropical elements); given that the immigration took place gradually in a gradient toward the newly colonized areas, Mexico benefited more than other countries, as it is in a geographically intermediate position with respect to the Panama land bridge and has extensive mountain areas that provided suitable habitats for temperate plants (Gentry 1982; Burnham and Graham 1999; Graham 1999). Additionally, the historical role of Mexico as a refuge for Holarctic flora during the Pleistocene glaciations (Rzedowski 1965, 1978) could have provided temporal stability for *Salvia* diversification. Hence, the amalgam and interaction of the factors and historical context already mentioned would have made Mexican territory an evolutionary laboratory where many lineages evolved, producing a diverse endemic flora (Rzedowski 1993; Villaseñor 2016) together with a significant portion of Nearctic and Neotropical elements. In fact, Mexico is supported as the center of origin and principal center of diversification of *Calosphace* (Jenks et al. 2013; Fragoso-Martínez et al. 2018; Kriebel et al. 2019), which would have provided greater opportunities for multiple speciation events than elsewhere in Central and South America.

Among the Caribbean islands, the Greater Antilles (Cuba, the Dominican Republic, Haiti, Jamaica, and Puerto Rico) harbor a high number of species (figs. 3, 4). Altogether, they have 50 species; 41 of these are endemic to the region (i.e., about 80%). This might be partially explained by the fact that these islands are much larger than the other islands; at the same time, they possess a more heterogeneous topographic relief. Particularly, Hispaniola stands out for its richness and unique *Salvia* composition (36 spp., 86% endemic); this could have been favored by a complex history with more than one introduction of both Mexican and Andean ancestors, as suggested by Zona et al. (2016). Additionally, a biogeographic node, which can be understood as a complex biotic and tectonic convergence, an evolutionarily very active area (Heads 2004), has been identified in Hispaniola (Echeverry and Morrone 2013).

The groups of countries recovered by the UPGMA analysis are mostly congruent with geographic distance, so neighboring countries are similar in the compositions of their flora (fig. 5). Only Bolivia and the United States slightly deviate from this general pattern. It might be expected that the United States would be closer to Mexico than a group composed of Mesoamerican countries is; however, this was not recovered because the United

States has a markedly lower *Salvia* diversity than the other countries. Hence, the number of species that it shares with Mexico is much lower than the number of species that Mexico shares with the other Mesoamerican countries (supplemental material 6). A similar situation explains why Bolivia is not similar to Peru, as only 11 of its 28 species of *Salvia* are also found in Peru (supplemental material 6). In addition to geographical proximity, the predominance of mountainous terrain and shared continuous patches of habitats or ecoregions also has a major role in the similarity of *Salvia* composition among countries. This helps to explain why Brazil is grouped with Paraguay and Uruguay instead of with Colombia or Peru; the country lacks mountain ranges, it is dominated by lowlands, and it mainly shares tropical rain forests—a habitat where *Salvia* is poorly represented—with Colombia and Peru. Although biological information about species composition by country is limited, a close correspondence with the bioregionalization of the Neotropical region postulated by Morrone (2014) can be demonstrated: group C (Caribbean islands and Belize) corresponds to the Antillean subregion, group B (specifically, Central America and northern South America) mirrors part of both American transition zones and two domains (Mesoamerican and Pacific) of the Brazilian subregion, and group A (eastern and southern South America) corresponds to the Chaco subregion. Hence, the groups retrieved can be useful as a baseline for the organization of species by geographical criteria, for example, when preparing an identification key for the whole subgenus or in the planning of conservation strategies. At the same time, it represents a first look into the geographical structure of species in the subgenus, which in turn can be substantially improved with more intensive biogeographical analyses.

The three biomes with the highest number of *Salvia* species geographically coincide with the countries with the highest richness. The tropical and subtropical coniferous forest biome has the most species; more than half of the biome is found in Mexico, with the rest in the north of Central America. The tropical and subtropical moist broad-leaved forest biome also includes parts of Mexico and Central America but primarily covers northern South America, including large portions of the species-rich countries Colombia, Ecuador, and Peru. Finally, the montane grassland and shrubland biome corresponds to the higher land in the Andes Cordillera, where a large proportion of the endemic *Salvia* species from Bolivia, Ecuador, and Peru are concentrated. Moreover, similar to the patterns exhibited by the countries, the biomes are more similar to those geographically closer (fig. 6) in terms of the composition of their *Salvia* species.

The present contribution constitutes a valuable tool for improving and guiding sampling representation in phylogenetic studies of *Calosphace* as well as for identifying subgroups whose evolutionary history is crucial in understanding the complete evolution of the subgenus. It is an indispensable nomenclatural tool for use in restructuring the sectional classification of this *Salvia* lineage on the basis of phylogenetic research, and in the context of natural resource management, the checklist is also useful for horticulturalists working on this genus of considerable horticultural importance and for conservation studies.

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Appendix A

Salvia subg. *Calosphace* (Benth.) Epling checklist. Unresolved species are marked with an asterisk at the beginning of the name. Sections mostly according to Epling's (1939) classification are given between parentheses. The distribution of each species by American country or territory can be consulted in supplemental material 3.

1. *Salvia acerifolia* B.L. Turner, Phytologia 90: 138. 2008. (*Sphacelioides*).
2. *Salvia acuminata* Ruiz & Pav., Fl. Peruv. 1: 24. 1798. (*Longiflorae*).
3. *Salvia adenophora* Fernald, Proc. Amer. Acad. Arts 35: 538. 1900. (*Holwaya*).
4. *Salvia aequidistans* Fernald, Proc. Amer. Acad. Arts 35: 512. 1900. (*Scorodonia*).
5. **Salvia agnes* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 41. 1938. (*Lavanduloideae*).
6. *Salvia alamosana* Rose, Contr. U.S. Natl. Herb. 1: 110. 1891. (*Sigmoideae*).
7. *Salvia alata* Epling, Brittonia 12: 147. 1960. (*Macrostachyae*).
8. *Salvia alba* J.R.I. Wood, Kew Bull. 62: 210. 2007. (*Angulatae*).
9. *Salvia albicalyx* J.G. González, Phytotaxa 77: 10. 2013. (not assigned).
10. *Salvia albiflora* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 76. 1844. (*Angulatae*).
11. *Salvia albiterrarum* J.G. González & Art. Castro, Phytotaxa 93: 54. 2013. (*Sigmoideae*).
12. *Salvia albocaerulea* Linden, Belgique Hort. 7: 199. 1857. (*Fernaldia*).
13. *Salvia alborosea* Epling & Játiva, Brittonia 18: 260. 1966. (*Lopeziana*).
14. *Salvia aliciae* E.P. Santos, Bradea 6(30): 259. 1993. (*Rudes*).
15. *Salvia altissima* Pohl, Pl. Bras. Icon. Descr. 2: 140. 1833. (*Hoehneana*).
16. *Salvia alvajaca* Oerst., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1853: 38. 1854. (*Angulatae*).
17. *Salvia amarissima* Ortega, Nov. Pl. Descr. Dec.: 4. 1797. (*Scorodonia*).

18. *Salvia amethystina* Sm., Pl. Icon. Ined. 2: 27. 1790. (*Rubescentes*).
19. *Salvia amissa* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 187. 1938. (*Farinaceae*).
20. *Salvia ampelophylla* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 76. 1935. (*Rubescentes*).
21. *Salvia amplifrons* Briq., Bull. Herb. Boissier 4: 863. 1896. (*Angulatae*).
22. *Salvia anastomosans* Ramamoorthy, J. Arnold Arbor. 65: 135. 1984. (*Tomentellae*).
23. *Salvia anguicoma* Epling, Bull. Torrey Bot. Club 74: 517. 1947. (*Purpureae*).
24. *Salvia angulata* Benth., Labiat. Gen. Spec.: 721. 1835. (*Angulatae*).
25. *Salvia angustiarum* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 315. 1939. (*Brandegeia*).
26. *Salvia aratocensis* (J.R.I. Wood & Harley) Fern. Alonso, Caldasia 25: 240. 2005. (*Angulatae*).
27. *Salvia arborescens* Urb. & Ekman, Ark. Bot. 20A(15): 91. 1926. (*Wrightiana*).
28. *Salvia arduinervis* Urb. & Ekman, Ark. Bot. 20A(15): 89. 1926. (*Ekmania*).
29. *Salvia arenaria* A. St.-Hil. ex Benth., Labiat. Gen. Spec.: 257. 1833. (*Angulatae*).
30. *Salvia areolata* Epling, Bull. Torrey Bot. Club 71: 493. 1944. (*Purpureae*).
31. *Salvia arizonica* A. Gray, Syn. Fl. N. Amer. 2(1): 370. 1878. (*Uliginosae*).
32. *Salvia arthrocoma* Fernald, Proc. Amer. Acad. Arts 43: 63. 1907. (*Angulatae*).
33. *Salvia articulata* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 49. 1935. (*Nobiles*).
34. *Salvia aspera* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 71. 1844. (*Conzattiana*).
35. *Salvia assurgens* Kunth, Nov. Gen. Sp. 2: 293. 1818. (*Uliginosae*).
36. *Salvia atrocalyx* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 65. 1935. (*Macrostachyae*).
37. *Salvia atrocyanea* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 44. 1935. (*Coeruleae*).
38. *Salvia atropaenulata* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 270. 1939. (*Briquetia*).
39. *Salvia austromelissodora* Epling & Játiva, Brittonia 18: 260. 1966. (*Scorodonia*).
40. *Salvia axillaris* Moc. & Sessé ex Benth., Labiat. Gen. Spec.: 270. 1833. (*Axillares*).
41. *Salvia axilliflora* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 33. 1935. (*Fendlera*).
42. *Salvia ayavacensis* Kunth, Nov. Gen. Sp. 2: 298. 1818. (*Cylindriflorae*).
43. *Salvia azurea* Michx. ex Vahl, Enum. Pl. Obs. 1: 253. 1804. (*Farinaceae*).
44. *Salvia bahorucona* Urb. & Ekman, Ark. Bot. 22A(10): 47. 1929. (*Ekmania*).
45. *Salvia balaustina* Pohl, Pl. Bras. Icon. Descr. 2: 133. 1833. (*Nobiles*).
46. *Salvia ballotiflora* Benth., Labiat. Gen. Spec.: 270. 1833. (*Tomentellae*).
47. *Salvia benthamiana* Gardner ex Fielding, Sert. Pl.: t. 19. 1843. (*Nobiles*).
48. *Salvia biserrata* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 66. 1844. (*Dusenostachys*).
49. *Salvia blepharophylla* Brandegee ex Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 314. 1939. (*Brandegeia*).
50. *Salvia boegei* Ramamoorthy, J. Arnold Arbor. 65: 137. 1984. (*Scorodonia*).
51. *Salvia bogotensis* Benth., Prodr. 12: 312. 1848. (*Angulatae*).
52. *Salvia borjensis* E.P. Santos, Biogeographica 71: 22. 1995. (*Rudes*).
53. *Salvia brachyloba* Urb., Symb. Antill. 7: 362. 1912. (*Gardoquiflorae*).
54. *Salvia brachyodonta* Briq., Annuaire Conserv. Jard. Bot. Genève 2: 149. 1898. (*Polystachyae*).
55. *Salvia brachyphylla* Urb., Symb. Antill. 3: 368. 1903. (*Urbania*).
56. *Salvia breviflora* Moc. & Sessé ex Benth., Labiat. Gen. Spec. 274. 1833. (*Scorodonia*).
57. *Salvia brevipes* Benth., Prodr. 12: 321. 1848. (*Rudes*).
58. *Salvia buchananii* Hedge, Bot. Mag. 174: t. 430. 1963. (*Brandegeia*).
59. *Salvia buchii* Urb., Symb. Antill. 3: 369. 1903. (*Gardoquiflorae*).
60. *Salvia bullulata* Benth., Prodr. 12: 327. 1848. (*Corrugatae*).
61. *Salvia bupleuroides* C. Presl. ex Benth., Labiat. Gen. Spec. 271. 1833. (*Membranaceae*).
62. *Salvia caaguazuensis* Briq., Bull. Herb. Boissier sér. 2 7: 608. 1907. (*Rudes*).
63. *Salvia cabonii* Urb., Symb. Antill. 7: 361. 1912. (*Tenuistachya*).
64. *Salvia cacaliifolia* Benth., Prodr. 12: 348. 1848. (*Standleyana*).
65. *Salvia cacomensis* J.G. González, J.G. Morales & J.L. Rodr., Revista Mex. Biodivers. 83: 342. 2012. (*Tubiflorae*).
66. *Salvia caeruleobracteata* Mart. Gord., D. Sandoval & García-Mend., J. Pl. Sci. 5: 146. 2017. (*Scorodonia*).
67. *Salvia calaminthifolia* Vahl, Enum. Pl. Obs. 1: 233. 1804. (*Urbania*).
68. *Salvia calcicola* Harley, Kew Bull. 29: 138. 1974. (*Malacophyllae*).
69. *Salvia calderoniae* Bedolla & Zamudio, Phytotaxa 217: 39. 2015. (*Angulatae*).
70. *Salvia calolophos* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 57. 1935. (*Tomentellae*).
71. *Salvia camarifolia* Benth., Prodr. 12: 342. 1848. (*Tubiflorae*).
72. *Salvia camporum* Epling, Bull. Torrey Bot. Club 61: 489. 1944. (*Macrostachyae*).
73. *Salvia candicans* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 61. 1844. (*Tomentellae*).
74. *Salvia carbonoi* Fern. Alonso, Caldasia 25: 245. 2003. (*Angulatae*).
75. *Salvia cardenasii* J.R.I. Wood, Kew Bull. 62: 206. 2007. (*Malacophyllae*).
76. *Salvia cardiophylla* Benth., Labiat. Gen. Spec.: 721. 1835. (*Rudes*).
77. *Salvia carnea* Kunth, Nov. Gen. Sp. 2: 300. 1818. (*Carneae*).

78. *Salvia carranzae* Zamudio & Bedolla, Phytotaxa 217: 36. 2015. (*Fulgentes*).
79. *Salvia carreyesii* J.G. González, Revista Mex. Biodivers. 84: 8. 2013. (*Briquetia*).
80. *Salvia carrilloi* Véliz & Quedensley, J. Bot. Res. Inst. Texas 5: 471. 2011. (*Tubiflorae*).
81. *Salvia caudata* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 243. 1939. (*Angulatae*).
82. *Salvia caymanensis* Millsp. & Uline, Publ. Field Columb. Mus. Bot. Ser. 2: 94. 1900. (*Micranthae*).
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538. *Salvia trifilis* Epling, Bull. Torrey Bot. Club 68: 560. 1941. (*Flocculosae*).
539. *Salvia tubifera* Cav., Icon. 1: 16. 1791. (*Curtiflorae*).
540. *Salvia tubiflora* Sm., Pl. Icon. Ined. 1: 26. 1789. (*Biflorae*).
541. *Salvia tubulosa* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 41. 1935. (*Longiflorae*).
542. *Salvia tuerckheimii* Urb., Symb. Antill. 7: 364. 1912. (*Ekmania*).
543. *Salvia turneri* Ramamoorthy ex B.L. Turner, Phytologia 81: 330. 1997. (*Caducae*).
544. *Salvia tuxtlensis* Ramamoorthy, Pl. Syst. Evol. 146: 142. 1984. (not assigned).
545. *Salvia uliginosa* Benth., Labiat. Gen. Spec.: 251. 1833. (*Uliginosae*).
546. *Salvia umbraticola* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 265. 1939. (*Maxonia*).
547. *Salvia umbratilis* Fernald, Proc. Amer. Acad. Arts 45: 421. 1910. (*Briquetia*).
548. *Salvia uncinata* Urb., Symb. Antill. 7: 364. 1912. (*Ekmania*).
549. *Salvia unguella* Epling, Bull. Torrey Bot. Club 67: 533. 1940. (*Secundae*).
550. *Salvia unicostata* Fernald, Proc. Amer. Acad. Arts 35: 501. 1900. (*Uliginosae*).
551. *Salvia univerticillata* Ramamoorthy ex Klitg., Novon 17: 208. 2007. (*Holwaya*).
552. *Salvia uribei* J.R.I. Wood & Harley, Kew Bull. 44: 261. 1989. (*Angulatae*).
553. *Salvia urica* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 175. 1939. (*Scorodonia*).
554. *Salvia urolepis* Fernald, Proc. Amer. Acad. Arts 45: 417. 1910. (*Angulatae*).
555. *Salvia urticifolia* L., Sp. Pl.: 24. 1753. (*Uliginosae*).
556. *Salvia uruapana* Fernald, Proc. Amer. Acad. Arts 45: 418. 1910. (*Angulatae*).
557. *Salvia vargas-llosae* Sagást. & E. Rodr., Revista Peru. Biol. 19: 139. 2012. (*Cylindriflorae*).

558. *Salvia vargasii* Epling, Bull. Torrey Bot. Club 74: 514. 1947. (*Tomentellae*).
559. **Salvia variana* Epling, Repert. Spec. Nov. Regni Veg. Beih. 110: 170. 1939. (*Scorodonia*).
560. *Salvia vazquezii* Iltis & Ramamoorthy, Brittonia 64: 345. 2012. (*Holwaya*).
561. *Salvia venturana* B.L. Turner, Phytoneuron 2013-36: 7. 2013. (*Flocculosae*).
562. *Salvia venulosa* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 35. 1935. (*Tubiflorae*).
563. *Salvia verecunda* Epling ex M.E. Jones, Contr. W. Bot. 18: 53. 1933. (*Membranaceae*).
564. *Salvia veronicifolia* A. Gray, Proc. Amer. Acad. Arts 22: 444. 1887. (*Uliginosae*).
565. *Salvia vestita* Benth., Prodr. 12: 346. 1848. (*Longiflorae*).
566. *Salvia villosa* Fernald, Proc. Amer. Acad. Arts 35: 518. 1900. (*Uliginosae*).
567. *Salvia viscida* A. St.-Hil. ex Benth., Labiat. Gen. Spec.: 268. 1833. (*Rudes*).
568. *Salvia vitifolia* Benth., Labiat. Gen. Spec.: 724. 1835. (*Blakea*).
569. *Salvia wagneriana* Pol., Linnaea 41: 591. 1878. (*Holwaya*).
570. *Salvia weberbaueri* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 42. 1935. (*Longiflorae*).
571. *Salvia whitefoordiae* Klitg., Novon 17: 209. 2007. (*Holwaya*).
572. *Salvia wixarika* J.G. González, Phytotaxa 260: 178. 2016. (not assigned).
573. **Salvia xalapensis* Benth., Prodr. 12: 308. 1848. (*Angulatae*).
574. *Salvia xanthophylla* Epling & Játiva, Brittonia 15: 374. 1963. (*Flocculosae*).
575. *Salvia xanthotricha* Harley ex E.P. Santos, Kew Bull. 59: 290. 2004. (*Secundae*).
576. *Salvia xeropapillosa* Fern. Alonso, Revista Acad. Colomb. Ci. Exact. 74: 471. 1995. (*Rubescentes*).
577. *Salvia xolocotzii* Bedolla & Zamudio, Phytotaxa 217: 43. 2015. (*Uliginosae*).
578. *Salvia yukoyukparum* Fern. Alonso, Novon 18: 38. 2008. (*Tomentellae*).
579. *Salvia zamoranensis* Zamudio & Bedolla, Phytotaxa 217: 48. 2015. (*Brandegeia*).
580. *Salvia zaragozana* B.L. Turner, Phytologia 90: 172. 2008. (*Farinaceae*).

Appendix B

Salvia subg. *Calosphace* (Benth.) Epling, checklist of infraspecific taxa.
1. *Salvia amethystina* Sm. subsp. *amethystina*
2. *Salvia amethystina* subsp. *sumapacis* Fern. Alonso, Caldasia 25: 268. 2003.
3. *Salvia amethystina* subsp. *vetasiana* Fern. Alonso, Caldasia 25: 270. 2003.
4. *Salvia aratocensis* (J.R.I. Wood & Harley) Fern. Alonso subsp. *aratocensis*
5. *Salvia aratocensis* subsp. *suratensis* (J.R.I. Wood & Harley) Fern. Alonso, Caldasia 25: 241. 2005.
6. *Salvia arenaria* A. St.-Hill. var. *arenaria*
7. *Salvia arenaria* var. *selowii* Benth., Prodr. 12: 306. 1848.
8. *Salvia azurea* Michx. ex Vahl subsp. *azurea*
9. *Salvia azurea* subsp. *pitcheri* (Torr. ex Benth.) Epling, Bull. Geol. Nat. Hist. Surv. 9: 76. 1894.
10. *Salvia camarifolia* Benth. subsp. *camarifolia*
11. *Salvia camarifolia* Benth. subsp. *ibiricensis* Fern. Alonso, Anales Jard. Bot. Madrid 59: 346. 2002.
12. *Salvia concolor* Lamb. ex Benth. var. *concolor*
13. *Salvia concolor* var. *iltisii* J.G. González & A. Vázquez, Revista Mex. Biodivers. 83: 592. 2012.
14. *Salvia cualensis* J.G. González var. *cualensis*
15. *Salvia cualensis* var. *perezii* J.G. González, Phytotaxa 74: 47. 2012.
16. *Salvia cuspidata* Ruiz & Pav. subsp. *cuspidata*
17. *Salvia cuspidata* subsp. *bangii* (Rusby) J.R.I. Wood, Kew Bull. 62: 186. 2007.
18. *Salvia cuspidata* subsp. *gilliesii* (Benth.) J.R.I. Wood, Kew Bull. 62: 186. 2007.
19. *Salvia cuspidata* subsp. *rosea* J.R.I. Wood, Kew Bull. 62: 188. 2007.
20. *Salvia cyanocephala* Epling subsp. *cyanocephala*
21. *Salvia cyanocephala* subsp. *macrosigmantha* Fern. Alonso, Repert. Spec. Nov. Regni Veg. Beih. 85: 126. 1936.
22. *Salvia elegans* Vahl var. *elegans*
23. *Salvia elegans* var. *sonorensis* Fernald, Proc. Amer. Acad. Arts 35: 550. 1900.
24. *Salvia erythrostoma* Epling subsp. *erythrostoma*
25. *Salvia erythrostoma* subsp. *isabelina* Fern. Alonso, Anales Jard. Bot. Madrid 53: 43. 1995.
26. *Salvia gachantivana* Fern. Alonso subsp. *gachantivana*
27. *Salvia gachantivana* Fern. Alonso subsp. *woodii* Fern. Alonso, Revista Acad. Colomb. Ci. Exact. 19: 472. 1995.
28. *Salvia melaleuca* Epling subsp. *melaleuca*
29. *Salvia melaleuca* subsp. *totensis* J.R.I. Wood & Harley, Kew Bull. 44: 234. 1989.
30. *Salvia mexicana* L. var. *mexicana*
31. *Salvia mexicana* var. *minor* Benth. Prodr., 12: 337. 1848.
32. *Salvia orthostachys* Epling subsp. *orthostachys*
33. *Salvia orthostachys* Epling subsp. *soatensis* Fern. Alonso, Revista Acad. Colomb. Ci. Exact. 19: 470. 1995.

34. *Salvia ovalifolia* A. St.-Hill. ex Benth. var. *ovalifolia*
35. *Salvia ovalifolia* var. *nitidula* (Briq.) E.P. Santos, Mém. Soc. Biogéogr. III 4: 17. 1994.
36. *Salvia ovalifolia* var. *villosa* Benth., Labiat. Gen. Spec. 267. 1833.
37. *Salvia pauciserrata* Benth. subsp. *pauciserrata*
38. *Salvia pauciserrata* subsp. *calocalicina* (Benth..) J.R.I. Wood & Harley, Kew Bull. 44: 245. 1989.
39. *Salvia pauciserrata* subsp. *derasa* (Briq.) J.R.I. Wood & Harley, Kew Bull. 44: 244. 1989.
40. *Salvia pauciserrata* subsp. *erythrocalicina* J.R.I. Wood & Harley, Kew Bull. 44: 245. 1989.
41. *Salvia pauciserrata* subsp. *lasiocalicina* J.R.I. Wood & Harley, Kew Bull. 44: 245. 1989.
42. *Salvia punctata* Ruiz & Pav. var. *punctata*
43. *Salvia punctata* var. *glabra* Epling, Repert. Spec. Nov. Regni Veg. Beih. 85: 58. 1935.
44. *Salvia raymondii* J.R.I. Wood subsp. *raymondii*
45. *Salvia raymondii* subsp. *mairanae* J.R.I. Wood, Kew Bull. 62: 207. 2007.
46. *Salvia rubescens* Kunth subsp. *rubescens*
47. *Salvia rubescens* subsp. *colombiana* (Epling) J.R.I. Wood & Harley, Kew Bull. 44: 232. 1989.
48. *Salvia rubescens* subsp. *dolichothrix* J.R.I. Wood & Harley, Kew Bull. 44: 229. 1989.
49. *Salvia rubescens* subsp. *truxillensis* (Briq.) J.R.I. Wood & Harley, Kew Bull. 44: 231. 1989.
50. *Salvia rufula* Benth. subsp. *rufula* var. *rufula*
51. *Salvia rufula* subsp. *latens* (Benth.) J.R.I. Wood & Harley, Kew Bull. 44: 268. 1989.
52. *Salvia rufula* subsp. *paezorum* J.R.I. Wood & Harley, Kew Bull. 44: 265. 1989.
53. *Salvia rufula* Benth. subsp. *rufula* var. *nutans* (Briq.) J.R.I. Wood & Harley, Kew Bull. 44: 265. 1989.
54. *Salvia rypara* Briq. subsp. *rypara*
55. *Salvia rypara* subsp. *platystoma* (Epling) J.R.I. Wood, Bull. Herb. Boissier 4: 850. 1896.
56. *Salvia sphacelioides* Benth. subsp. *sphacelioides*
57. *Salvia sphacelioides* subsp. *anaglypha* (Briq.) Fern. Alonso, Caldasia 25: 251. 2005.
58. *Salvia sphacelioides* subsp. *paxfluminensis* Fern. Alonso, Caldasia 25: 253. 2003.
59. *Salvia sphacelioides* subsp. *trianae* J.R.I. Wood & Harley, Kew Bull. 44: 257. 1989.
60. *Salvia uliginosa* Benth. var. *uliginosa*
61. *Salvia uliginosa* var. *rufescens* Benth., Prodr. 12: 306. 1848.
62. *Salvia vazquezii* Iltis & Ramamoorthy subsp. *vazquezii*
63. *Salvia vazquezii* subsp. *tancitaroensis* J.G. González & A. Vázquez, Brittonia 64: 348. 2012.

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