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Rediscovery of *Salvia dugesiana* (Lamiaceae) in Guanajuato, Mexico, after 129 years

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Abstract

A wild population of *Salvia dugesiana* is recorded for the first time after 129 years since the last collections made of the species. It was known only in base to two different gatherings with imprecise localities by Alfred A. D. Dugès in 1880 and 1894. The taxon was detected by a photograph published in an online website for citizen science, iNaturalist. The population was found in southern Guanajuato, in tropical deciduous forest. The species is akin to *S. karwinskii* (sect. *Holwaya*). A lectotype was designated, and a detailed description, photographs and distribution map are presented. Additionally, an identification key to Mexican *Salvia* species with red or orangish corollas is provided, which helps to contrast *S. dugesiana* against the rest of Mexican species with these colors in their corollas.

Key words: A. Dugès, El Bajío region, *Salvia* sect. *Holwaya*, iNaturalist.

Resumen

Se registra por primera vez una población silvestre de *Salvia dugesiana* después de 129 años desde las últimas colecciones hechas de la especie. Era solo conocida de dos colectas de localidades imprecisas de Alfred A. D. Dugès en 1880 y 1894. El taxón se detectó a través de una foto publicada en una plataforma de ciencia ciudadana, Naturalista. La población se encontró en la parte sur del estado de Guanajuato, en bosque tropical caducifolio. La especie es afín a *S. karwinskii* (sect. *Holwaya*). Se designa un lectotipo y se presenta una descripción detallada, fotografías y un mapa de la distribución geográfica de la especie. Adicionalmente, se presenta una clave para la identificación de las especies mexicanas de *Salvia* con corolas rojas o anaranjadas, lo que ayuda a contrastar a *S. dugesiana* respecto al resto de especies mexicanas con estos colores en sus corolas.

Palabras clave: A. Dugès, Naturalista, región de El Bajío, *Salvia* sect. *Holwaya*.

Introduction

Salvia Linnaeus (1753: 23) is rich in species useful to humans especially for their content of essential oils (e.g. Galimuhstasib *et al.* 2000, Cui *et al.* 2015, Casella *et al.* 2023, La Face *et al.* 2023, Perrino *et al.* 2023), and is the biggest genus within the Mexican Flora adding up to 318 species (Villaseñor 2016, Martínez-Gordillo *et al.* 2017a, 2017b, 2023, González-Gallegos *et al.* 2018, 2019, 2020, 2021a, 2021b, González-Gallegos & Carnahan 2019, Martínez-Ambríz *et al.* 2019, Fragoso-Martínez *et al.* 2021). In the recent years, the taxonomic research on *Salvia* has been very active in the country. Lamiaceae fascicles for some regional Flora projects have been prepared: *Flora de Jalisco y Áreas Colindantes* (González-Gallegos *et al.* 2016), *Flora Fanerogámica del Valle de México* (Ramamoorthy 2005), *Flora Mesoamericana* (Klitgaard 2012) and *Flora del Valle de Tehuacán-Cuicatlán* (Martínez-Gordillo *et al.* 2019); together these cover 51 % national diversity (González-Gallegos *et al.* 2021a), including update descriptions, distribution maps, photographs or illustrations and sections about phenology, habitat, distribution and diagnostic discussions. Also, 74

new species have been described within the last 40 years and remain as accepted taxa (González-Gallegos *et al.* 2020, 2021a, 2021b, Martínez-Gordillo *et al.* 2023), contributing with an additional 13 % of the species diversity addressed through thorough descriptions according to current standards. Hence, a significant advance in documenting the taxonomic diversity of the genus in Mexico has been achieved, though, there is still the need to complete, compile and homogenize all this information in a single publication, and there are some species poorly understood due to the scarce herbarium specimens available. González-Gallegos & Marinero-Sobal (2023) points out that the extreme examples are those species known only from the type specimens and some few additional ones collected before 1940, even being possible that some of these could be considered as possibly extinct (IUCN 2022). They identified six species under this condition: *Salvia dugesiana* Epling (1939: 343), *S. inornata* Epling (1939: 161), *S. iodophylla* Epling (1939: 141), *S. jacobi* Epling (1940: 522), *S. leninae* Epling (1941: 565) and *S. synodonta* (Epling 1940: 528); and in that publication they present the rediscovery of *S. iodophylla*.

Of the remaining five species, *Salvia inornata*, *S. jacobi* and *S. leninae* are known only based on a single gathering number, corresponding to the type specimens: eight, sixteen, and ten, respectively (JSTOR Global Plants 2023, SEINet 2023, IBdata v3 2023). *Salvia dugesiana* and *S. synodonta* have two gatherings, with a total of two specimens the first, and fifteen the other (Jstor Global Plants 2023, SEINet 2023, IBdata v3 2023). *Salvia jacobi*, *S. leninae* and *S. synodonta* grow in remote and difficult localities to be explored, the two first in Sierra Madre del Sur region in Guerrero state, and the other in the Pacific Lowlands in Michoacán, following Morrone (2017) biogeographic regionalization. As far as known, no specific attempts to trace and collect these species have been made. In contrast, several botanical explorations have been conducted by us and other colleagues to find *S. inornata* in La Esperanza, Puebla, the type locality, but with no success (Martínez-Gordillo *et al.* 2019). La Esperanza is a town that flourished around a train station, active at the time when Carl A. Purpus collected the plant (Sousa-Sánchez 1969); we have explored the surrounding xeric hills to the town since the shrubby and small thick leaves of *S. inornata* suggest this kind of environment; however, lines of wind generators have been installed there and it is not clear if the plant could have been extirpated by the impact of such disturb, or if Purpus mentioned La Esperanza just as a general reference when he might have collected it in a more distant area. Finally, *S. dugesiana* represented the most challenging of the poorly known Mexican salvias to be rediscovered. There are two syntypes collected by Alfred Dugès: a) one in 1880 with no locality description but the name of Guanajuato state, and no gathering number assigned, b) the other was made in 1894 and has two labels, the first describing the plant as a “big sage with red bright flowers” [from] “rocky mountains”, and the other pointing again only the name of the state, the gathering number 226 and the year. Alfred Dugès was a French physician with a strong naturalist interest who migrated to Mexico in 1853, he lived in several cities but after he finally established in Guanajuato city in 1861, he started to collect animal and plants specimens regularly (Rzedowski *et al.* 2009, Flores-Villela *et al.* 2018); however, most of his plant specimens lack of a referred locality. Due to the above there was no clue where to start the search for this species. Fortunately, a recent observation in Naturalista (iNaturalist) from Huanímaro, Guanajuato (user betootero, Roberto Otero Zaragoza, August 13th, 2022; Naturalista 2023; <https://naturalista.mx/observations/130938993>), though with a fuzzy photograph and hence not at all unambiguous, triggered our attention as a possible *S. dugesiana* population and led us to rediscover the species, what it is here reported.

Materials and methods

A botanical exploration was conducted to locate the purportedly *Salvia dugesiana* population in Huanímaro, Guanajuato, in August 2023. The specimens were gathered and prepared according to standard recommendations (Lot & Chiang 1986). Photographs of the habitat and different morphological structures of the plants were taken with a Nikon D5600 camera. A Karl Zeiss Stemi 508 dissecting microscope was used to observe and assess the morphological variation of the specimens. The morphology of the specimens was collated against the protologue of *S. dugesiana* (Epling 1939) and syntypes to confirm its identity.

Additionally, different sources were consulted in search of some insights that could have provided data to uncover the precise type locality of *S. dugesiana*, including online databases of those herbaria where Dugès used to send duplicates of its specimens (Bean 1892, Beltrán *et al.* 1990, Flores-Villela *et al.* 2018, Harvard University & Libraries 2023, IBdata v3 2023, SEINet 2023, Smithsonian National Museum of Natural History 2023). The correspondence with Sereno Watson from the Gray Herbarium available at Biodiversity Heritage Library (2023a), to whom he sent duplicates of his specimens and who helped him to identify them, was also examined, as well as the Gray Herbarium Miscellaneous Plant Lists summarizing Dugès specimens (Biodiversity Heritage Library 2023b).

An identification key to Mexican *Salvia* species with red or orangish corollas was also prepared to help in the identification of the poorly known *S. dugesiana*. The key was prepared based on specialized literature (Walker & Elisens 2001, Klitgaard 2012, González-Gallegos *et al.* 2016, Martínez-Gordillo *et al.* 2019) and our own observations on herbarium specimens to confirm or assess some morphological characters.

Results

Taxonomy

Salvia dugesiana Epling (1939: 343)

Type:—MEXICO. Guanajuato. Montagnes pierreuses, 1894, *A. Dugès* 226 (lectotype GH (barcode 00001614); here designated).

Perennial herb to subshrub, 0.6–1.5 m tall; stem densely pilose and covered with light amber glandular dots, also with some glandular-capitate hairs along young branches. Leaves with petiole (1.4–)2.5–5 cm long, pubescent as the stems; leaf blade ovate to ovate-lanceolate, (4.4–)8–14 × (2.1–)4–8.3 cm, apex acute, base short cuneate to oblique, margin crenate to serrate, sparsely pilose above, moderately pilose beneath with the hairs mainly along the veins, and with translucent amber glandular dots. Inflorescence in racemes 7.8–17(–27) cm long, with 3–8(–10) floral nodes, each one (4–)6–12(–18)-flowered, the lowermost 2.2–2.7 cm apart from each other; flora axis densely covered with pilose and glandular-capitate hairs, puberulent and with light amber glandular dots. Floral bracts deciduous, usually red, ovate to ovate-lanceolate, 3.7–10 × 1.7–6 mm, apex caudate, base truncate, margin entire, outer surface pilose and covered with light amber glandular dots; occasionally the lowermost floral bracts seem to be reduced leaves, reaching 13–22 × (6.2–)9–12 mm, and with serrate margin in the lower half portion. Flowers with pedicel 6.2–10 mm long, hirtellous with glandular-capitate hairs. Calyx red, hirtellous with glandular-capitate hairs and covered with amber glandular dots, internally short hispidulous with antrorse hairs, 10–16 × 3.8–5.2(–7) mm, lips acuminate and then long caudate, upper one 7-veined and entire. Corolla red, short pilose and with some tiny glandular-capitate hairs in the lips, tube 20–26 × 6.3–8.7 mm, slightly ventricose, not invaginated near the base and internally epapillate; upper lip 7–10.3 mm long; lower lip 6–11 × 5–8 mm, incurve-concave. Stamens included; filament 3–5 mm long; connective 17–22 mm long, ornated with a ventral cleft with short acute teeth at its extremes; theca 3.2–3.5 mm long; staminodes filiform, 0.9–1 mm long, placed above and behind filament insertion in corolla basal third. Gynobasic horn 1.3–2.6 mm long; style 24–36(–40) mm long, scarcely short pilose, upper stigmatic branch arcuate and longer, the lower one acute at the apex. Immature mericarp ovoid, 3–4 × 1.8–2 mm, mature ones not seen.

Phenology:—The plant was found in full bloom in mid-August and with immature fruits, so it is very probable that blooming extends from late June to at least late November; and fruits should be maturing from late August to November as well.

Distribution, habitat and ecology:—*Salvia dugesiana* is known exclusively from the locality near Cueva de Santa Regina in Huanímaro, southwestern Guanajuato, very close to the boundaries with Michoacan state (Fig. 1). It inhabits in shady ravines with tropical deciduous forest with the trees *Agonandra racemosa* (de Candolle 1825: 41) Standley (1920: 506) and *Heliocarpus terebenthinaceus* (de Candolle 1813: 114) Hochreutiner (1914: 125) as dominant, and *Euphorbia tanquahuete* Sessé & Mociño (1894: 122) and *Ipomoea murucoides* Roemer & Schultes (1819: 248) at the upper edges of the ravine. It shares habitat also with the herbs and shrubs *Dioscorea* Linnaeus (1753: 1032) sp., *Euphorbia graminea* Jacquin (1763: 151), *Jaltomata procumbens* (Cavanilles 1791: 53) Gentry (1973: 287), *Justicia candicans* (Nees 1847: 396) Benson in Benson & Darrow (1981: 218), *J. caudata* Gray (1886: 405) and *Schizocarpum parviflorum* Robinson & Greenman (1894: 386).

Etymology:—The species was named in honor of its first collector, Alfred Dugès. The prolific field work done by Dugès is recognized by a total of 55 species dedicated to him, including fungi, plants, invertebrates, and vertebrates (Ríos-Muñoz *et al.* 2018). There are still 10 flowering plants species retaining the epithets *dugesii* or *dugesiana* in their accepted names, and the monotypic genus *Dugesia* Gray (1882: 215) of the Asteraceae.

Additional specimens examined:—MEXICO. Guanajuato. Guanajuato, 1880, *A. Dugès* s.n. (GH!); mpio. Huanímaro, Cueva de Santa Regina, cañada junto a la vereda de ascenso, 1.7–1.8 km al N de Huanímaro, 20°22.99'N 101°30.22'W, 1830 m, 30 August 2023, *J.G. González-Gallegos*, *B.Y. Bedolla-García*, *L. Ruacho-González*, *J. Noriega-Villa*, *M.H. Sandoval-Ortega* & *S. Ruiz* 2926 (CIIDIR!, IBUG!, IEB!, MEXU!, XAL!).

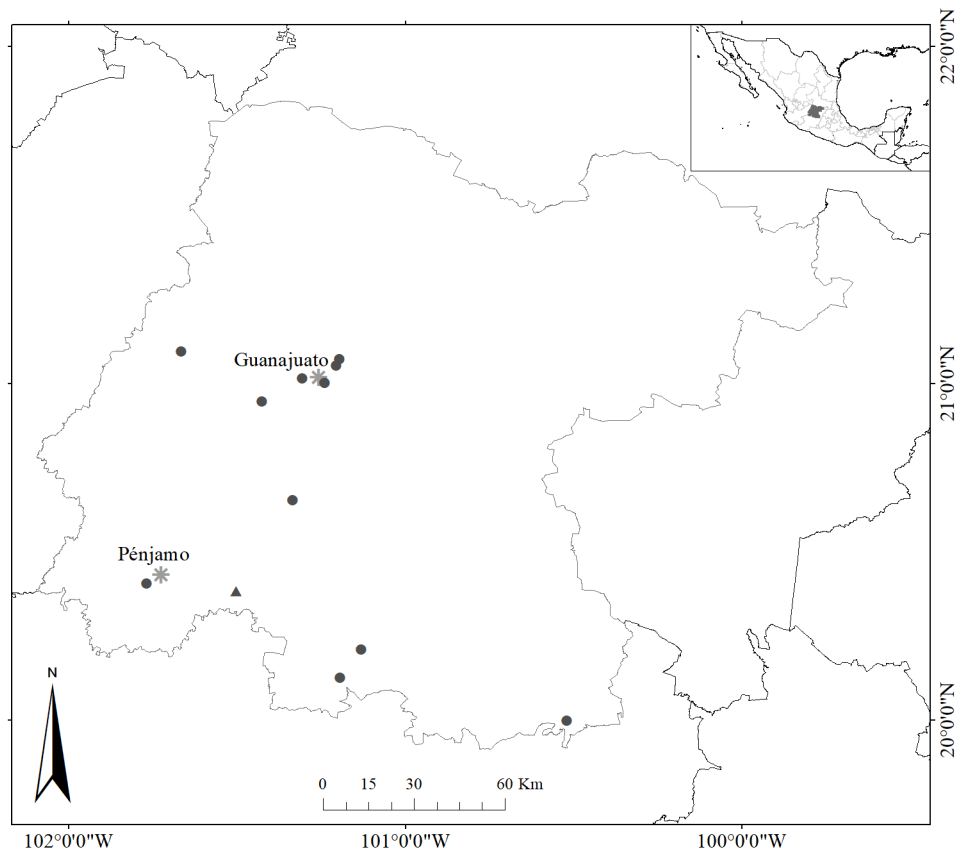


FIGURE 1. Distribution map of *Salvia dugesiana* (triangle) and those localities visited by A. Dugès in Guanajuato state (circles). Guanajuato and Pénjamo cities are highlighted with an asterisk to serve as reference.

Discussion:—*Salvia dugesiana* was originally placed in *Salvia* sect. *Secundae* (Bentham 1848: 331) Epling (1939: 342), a group made up of South American species (except *S. dugesiana*). Epling (1939) pointed out that the assignment was provisional until more material with mature corollas could be observed, and indeed, the current examination of floral characters reveals a better match with sect. *Holwaya* Ramamoorthy (1984: 323), equivalent partially to the Mexican species recognized by Epling as part of sect. *Nobiles* (Bentham 1848: 328) Epling (1939: 280). *Salvia* sect. *Holwaya* was coined to embrace the Mexican species previously placed in sect. *Cardinales* Epling (1939: 295) but left out of this when Ramamoorthy (1984) synonymized the type species, *S. cardinalis* Kunth (1817: 301), with *S. fulgens* Cavanilles (1791: 15), which is the type of sect. *Fulgentes* Epling (1939: 273); hence, merging both sections into one, but leaving the former species of sect. *Cardinales*, not morphologically cohesive with *S. cardinalis*, out. The new section suffered an additional arrangement due to the transfer of the Mexican species formerly in sect. *Nobiles* by dos Santos (1991), who justified it supported on morphological evidence to circumscribe the section only to South American species.

According to the current delimitation of the section and based on the combination of characters of the former section *Cardinales* and Mexican species of *Nobiles*, *Salvia* sect. *Holwaya* includes herbs and suffrutescent herbs, with simple or branched hairs, ovate leaves, acuminate at apex, mostly rounded to cordate/subcordate at base, floral axis with many flowers, bracts early deciduous, large, 5 or 7-veined upper calyx lip, brightly red, pink to magenta colored, showy red corolla, tube papillate or epapillate near the base, frequently invaginate and ventricose, stamens included, connective ornated with a tooth, and pilose style (Epling 1939, Ramamoorthy 1984, González-Gallegos & Aguilar-Santelises, Bedolla-García & Zamudio 2017). It is currently made up of 10 species: *S. adenophora* Fernald (1900: 538), *S. disjuncta* Fernald (1900: 533), *S. gesneriiflora* Lindley & Paxton (1853: 49), *S. guevarae* Bedolla & Zamudio (2017: 6), *S. holwayi* Blake (1920: 113), *S. karwinskii* Bentham (1833: 725), *S. involucrata* Cavanilles (1793: 3), *S. stolonifera* Bentham (1840: 70), *S. wagneriana* Polakowski (1875: 591), *S. tilantongensis* González-Gallegos & Aguilar-Santelises (2014: 13). However, it is necessary to wait for the progress of phylogenetic studies to definitively locate the species; now, most of the sequenced species of the *Holwaya* section are nested in the *Fulgentes* clade

(Fragoso *et al.* 2018). This clade groups members of the sections *Fulgentes*, *Holwaya*, and *Flocculosae* (Epling 1935: 77) Epling (1939:153); in the near future, it is possible that it will be recognized as a monophyletic group.

Among the species of sect. *Holwaya*, *Salvia dugesiana* is morphologically most similar to *S. karwinskii*, particularly with regard to the appearance of the leaves, inflorescence size, number of the flowers per floral node, presence of glandular-capitate hairs along floral axis and calyx, upper lip acuminate and then long caudate, and corolla tube slightly ventricose. *Salvia dugesiana* differs by having stems and leaves moderately pilose with simple hairs (*vs.* tomentose with dendritic hairs), lacking bracteoles additional to floral bracts, corolla tube not invaginated (*vs.* invaginated) and internally epapillate (*vs.* papillate) (see Table 1 and Fig. 2 for more details; Epling 1939, Klitgaard 2012, Martínez-Gordillo *et al.* 2019). Furthermore, if *S. karwinskii* is discarded due to its indumentum with branched hairs, *S. dugesiana* groups with a set of three Mexican shrubby *Salvia* surpassing 80 cm tall, having petioles and leaf blades longer than 10 mm and 25 mm, respectively, calyces longer than 11 mm, 5 or 7-veined upper calyx lip, corolla tube ventricose, 20 mm long or longer, epapillate inside, and included stamens: *S. guevarae*, *S. gesneriiflora* and *S. tilantongensis*; all in fact, members of sect. *Holwaya*. Considering these three species, *S. dugesiana* is most similar to *S. guevarae* due to the corolla tube shorter than 3 cm long, and relatively small corolla lips (upper 7–10.3 mm long, lower 6–12 mm long, *vs.* 16–25 mm long and 12–27 mm long). *Salvia dugesiana* can be set apart from *S. guevarae* by means of the cuneate to oblique leaf base (*vs.* slightly truncate, rounded to cordate), caudate calyx lobes (*vs.* short acuminate), narrower corolla tube (6.3–8.7 mm *vs.* 9–13 mm long) and filiform staminodes (*vs.* claviform) (Fig. 2). Besides, *S. guevarae* grows in temperate forest rather than in tropical, including pine-oak and cloud montane forests and has not been recorded in Guanajuato but in Hidalgo, Querétaro and San Luis Potosí.

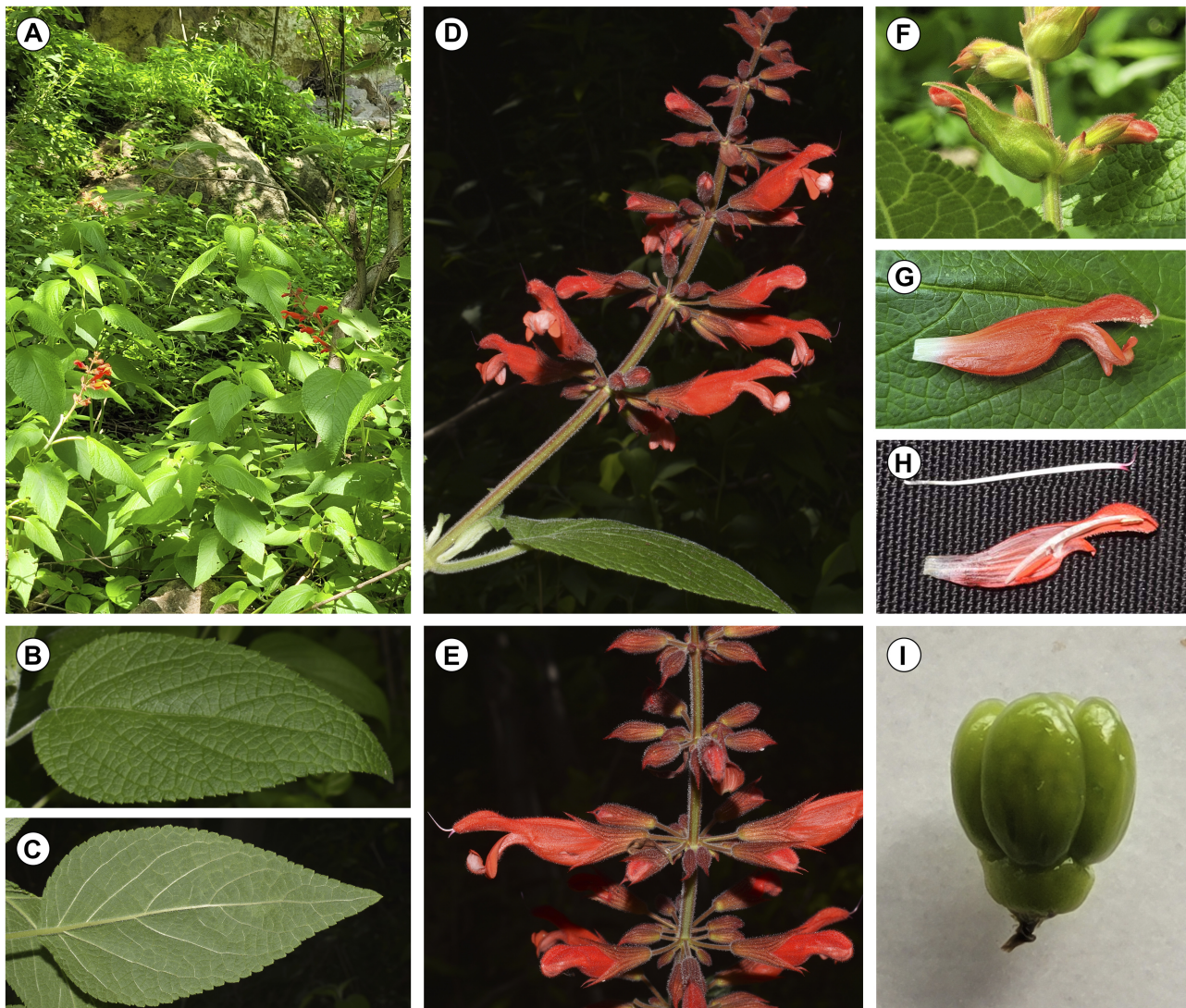


FIGURE 2. A. Habitat, B. Above leaf blade, C. Beneath leaf blade, D. Inflorescence, E. Detail of the floral node and lateral view of the corolla, F. Detail of the lowermost floral bracts, G. Lateral view of the corolla, H. Style and connective, I. Immature mericarps. Photographs taken by Brenda Bedolla (A, F, G, I), Jesús G. González-Gallegos (B–E, H).

TABLE 1. Comparison of morphological characters, habitat and distribution between *Salvia dugesiana* and *S. karwinskii*.

Characters	<i>S. dugesiana</i>	<i>S. karwinskii</i>
Habit	perennial herb to subshrub	subshrub
STEAM		
Indument	densely pilose with simple hairs, and some glandular-capitate along young branches	tomentose with dendritic hairs
LEAVES		
blade shape	ovate to ovate-lanceolate	ovate to elliptic-ovate
blade size (cm)	(4.4–)8–14 × (2.1–)4–8.3	(4–)10–13 × (2–)3.5–6
base shape	short cuneate to oblique	rounded to truncate, rarely rounded and then attenuate
apex shape	acute	acuminate to acute
pubescence on beneath surface	moderately pilose with simple hairs mainly along the veins	tomentose with dendritic hairs dispersed throughout the surface
INFLORESCENCE		
length (cm)	7.8–17(–27)	10–18(–25)
pubescence of floral axis	pilose with glandular-capitate hairs	pilose with glandular-capitate hairs, and scarce dendritic hairs dispersed on the surface
number of flowers per floral nodes	(4–)6–12(–18)	(4–)6–14
FLORAL BRACT		
shape	ovate to ovate-lanceolate	ovate
size (mm)	3.7–10 × 1.7–6	12–17(–30) × 1.5–4
color	red	red
apex shape	caudate	caudate
duration	deciduous	deciduous
bracteoles	absent	present
CALYX		
size (mm)	10–16 × 3.8–5.2(–7)	12–18 × 7–10
pubescence	hirtellous with glandular-capitate hairs	hirtellous with glandular-capitate hairs
upper lip shape	acuminate and then long caudate	acuminate and then long caudate
COROLLA		
color	red	red
pubescence	short pilose and with some tiny glandular-capitate hairs in the lips	short pilose and with some tiny glandular-capitate hairs in the lips
tube size (mm)	20–26 × 6.3–8.7	(18–)21–30 × 4.5–6
tube shape	slightly ventricose and straight at base	slightly ventricose and invaginated at base
number of internal papillae	0	2
habitat	tropical deciduous forest	pine-oak forest and montane cloud forest
distribution	Guanajuato	Southern Mexico (Chiapas, Oaxaca, Puebla and Veracruz) and northern Central America (Guatemala, Honduras, El Salvador and Nicaragua)

Alfred Dugès contributed greatly to documenting the Mexican biodiversity thanks to his extensive collections, mainly in the central area of the country, a territory known as El Bajío Region. Unfortunately, most of his samples lack a precise description of the locality or even a simple reference to a town or geographical accident that could be located. The above makes difficult to trace and have an idea of his exploration itineraries, and that is why there was no clue about where to look for *S. dugesiana*, what in turn promoted taxonomic turmoil that made botanists to hesitate on the recognition of this species. Proof of the later is that the species was overlooked in floristic inventories in Guanajuato (Carranza-González 2005, Zamudio & Galván-Villanueva 2011), or even in a global checklist of vascular plants in Mexico (Villaseñor 2014). However, the rediscovery of a population of the species makes clear that this deserve to

be recognized, being a distinctive species within salvias with red corollas, a taxon that should be added to the list of those taxa restricted to the biogeographical province of the Trans-Mexican Volcanic Belt (Rzedowski 2020). It is worth noting that *S. dugesiana* is not the only reported case of a species described based on Dugès specimens and lost for over 100 years; *Pachyphytum brevifolium* Rose in Britton & Rose (1905: 12) represents an additional example, a plant rediscovered a couple decades ago by Pérez-Calix & Glass (1999) in surrounding areas to the capital city of the state, Guanajuato.

The rediscovery of *S. dugesiana* was possible only to the fortunate event that the iNaturalist (known as Naturalista in Mexico) user *betootero* (Roberto Otero Zaragoza) uploaded and observation of the plant, which triggered our attention in its possible identity as this long-forgotten species. This is especially true considering the lack of information commented before, as well as the morphological characters of *S. dugesiana* and similarity with species of cloud montane, pine-oak and oak forests, what suggested that the species should be found also in that kind of vegetation and not in tropical dry forests. However, there are no elements to ensure that the population in Huanímaro corresponds to the type locality of the species. In the literature and different sources consulted in search of additional information that could clarify some of the localities visited by Dugès, the direct mentions to any geographical name are scarce (Bean 1892, Biodiversity Heritage Library 2023a, 2023b, Harvard University & Libraries 2023, IBdata v. 2023, SEINet 2023, Smithsonian National Museum of Natural History 2023). The only localities extracted from that sources and which undoubtedly were visited by Dugès in El Bajío Region and adjacent areas are: Guadalajara in Jalisco state; Cuitzeo, Morelia, Tangancicuaro and Tengüecho in Michoacán state; Campo Santo de [graveyard of] San Sebastián (most probably the one in the city León), Hacienda de Tupátaro, Moroleón, Pénjamo, Santa Rosa mountains, Silao, Tarandacuao and Yuriria lake in Guanajuato state, as well as the capital city with the same name (referring a couple of specific points in the surroundings of the city, or between this and Santa Rosa, Presa de la Olla and San Nicolás Mountain). Of all the listed localities the closest one to Huanímaro is Pénjamo, about 24 km straight line distance (Fig. 2), and being historically a bigger settlement than Huanímaro at the foot of a more massive mountain, it is highly probable that Dugès collected the original material in that mountains. Hence, future botanical exploration in that range might result in additional populations of *S. dugesiana*.

Identification key to Mexican species of *Salvia* with red or other orange corollas

1. Basal leaves often pinnately 3–5-foliolate; stamens bearing two fertile thecae at the connective extremes, though the posterior ones sometimes reduced, posterior connective branches of both stamens free2
1. Basal leaves simple; stamens bearing only one fertile theca at connective anterior point, posterior connective branches connate between both stamens.....3
2. Calyx lobes bearded; corolla straight and parallel to calyx longitudinal axis, lower corolla lip shorter than the upper *S. henryi*
2. Calyx lobes glabrous; corolla arcuate upwards in respect to calyx longitudinal axis, lower corolla lip subequal or longer than the upper *S. roemeriana*
3. Calyces inflated such as the dorsal and ventral margins are rounded4
3. Calyces not inflated, with both dorsal and ventral lines straight and almost parallel or divergent.....6
4. Shrub, 0.8–1.6 m tall; leaves mostly deltoid or deltoid-ovate; mericarp 4.5–5.7 mm long. Plants from desert shrub or arid oak and pine-oak forests, usually above 2000 m elevation..... *S. regla*
4. Arborescent shrub, (1.5–)2–4(–6.5) m tall; leaves ovate, ovate-lanceolate to lanceolate; mericarp 2.8–3.5 mm long. Plants infrequent in desert shrub, but mostly in tropical deciduous forests or subtropical shrub, as well as in oak and pine-oak forest, usually below 2000 elevation5
5. Calyx constricted around its base; style glabrous..... *S. pubescens*
5. Calyx rounded from the base with no constriction; style short pilose near the apex *S. sesssei*
6. Upper calyx lip 3-veined7
6. Upper calyx lip 5 or 7-veined.....13
7. Corolla tube ventricose.....8
7. Corolla tube tubular and widened towards the throat.....9
8. Leaf blade ovate, subcordate at base; calyx (5.7–)6.5–7.9 mm long; corolla tube (16.2–)17–20.4 mm long, upper corolla lip subequal to the lower..... *S. durangensis*
8. Leaf base elliptic to elliptic lanceolate, attenuate at base; calyx 8.5–10 mm long; corolla tube 21–26 mm long, upper corolla lip shorter than the lower *S. miniata*
9. Leaf base truncate to rounded and abruptly short cuneate; stamens included in the corolla10
9. Leaf base cordate to rounded; stamens exserted from the corolla.....12
10. Leaf blade serrate-erose at margin, glabrescent; calyx red; corolla lips subequal in length, the lower reflexed but not folded backwards around the tube *S. subrubens*
10. Leaf blade dentate to serrate at margin, pubescent to tomentose; calyx green, and sometimes with a shade of purple to the lips; lower corolla lip patently shorter than the upper, and strongly reflexed and folded backwards around the tube11

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