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.


Introduction

*Salvia* Linnaeus (1753: 23) is rich in species useful to humans especially for their content of essential oils (e.g. Gali-Muhtasib 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-Ambriz 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 fussy 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

*S. 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 epappulate; 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* sp., *Euphorbia graminea* Jacquin (1763: 151), *Jaltomata procumbens* (Cavanilles 1791: 53) Gentry (1973: 287), *Justicia candidans* (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 (Rios-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.

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.

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

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

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 those 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 Túpátoro, 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 ocher orange corollas

1. Basal leaves often pinnately 3–5-foliolate; stamens bearing two fertile thecae at the connective extremities, though the posterior ones sometimes reduced, posterior connective branches of both stamens free ................................................................. 2
2. Basal leaves simple; stamens bearing only one fertile theca at connective anterior point, posterior connective branches connate between both stamens. ................................................................. 3
3. Calyces inflated such as the dorsal and ventral margins are rounded ........................................................................................................ 4
4. Calyces not inflated, with both dorsal and ventral lines straight and almost parallel or divergent ................................................................. 5
5. 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. ....................................................................................................................... 6
6. 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 forests, usually below 2000 elevation ................................................................. 7
7. 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 tube ........................................................................................................ 8
8. Leaf blade elliptic to elliptic lanceolate, attenuate at base; calyx 8.5–10 mm long; corolla tube 21–26 mm long, upper corolla lip subequal to the lower ........................................................................................................ 9
9. Leaf blade truncate to rounded and abruptly short cuneate; stamens included in the corolla ....................................................................................................................... 10
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 ........................................................................................................ 11

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11. Floral node 2–4(–6)-flowered; calyx lips acuminate and apiculate at apex; corolla 38–45 mm long; upper corolla lip 8–15 mm long.................................................................S. nervata

12. Calyx 18.5–19.6 mm long, lips long caudate-aristate; corolla tube 27–35 mm long, internally epapillate towards the base, upper corolla lip longer than the lower; style short pilose near the apex.................................................................................................................S. tubifera

13. Stems short pilose to pilose; lower corolla lip narrow, 2.2–6 mm wide. Plants growing mostly in temperate forest (oak, pine-oak, cloud montane forests), regularly above 1800 m elevation ........................................................................................................S. longistyla

14. Indument of branched hairs throughout the different plant structures (stem, petiole, both leaf surfaces, floral axis and bract, and calyx); corolla ochre orange; mericarp short pilose at apex ......................................................................................................................................................S. lasiantha

15. Leaf blade ovate to ovate-deltoid, bullate above, green beneath; floral bract rhomboid-elliptic to lanceolate 3.7–4.7 mm long, lower corolla lip incurved-concave; connective with a tiny tooth at midportion; style sparsely pilose near midportion; mericarps brownish gray and irregularly punctate with a darker tone .........................................................S. patriciae

16. Stems with simple hairs, or if glandular present, then tiny or sparse; leaves ovate, ovate lanceolate to elliptic, mostly less than two times longer than wide; corolla tubular and/or widened towards the throat. Plants not restricted to Guerrero ....................................................................................S. perlonga

17. Calyx violet to violet red with the veins slightly inconspicuous, 12–14.8 mm long, arcuate from the base, upper lip longer than the lower .................................................................S. coccinea

18. Leaf blade ovate to elliptic lanceolate, smooth above, usually violet beneath; floral bract ovate, 2.5–3.3 mm long; corolla straight, internal basal papillae 1–1.4 mm long, lower corolla lip reflexed; connective entire at midportion; style glabrous; mericarps bright black ......................................................................................................................................................S. iodophylla

19. Stems hirsute; lower corolla lip wide, 6–14 mm wide. Plants usually from secondary vegetation and tropical deciduous forests, growing mainly below 1600 m elevation ..............................................................................................................................................................S. iodophylla

20. Leaves smooth above, glabrous on both surfaces except by the short pilose midvein, margin long ciliolate with simple hairs (1.8–2 mm long); flowers 2 on each floral node; corolla internally ornate with a couple papillae towards the base.................................................................................................................................S. karwinskii

21. Corolla tube with a couple papillae inside towards the base .................................................................................................................................S. praestans

22. Stems with branched hairs ..........................................................................................................................................................................................S. elegans

23. Leaf ovate to elliptic lanceolate, 3–12.5 cm long, sparsely yellowish tomentose beneath; floral nodes with 4–12 flowers; upper calyx entire and long caudate; corolla tube internally ornate with a couple papillae towards the base ......................................................................................................................S. disjuncta

24. Leaf blade ovate-deltoid, 0.8–3 cm long, densely white tomentose beneath; floral nodes with 2 flowers; upper calyx lip truncate and acuminate; corolla tube epapillate inside towards the base ........................................................................................................................................S. oaxacana

25. Corolla tube internally ornate with a couple folds or papillae towards the base .................................................................S. arnoldiana

26. Leaves smooth above, glabrous on both surfaces except by the short pilose midvein, margin long ciliolate with simple hairs (1.8–2 mm long); flowers 2 on each floral node; corolla internally ornate with a couple folds towards the base................................................................................................................................................S. holwayi

27. Leaf smooth above; racemes with 4–18 floral nodes; both corolla lips less than 6 mm long .................................................................................................................................S. holwayi

28. Perennial herb, decumbent, mostly subcapsule with the leaves concentrated in the lower third or quarter of its length; connective with a retrorse tooth near ventral midpoint at the anterior end of a constricted portion in width, short pilose in the border opposite to the tooth and in the dorsal midvein; papillae inside corolla tube and near the base bent forwards by 4–5 mm .........................................................................................................................................................S. stolonifera

29. Perennial herbs, subshrubs to shrubs, mostly erect and with the leaves distributed almost equally along their length; connective with a retrorse tooth near ventral midpoint, with no constriction, glabrous or puberulent; papillae inside corolla tube erect, or if bent forwards, no more than 2 mm ........................................................................................................................................S. univerticillata
29. Corolla tube 2.2–3.9 (–4.4) cm long or longer, upper corolla lip 1.2–1.9(–2.1) cm long ................................................................. 30
29. Corolla tube 1.2–2.1 cm long, upper corolla lip 0.6–1.1 mm long ........................................................................................................ 32
30. Floral bract longer than 1.8 cm; corolla tube straight at the base ................................................................................................. 32
30. Floral bract less than 1.1 cm; corolla tube invaginate at the base ................................................................................................. 31
31. Leaves with glandular capitate hairs only beneath; connective 18–19 mm long; plants from southern Mexico (Oaxaca and Puebla) ........................................................................................................................................ 31
31. Leaves covered with glandular-capitate hairs above and beneath; connective 20–23 mm long; plants from northeastern Mexico (Coahuila, Nuevo León, San Luis Potosí and Zacatecas) ........................................................................................................................................ 31
32. Leaves (2.5–)7–14 cm long, the uppermost sessile; floral bract 15–20 mm long ................................................................................ 32
32. Leaves 1–3.3(–4) cm long, the uppermost petiolate; floral bract 2.8–8.4 mm long ........................................................................ 33
33. Margin of the floral bract denticulate; papillae at the inside of basal corolla tube bidentate at apex; upper corolla lip longer than the lower ........................................................................................................................................ 33
33. Margin of the floral bract entire; papillae at the inside of basal corolla tube entire at apex; upper corolla lip shorter than the lower ........................................................................................................................................ 33
34. Perennial herb to shrub, (30–)40–120 cm tall; leaf short pilose to hispidulous (rarely glabrous), base truncate to subcordate; floral bract 3–8.4 mm long, acuminate at apex .............................................................. 34
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35. Corolla tube with the same width all along, with no ventricose portion; usually the thecae and small portion of the filament exserted from the upper corolla lip ........................................................................................................................................ 35
35. Corolla tube ventricose; stamens included below the upper corolla lip ......................................................................................... 36
36. Plants up to 60 cm tall; leaves with petioles (0.7–)2–5 mm long or sessile, leaf blade (0.5–)1–2.5 × 0.2–0.3 cm; plants mostly from desert shrub and Juniperus forest ........................................................................................................................................ 36
36. Plants mostly taller than 80 cm; leaves with petioles longer than 10 mm, leaf blade 2.5 cm long or longer, and wider than 1.4 cm; plants mostly from temperate (pine, pine-oak and cloud montane) or tropical (tropical deciduous) forests ........................................................................................................................................ 37
37. Calyx less than 11 mm long, upper lip 5-veined; corolla tube less than 18 mm long ........................................................................................................................................ 37
38. Calyx 11 mm long or longer, upper lip 5 or 7-veined; corolla tube 20 mm long or longer ........................................................................ 38
38. Floral bract deciduous, 3–5 mm long; corolla tube 15–17 mm long .................................................................................................. 38
39. Floral bract persistent, 6.3–15.9 mm long; corolla tube 9.9–12.3 .............................................................. 39
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40. Erect perennial herbs to shrubs; upper stigmatic branch longer than the lower ................................................................. 40
40. Corolla tube shorter than 3 cm long, upper lip 7–10.3 mm long, lower lip 6–12 mm long ................................................................. 40
41. Leaf base cuneate to oblique; calyx lobes triangular and caudate at apex; corolla tube 6.3–8.7 mm wide; staminodes filiform. Plants from tropical deciduous forest in Guanajuato ................................................................. 41
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42. Stem with exfoliating bark; petiole directly attached to the stem; floral bract (0.6–)0.7–2(–2.4) cm long; calyx lobes not aristate; middle lobe of the lower corolla lip reflexed ........................................................................................................ 42
42. Stem without exfoliating bark; petiole articulated to a widened basal portion; floral bracts 0.2–0.5(–0.8) cm long; calyx lobes aristate with an extension of 3–4.5 mm; middle lobe of the lower corolla lip incurve concave ........................................................................................................ 42

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