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Notes on *Salvia* subgenus *Calosphace* section *Macrostachyae* (Lamiaceae) from Ecuador with a new record

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Abstract

Salvia alata is reported as new record for Ecuador. This species belongs to *S.* sect. *Macrostachyae*, thus an updated identification key to species of this section is provided. The descriptions of *Salvia alata* and the species most morphologically similar to it (*Salvia speciosa*) are complemented with new information and photographs taken in the field. *Salvia alata* is distributed in Ecuador and Peru and can be distinguished from *Salvia speciosa* by its pilose vegetative organs, flowers with white stamens and styles, and mericarps with a deltoid apex. On the other hand, *Salvia speciosa* is endemic to Peru, and it has glabrescent vegetative organs, flowers with burgundy to deep purple stamens and styles, and mericarps with a bifurcate apex.

Resumen

Salvia alata se reporta como un nuevo registro para Ecuador. Esta especie pertenece a *S.* sección *Macrostachyae*, por lo que se provee una clave de identificación actualizada para las especies de esta sección. Las descripciones de *Salvia alata* y la especie que es más similar morfológicamente a ella (*Salvia speciosa*) son complementadas con nueva información y fotografías tomadas en el campo. *Salvia alata* se distribuye en Ecuador y Perú y se distingue de *Salvia speciosa* por sus órganos vegetativos pilosos, flores con estambres y estilos blancos, y mericarpos con un ápice deltoideo. Por su parte, *Salvia speciosa* es endémica a Perú, tiene órganos vegetativos glabrescentes, flores con estambres y estilos vináceos y mericarpos con un ápice bifurcado.

Key words: Andes, diversity, Neotropics, South America, sages

Introduction

Salvia Linnaeus (1753: 23) is the most diverse genus of the mint family (Lamiaceae), with almost 1,000 described species (Harley *et al.* 2004). Within this genus, the New World endemic lineage, *S.* subg. *Calosphace* (Bentham 1833:

198) Epling (1939: 4) comprises more than one-half of that diversity (ca. 580 species; González-Gallegos *et al.* 2020). Species of *S.* subg. *Calosphace* are mainly distributed in the Neotropics, with four diversity centers: Mexico and Central America, the Andean region, eastern South America, and the Antilles (Jenks *et al.* 2013).

The Andean region is the second most important diversity center of *S.* subg. *Calosphace*, containing ca. 155 species (Jenks *et al.* 2013). It has been considered a key area for the evolutionary history of *S.* subg. *Calosphace* due to the high frequency of ornithophily (Wester & Claßen-Bockhoff 2011) and the presence of polyploid taxa (Alberto *et al.* 2003), compared to Mexico and Central America, where both conditions are less frequent. These two features have been associated with an increase in evolutionary rates in other flowering plant groups (Lagomarsino *et al.* 2016; Tank *et al.* 2015).

Ecuador harbors 17,548 species of vascular plants, 31% of them endemic, ranking as the fourth South American country in terms of vascular plant diversity (Ulloa-Ulloa *et al.* 2017). Regarding *Salvia* subg. *Calosphace*, Ecuador is the sixth most-diverse country, with 41 species, 17 of them endemic (González-Gallegos *et al.* 2020). However, several of these species are only known from the type specimens—i.e., *Salvia austromelissodora* Epling & Játiva (1966:260), *Salvia peregrina* Epling (1951:134), and *Salvia unguella* Epling (1940:533)—or from a few specimens with imprecise geographic information housed in historic collections at Q and QPLS herbaria (Harley 1999; Moscoso *et al.* 2011).

Epling organized the species of *S.* subg. *Calosphace* in 102 sections (Epling 1939, 1940, 1941, 1944, 1947, 1951, 1960; Epling & Játiva 1963, 1966, 1968; Epling & Mathias 1957). *Salvia* sect. *Macrostachyae* (Benth 1848: 322) Epling (1937: 64) is a group of South American plants characterized by the following combination of characters: presence of more or less persistent bracts, 5–9 veined upper calyx lobes, epapillate corolla tubes, long and exerted stamens and styles, entire connectives, styles with reduced posterior lobes, and complanate mericarps, often with emarginate tips (Epling 1937, 1939). The section consists of six species, five of them endemic to Peru and one distributed in Colombia and Ecuador (González-Gallegos *et al.* 2020).

As a part of a joint project between Ecuador's Instituto Nacional de Biodiversidad and Instituto de Biología of Mexico's National University (UNAM), during 2017 and 2018 we conducted four trips of botanical exploration in Ecuador, covering great part of the Andean provinces, collecting specimens of Lamiaceae. During one such trips in the province of Azuay, we found plants belonging to *Salvia* sect. *Macrostachyae* which differed from the other species of that section previously reported for Ecuador (Harley 1999), namely *Salvia macrostachya* (Kunth 1818: 298). After reviewing the morphology of these specimens, we identified it as *S. alata* Epling (1960: 147), which represents an addition to the sage flora of Ecuador. In the following study, we provide expanded descriptions for *S. alata* and the similar species *S. speciosa* Presl ex Benth (1833: 272), with which it could be confused, along with an updated key to the species of *S.* sect. *Macrostachyae*.

Material and methods

Field and herbarium work:—The collected specimens were identified using the most comprehensive keys and descriptions for *Salvia* subg. *Calosphace* currently available (Epling 1937, 1939). However, since some of the species of *S.* sect. *Macrostachyae* were described by Epling after such revisions (Epling 1944, 1960), and as some specimens were collected in southern Ecuador, we also used the keys from Flora of Peru (MacBride 1960).

We studied the herbarium specimens of *S.* sect. *Macrostachyae* housed at two major Ecuadorian herbaria (QCA, QCNE) and one historical herbarium (QPLS). Additional morphological data was obtained from live plants of species belonging to *Salvia* sect. *Macrostachyae* maintained in a private collection in Mar del Plata, Argentina (<http://salvias.com.ar/>).

We compared the morphology of the involved species with the protologues and the type material requested to the PR herbarium or available in the online databases of G (<http://www.ville-ge.ch/musinfo/bd/cjb/chg>), K (<http://apps.kew.org/herbcat/navigator.do>), and LA in UC (https://ucjeps.berkeley.edu/db/types/types_table.html) herbaria.

We assembled expanded descriptions for *Salvia alata* and the similar *S. speciosa*, focusing on floral characters, and constructed an identification key to all species of *S.* sect. *Macrostachyae*.

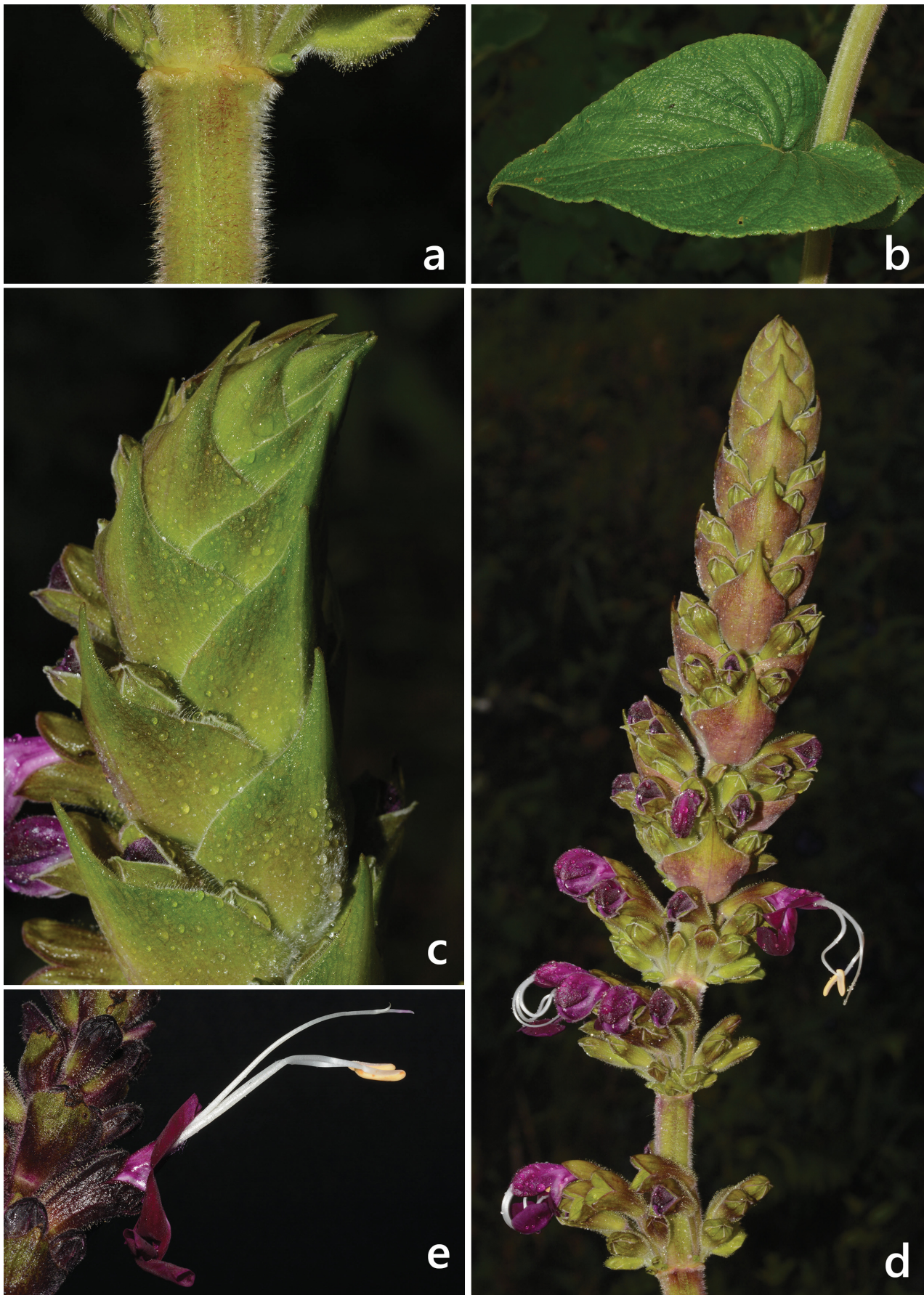


FIGURE. 1. *Salvia alata* **A** Portion of a stem covered with simple trichomes. **B** Upper leaf surface. **C** Young inflorescence with bracts. **D** Inflorescence with flowers approaching anthesis and flower buds; some of the bracts from the lower verticillasters already shed. **E** Close-up of the flower at anthesis [Photographs by G. Salazar from *I. Fragoso-Martínez et al.* 770 (QCNE)].

Taxonomy

Salvia alata Epling (1960: 147). Fig. 1

Type:—PERU. Prov. La Libertad. Santiago de Chuco, Cachicadan, rocky slopes, 2740 m, 12 May 1952, *N. Angulo 1684* (Holotype: LA in UC!).

Suffruticose subshrubs, erect, 2–4 m tall; stems fistulose, surface densely hirsute to glabrescent, with copper-colored glandular-capitate hairs. Leaves membranaceous, with densely hirsute petioles 3–10.8 cm long; leaf blades ovate-lanceolate or ovate, (8–)10–25 × 6.5–13.5 cm, apex acute, margin crenate or crenulate, base rounded, cordate or truncate, in large leaves slightly asymmetric, upper surface sparsely hirsute, lower surface densely hirtellous on the veins, with clear sessile-globose glands. Inflorescences densely crowded, terminal, racemose, 20–40 cm long, peduncles ca. 10 cm long; with 8–20 flowers per verticillaster, verticillasters 1.5–2.5(–5) cm apart, rachis densely hirsute with copper-colored or purple glandular trichomes. Bracts commonly caducous at anthesis, green or pinkish, ovate, 1.2–3 × 0.8–2.5 cm, apex acuminate, margin repand or entire, ciliate. Flowers with pedicels 0.7–2 cm long, hirsute. Calyx purple or green with purplish lobes, 1.4–1.75 cm long, base glandular-pilose, lobes hirtellous to glabrous; calyx tube cylindrical, arcuate, 1–1.3 cm long; upper lobe 5-veined, obtuse, 4.5–6.5 mm long, lower lobes acute, 3–6 mm long. Corolla fuchsia or deep purple with white nectar guides, 1.6–2.8 cm long; corolla tube epapillate, cylindrical, arcuate, 1.2–2 cm long; upper lip straight, emarginate, 0.6–1 cm long, lower lip reflexed, 4-lobate, 0.8–1.8 cm long. Stamens exerted; filaments 0.5–1.6 cm long, white, glabrous; connectives 3–5.5 cm long, white, straight, glabrate, lacking teeth; thecae yellow; staminodes 2, filiform. Style white, exerted, 4.5–6.5 cm long, glabrous, bilobate; lobes complanate, upper lobe shorter than the lower lobe; nectar gland deltoid, trilobate, ventral surface with sessile glands, 4–5.5 mm long. Mericarps oblong, complanate, winged, 4.5–5.5 mm long, black, glabrous, apex deltoid.

Distribution, habitat and phenology:—*Salvia alata* is distributed in Ecuador and Peru, where it inhabits montane forests at elevations of 2560–3224 m. Flowering occurs from August to April.

Additional specimens examined:—ECUADOR. Azuay: cantón Santa Isabel, parroquia Shaglli, 6.2 km al NE de Cebadas, vía Hornillos-Cebadas, 3224 m, 25 April 2018, 3°2'6.81"S 79°26'13.03"W, 3224 m, *I. Fragoso-Martínez et al. 770* (QCNE!). “Lacha”, 3200 m, August 1913, *L. Sodiro s.n.*, (QPLS!). PERU. Áncash: Prov. Huaraz, Baños de Chaucos, 2560 m, January 1944, *C. Sanderman, 4638* (K!).

Salvia speciosa C.Presl ex Bentham (1833: 272). Fig. 2

Type:—PERU. Huánuco, 1832, *T. Haenke 24332* (Lectotype: PR[24332]! (designated by Epling 1935); isoelectotype: K[000479427]!).

Salvia mathewsii Bentham (1835: 722). Type:—PERU. Purrochuca & Obrajilla, 1833, *A. Mathews 660* (Lectotype: K[000479426]! (designated by Epling 1935); isoelectotypes, G[00435600]!, K[000479425]!).

Suffruticose subshrubs, erect, 2.5–4 m tall; stems fistulose, green or vinaceous, surface glabrescent. Leaves membranaceous, with sparsely hirsute to glabrescent petioles, (3)5–11 cm long; leaf blade ovate to ovate-lanceolate, (6.5–)10–23 × (4.5–)6.5–13 cm, apex acute to acuminate, margin crenate-serrate or serrate, base cordate, both leaf surfaces glabrescent, in young leaves the lower surface tomentose. Inflorescences densely crowded to lax, terminal, racemose, 20–40 cm long, peduncles ca. 10 cm long; with 3–12 flowers per verticillaster, verticillasters 1.5–2 cm apart, rachis densely hirsute with white to light yellow glandular trichomes. Bracts persistent at anthesis, green or vinaceous, broadly ovate, 1.3–2.3 × 0.7–2 cm, apex caudate, margin entire, ciliate. Flowers with pedicels 0.5–1.5 cm long, hirsute. Calyx vinaceous, glaucous or green with vinaceous to almost black lobes, 1.5–1.8(–2) cm long, base glandular-pilose, lobes hirtellous or glabrescent; calyx tube cylindrical, arcuate, 1–1.2(–1.4) cm long; upper lobe 5-veined, obtuse, 3–4 mm long, lower lobes acute, 2.8–3.4 mm long. Corolla burgundy to deep purple, almost black, nectar guides as a spot near the throat, lighter than the lips, 2.4–2.7 cm long; corolla tube epapillate, cylindrical, arcuate, 1.5–1.7 cm long; upper lip straight, emarginate, 0.7–1 cm long, lower lip reflexed, 4-lobate, 1–2 cm long. Stamens exerted; filaments 5–7 mm long, burgundy or deep purple, glabrous; connectives 4.5–6.5 cm long, burgundy or deep purple, straight, glabrate, lacking teeth; thecae yellow; staminodes 2, filiform. Style burgundy or deep purple, exerted, 6–7 cm long, glabrous, bilobate; lobes complanate, upper lobe shorter than the lower lobe; nectar gland deltoid, ventral surface with sessile glands ca. 4 mm long. Mericarps oblong, complanate, winged, 4–5 mm long, tan, glabrous, apex bifurcated.

Distribution, habitat and phenology:—*Salvia speciosa* is restricted to Peru, inhabiting montane forests at elevations of 2500–3510 m. Flowering occurs from April to September.

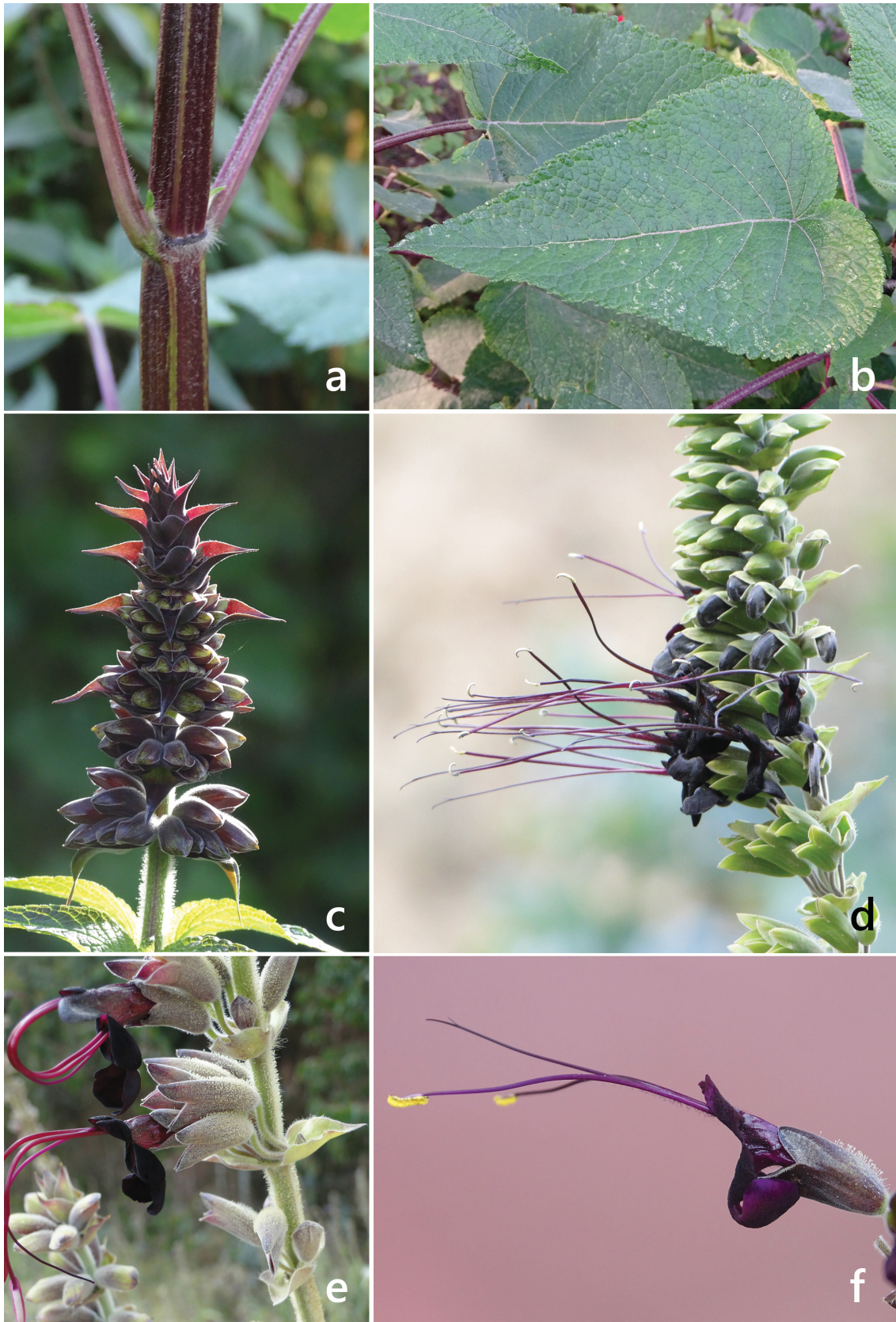


FIGURE 2. *Salvia speciosa*. **A** Portion of stem with sparse, simple trichomes. **B** Upper leaf surface. **C** Young inflorescence with bracts. **D** Inflorescence with flowers at anthesis, showing persistent bracts from the lower verticillasters. **E** Close-up of the flowers approaching anthesis. **F** Close-up of the flower at anthesis [Photographs by R. Uría from: Peru: Alrededores de Guzmango, 7°22'27"S, 78°53'28.9"W, 3050 m, 20 June 2016, R. Uría & F. Lozano Pe-16-0014; Porcón Alto, 7°4'13.7"S, 78°36'2.1"W, 3512 m, 20 June 2016, R. Uría & F. Lozano Pe-16-0023; alrededores de Huamachuco, 7°50'10"S, 78°4'9"W, 3240 m, 19 July 2016, R. Uría & F. Lozano Pe-16-0028 (live plants cultivated in the private collection of R. Uría in Mar del Plata, Argentina); R. Uría, R. Uría & F. Lozano Pe-16-0096 (MEXU)].

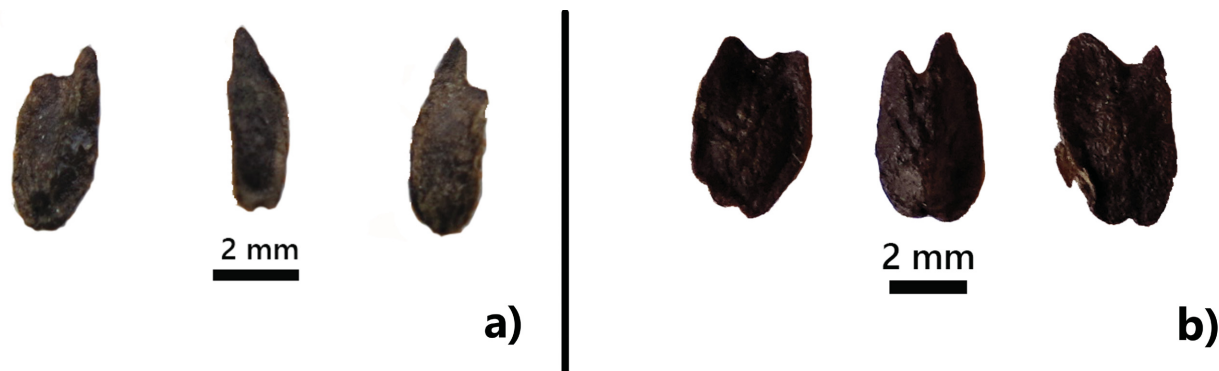


FIGURE 3. Winged mericarps of two species of *Salvia* sect. *Macrostachyae*. **A** *Salvia alata*, with a deltoid projection at the apex [*I. Fragoso-Martínez et al.* 770 (QCNE)]. **B** *Salvia speciosa*, with a bifurcated apex forming two deltoid projections [*R. Uría & F. Lozano Pe-16-0096* (MEXU)].

Additional specimens examined:—PERU. Cajamarca: Prov. Cajamarca, distrito Cajamarca, lugar Porcón Alto km 21, a unos 100 m del desvío, 3260 m, 10 June 1993, *J. Cabanillas & J. Guevara* 465 (CPUN!); El Chiche, 7°5'7.5"S, 78°23'58.5"W, 2888 m, 15 July 2016, *R. Uría & F. Lozano Pe-16-0096* (MEXU!). Prov. Contumazá, La Pampa, debajo de Guzmango, 2500 m, 24 July 1977, *A. Sagástegui & J. Mostacero* 9062 (K!). Prov. San Marcos, en la cúspide del cerro Quinua, 3200 m, 10 April 1991, *I. Sanchez Vega et al.* 5525 (CPUN!). La Libertad: Prov. Otuzco, Peña Loro (Sinsicap-San Ignacio), 2600 m, 22 April 1995, *A. Sagástegui et al.* 15681 (K!, QCA!); Prov. Santiago de Chuco, Santiago de Chuco-Cachicadán, 2700 m, 14 June 1984, *A. Sagástegui et al.* 11840 (MEXU!).

Discussion

Salvia sect. *Macrostachyae* includes six species. Four of these are endemic to Peru: *Salvia atrocalyx* (Epling 1935: 65), *S. camporum* (Epling 1944: 489), *S. psilostachya* (Epling 1935: 65), and *S. speciosa*. *Salvia macrostachya* is found both in Colombia and Ecuador (Fernández-Alonso 2003; Wood & Harley 1989) and *S. alata*, previously known only from Peru, is here recorded also for Ecuador. Two of the Peruvian species—*S. atrocalyx* and *S. camporum*—are considered critically endangered and endangered, respectively (Rodríguez 2006). The former is known only from the type collection and the latter only from a few records. The main threat factors affecting these species seems to be habitat alteration resulting from human activities such as agricultural expansion and mining activities (Fernández-Alonso & Rivera-Díaz 2006; Rodríguez 2006). Our botanical explorations in Ecuador allowed us to collect and document another little-known taxon—*Salvia unguella*—, suggesting that future field work in poorly-explored areas of both countries will likely continue to yield undescribed or little-known taxa. Thus, further fieldwork both in Ecuador and Peru is crucial to ascertain the conservation status of the species and learn more about their biology and geographical distribution.

Regarding the phylogenetic relationships of *S.* sect. *Macrostachyae*, its monophyly has not been tested yet due to taxon sampling limitations. The only species of this section that was included in the comprehensive molecular phylogenetic analysis of *Salvia* subg. *Calosphace* of Fragoso-Martínez *et al.* (2018) was *Salvia speciosa*. The resulting phylogeny, based on three molecular markers, showed that *S. speciosa* could be related to Peruvian and Ecuadorian species of *S.* sect. *Biflorae* (Benth) Epling (1937: 128). However, such relationship is pending confirmation since that clade received low support. Further work that includes a more thorough sampling of taxa and characters is needed to clarify the relationships of the Andean sages.

Salvia alata and *S. speciosa* have a similar overall morphology, which, combined with the poor type material of the former and the morphological variation occurring within each species (Figs. 1D–E; 2C–E), makes their identification challenging. The characters that are consistently useful to differentiate them are shown in Table 1. Of these, perhaps the most useful character is the morphology of the apex of the mericarp (Fig. 3). As described by Epling (1960), *S. alata* has a winged mericarp with a deltoid tip or appendage (Fig. 3A). This structure contrasts with the mericarp of *S. speciosa*, in which the tip is bifurcated, resulting in two deltoid projections (Fig. 3B).

TABLE 1. Morphological comparison between *Salvia alata* and *S. speciosa*.

Characters	<i>Salvia alata</i>	<i>Salvia speciosa</i>
Stem surface (middle portion of the stem)	Densely hirsute to glabrescent	Glabrescent
Stem color	Green to coppery	Green, sometimes vinaceous
Bract persistence at anthesis	Caducous	Persistent
Bract apex	Acuminate	Caudate
Stamen and style color	White	Deep purple or vinaceous
Mericaip apex	With a single deltoid projection	Bifurcated, with two deltoid projections

The presence of wings and appendages in the mericarps is rare in *Salvia* and only two Caribbean species of *S.* subg. *Calosphace* are known to have appendages (Zona 2017). However, no wings have been reported for the genus (Bouman & Meeuse, 1992) other than in the taxonomic treatment by Epling (1939). Generally, the wings in diaspores assist wind dispersal (Zona 2017). The presence of wings and the flattened shape of the mericarps from the species treated here (*S. alata* and *S. speciosa*; Fig. 3) are characters consistent with anemochory (Bouman & Meeuse, 1992). However, the size and weight of the mericarps are large compared to that of the wings, which could impair wind dispersal. Thus, future studies in the dispersal mechanisms of the Neotropical sages will be key to understand their biology and evolution.

We present an identification key for the species of *S.* sect. *Macrostachyae*, including the species described after Epling's (1939) revision of *S.* subg. *Calosphace*.

Key to species of *Salvia* sect. *Macrostachyae*

1. Bracts conduplicate *S. atrocalyx*
- Bracts applanate 2
2. Corolla white, occasionally with pinkish to reddish tones; stamen connectives and style pink or light red *S. psilostachya*
- Corolla blue, indigo or purple; stamen connectives and style blue, purple or white 3
3. Mericarps lacking wings; bracts caducous *S. camporum*
- Mericarps winged; bracts persistent or late caducous 4
4. Leaf blades orbicular; bracts orbicular, apex apiculate; corolla blue *S. macrostachya*
- Leaf blades ovate or ovate-lanceolate; bracts ovate, apex acuminate; corolla burgundy or deep purple 5
5. Stamen connectives and style white; apex of the mericaip entire, with a single deltoid projection *S. alata*
- Stamen connectives and style purple; apex of the mericaip bifurcated, with two deltoid projections *S. speciosa*

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References

- Alberto, C.M., Sanso, A.M. & Xifreda, C.C. (2003) Chromosomal studies in species of *Salvia* (Lamiaceae) from Argentina. *Botanical Journal of the Linnean Society*: 483–490.

<https://doi.org/10.1046/j.1095-8339.2003.t01-1-00178.x>

- Bentham, G. (1832–1836) *Labiatarum Genera et Species*. James Ridgway and Sons, London, 745 pp.
- Bentham, G. (1848) Labiatae. In: de Candolle, A. (Ed.) *Prodromus Systematis Naturalis Regni Vegetabilis*. Victor Masson, Paris, pp. 27–603.
- Bouman, F. & Meeuse, A.D.J. (1992) Dispersal in Labiatae. In: Harley, R.M. & Reynolds, T. (Eds.) *Advances in Labiate Science*. Royal Botanic Gardens Kew, Richmond. pp. 193–202.
- Epling, C. (1935–1937) Synopsis of the South American Labiatae. *Repertorium Specierum Novarum Regni Vegetabilis* 85: 1–341.
- Epling, C. (1939) A revision of *Salvia* subgenus *Calosphace*. *Repertorium Specierum Novarum Regni Vegetabilis* 110: 1–380.
- Epling, C. (1940) Supplementary Notes on American Labiatae. *Bulletin of the Torrey Botanical Club* 67: 509–534.
<https://doi.org/10.2307/2480972>
- Epling, C. (1941) Supplementary notes on American Labiatae-II. *Bulletin of the Torrey Botanical Club* 68: 552–568.
<https://doi.org/10.2307/2481456>
- Epling, C. (1944) Supplementary notes on American Labiatae-III. *Bulletin of the Torrey Botanical Club* 71: 484–497.
<https://doi.org/10.2307/2481241>
- Epling, C. (1947) Supplementary Notes on American Labiatae-IV. *Bulletin of the Torrey Botanical Club* 74: 512–518.
<http://dx.doi.org/10.2307/2481876>
- Epling, C. (1951) Supplementary Notes on American Labiatae-V. *Brittonia* 7: 129–142.
<https://doi.org/10.2307/2804702>
- Epling, C. (1960) Supplementary Notes on American Labiatae-VII. *Brittonia* 12: 140–150.
<http://dx.doi.org/10.2307/2805214>
- Epling, C. & Játiva, C. (1963) Supplementary Notes on American Labiatae-VIII. *Brittonia* 15: 366–376.
<http://dx.doi.org/10.2307/2805381>
- Epling, C. & Játiva, C. (1966) Supplementary Notes on American Labiatae-IX. *Brittonia* 18: 255–265.
<http://dx.doi.org/10.2307/2805366>
- Epling, C. & Játiva, C. (1968) Supplementary Notes on American Labiatae-X. *Brittonia* 20: 295–313.
<http://dx.doi.org/10.2307/2805687>
- Epling, C. & Mathias, M. (1957) Supplementary notes on American Labiatae-VI. *Brittonia* 8: 297–313.
<http://dx.doi.org/10.2307/2804980>
- Fernández-Alonso, J.F. (2003) Estudios en Labiatae de Colombia IV. Novedades en *Salvia* y sinopsis de las secciones *Angulatae* y *Purpureae*. *Caldasia* 25: 235–281.
- Fernández-Alonso, J.F. & Rivera-Díaz, O. (2006) Las labiadas (Familia Labiatae). In: García-Castro, N.J. & Galeano, G. (Eds.) *Libro Rojo de Plantas de Colombia. Volumen 3. Las bromelias, las labiadas y las pasifloras*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Ministerio de Ambiente, Vivienda y Desarrollo Territorial, Bogotá. pp. 385–582.
- Fragoso-Martínez, I., Martínez-Gordillo, M., Salazar, G.A., Sazatornil, F., Jenks, A.A., García Peña, M. del R., Barrera-Aveleida, G., Benítez-Vieyra, S., Magallón, S., Cornejo-Tenorio, G. & Granados Mendoza, C. (2018) Phylogeny of the Neotropical sages (*Salvia* subg. *Calosphace*; Lamiaceae) and insights into pollinator and area shifts. *Plant Systematics and Evolution* 304: 43–55.
<https://doi.org/10.1007/s00606-017-1445-4>
- González-Gallegos, J.G., Bedolla-García, B.Y., Cornejo-Tenorio, G., Fernández-Alonso, J.L., Fragoso-Martínez, I., García-Peña, M.R., Harley, R.M., Klitgaard, B., Martínez-Gordillo, M.J., Wood, J.R.I., Zamudio, S., Zona, S. & Xifreda, C.C. (2020) Richness and distribution of *Salvia* subgenus *Calosphace* (Lamiaceae). *International Journal of Plant Sciences* 181 (8): 831–856.
<https://doi.org/10.1086/709133>
- Harley, R.M. (1999) Lamiaceae. In: Jørgensen, P.M. & León-Yáñez, S. (Eds.) *Catalogue of vascular plants of Ecuador, Monographs in Systematic Botany from the Missouri Botanical Garden* 75, Missouri Botanical Press, St. Louis, pp. 519–526.
- Harley, R.M., Atkins, S., Budantsev, A.L., Cantino, P.D., Conn, B.J., Grayer, R., Harley, M.M., de Kok, R., Krestovskaja, T., Morales, R., Paton, A.J., Ryding, O. & Upson, T. (2004) Labiatae. In: Kadereit, J.W. (Ed.) *The families and genera of vascular plants. Vol 7*. Springer, Berlin, pp. 167–275.
- Jenks, A.A., Walker, J.B. & Kim, S.-C. (2013) Phylogeny of New World *Salvia* subgenus *Calosphace* (Lamiaceae) based on cpDNA (psbA-trnH) and nrDNA (ITS) sequence data. *Journal of plant research* 126: 483–496.
<https://doi.org/10.1007/s10265-012-0543-1>
- Kunth, C.S. (1818) *Nova genera et species plantarum*. The Greek-Latin-Germanic Library, Paris, 404 pp.
- Lagomarsino, L.P., Condamine, F.L., Antonelli, A., Mulch, A. & Davis, C.C. (2016) The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). *New Phytologist* 210: 1430–1442.
<https://doi.org/10.1111/nph.13920>

- Linnaeus, C. (1753) *Species plantarum*. Salvius, Stockholm, 1200 pp.
- MacBride, J.F. (1960) Labiatae. In: MacBride, J.F. (Ed.) *Flora of Peru*, Vol 13, pt V, no 2. Field Museum of Natural History, Chicago, pp. 721–829.
- Moscoso, A., Montúfar, R. & Tye, A. (2011) Lamiaceae. In: León-Yáñez, S., Valencia, R., Pitman, N., Endara, L., Ulloa Ulloa, C. & Navarrete, H. (Eds.) *Libro rojo de las plantas endémicas del Ecuador*; Publicaciones del Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito. pp. 367–371.
- Rodríguez, M. (2006) Lamiaceae endémicas del Perú. *Revista Peruana de Biología* 13: 371s–379s.
- Tank, D.C., Eastman, J.M., Pennell, M.W., Soltis, P.S., Soltis, D.E., Hinchliff, C.E., Brown, J.W., Sessa, E.B. & Harmon, L.J. (2015) Nested radiations and the pulse of angiosperm diversification: increased diversification rates often follow whole genome duplications. *New Phytologist* 207: 454–467.
<https://doi.org/10.1111/nph.13491>
- Ulloa-Ulloa, C., Acevedo-Rodríguez, P., Beck, S., Belgrano, M.J., Bernal, R., Berry, P.E., Brako, L., Celis, M., Davidse, G., Forzza, R.C., Robbert Gradstein, S., Hokche, O., León, B., León-Yáñez, S., Magill, R.E., Neill, D.A., Nee, M., Raven, P.H., Stimmel, H., Strong, M.T., Villaseñor, J.L., Zarucchi, J.L., Zuloaga, F.O. & Jørgensen, P.M. (2017) An integrated assessment of the vascular plant species of the Americas. *Science* 358: 1614–1617.
<https://doi.org/10.1126/science.aao0398>
- Wester, P. & Claßen-Bockhoff, R. (2011) Pollination syndromes of New World *Salvia* species with special reference to bird pollination. *Annals of the Missouri Botanical Garden* 98: 101–155.
<https://doi.org/10.3417/2007035>
- Wood, J. & Harley, R. (1989) The genus *Salvia* (Labiatae) in Colombia. *Kew Bulletin* 44: 211–278.
- Zona, S. (2017) Fruit and seed dispersal of *Salvia* L. (Lamiaceae): a review of the evidence. *The Botanical Review* 83: 195–212.
<https://doi.org/10.1007/s12229-017-9189-y>