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The west Mediterranean orophilous taxa of *Sideritis* L. (Lamiaceae): a new species of subsection *Hyssopifolia* from south-eastern Spain

SEGUNDO RIOS* and MANUEL B. CRESPO

Centro Iberoamericano de la Biodiversidad (CIBIO), Universidad de Alicante, Apdo. 99, E-03080 Alicante, Spain

DIEGO RIVERA

Departamento de Biología Vegetal, Facultad de Biología, Universidad de Murcia, E-30100 Murcia, Spain

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Orophilous taxa of *Sideritis* sect. *Sideritis* (Lamiaceae) are rare, although highly diversified in south-eastern Spain. Most of them belong to subsections *Hyssopifolia* and *Fruticulosa* and show very reduced distribution areas in the summits of the highest Betic mountains. The inaccessibility of their habitats has meant that many of them have been described only within the last twenty years. In this context, a new species ***Sideritis tugiensis*** is described in subsection *Hyssopifolia*, from the Oromediterranean summits of Sierra de Segura (south-eastern Spain). It is a woody, cushion-shaped plant, resembling both *S. carbonellis* Socorro (subsect. *Hyssopifolia*) and *S. glacialis* Boiss., *s.l.* (subsect. *Fruticulosa*), though important morphological divergences warrant recognition at species rank. Data on morphology, ecology and chorology of the new species are reported, and affinities and differences with regard to close taxa from other subsections are presented. Evolutionary trends in the whole aggregate are briefly discussed.

ADDITIONAL KEY WORDS: Betic mountains – biogeography – conservation – ecology – evolutionary trends – morphology – taxonomy.

INTRODUCTION

Sideritis L. sect. *Sideritis* (Lamiaceae) is endemic to the western Mediterranean and is highly diversified in the south-eastern part of the Iberian Peninsula. Most taxa of the section grow at low altitudes on rather disturbed soils, high mountain taxa being comparatively very scarce (Obón & Rivera, 1994; Rivera *et al.*, 1999). The majority of taxa of sect. *Sideritis* occur in the surroundings of the main Iberian and North African mountains.

Orophilous taxa of *Sideritis* belong to six subsections and show a clear polyphyletic origin (Rivera *et al.*, 1990; Obón & Rivera, 1994). Recently, Rivera *et al.* (1999) have presented an interesting approach to the aggregate of *S. glacialis* Boiss. and related taxa from south-eastern Spain and North Africa. They include six taxa, which grow in the summits of the Moroccan Atlas (*S. jahandiezii* Font Quer), Betic mountains of south-eastern Spain (*S. carbonellis* Socorro and *S. glacialis* subsp. *glacialis*, subsp. *vestita* Obón & D. Rivera, and subsp. *virens* (Boiss.) Obón & D. Rivera) and the southern Sistema Ibérico, eastern Spain (*S. glacialis* subsp. *fontqueriana* Obón & D. Rivera [= *S. fernandez-casasii* Roselló *et al.*]). On the basis of differences in micromorphological features of the indumentum, those taxa are currently included in two different groups, subsect. *Fruticulosa* Obón & D. Rivera (*S. fruticulosa* and *S. glacialis*, s.l.) and subsect. *Hyssopifolia* Obón & D. Rivera (*S. carbonellis*). However, they share a similar habit and similar macromorphological characters, perhaps due to convergence to the stressful climatic conditions of high mountain habitats.

In the course of field work in the Betic mountains

* Corresponding author. E-mail: rios@carn.ua.es

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of south-eastern Spain, we found populations of a peculiar plant resembling *S. carbonellis*, growing at an altitude above 2000 m on the summit of Sierra Seca (Sierra de Segura-Castril, Granada province). The site is located about 10 km from the Sierra de la Sagra, which is the classic locality of the latter taxon, an endemic orophilous plant only known from La Sagra and Baza (Granada province). Although both plants share several features, a more detailed comparison revealed the existence of very important divergences which warrant recognition of the plants from Sierra Seca as a new species. This plant has been hitherto neglected, probably due to both its relatively late flowering time (July–August) and its vegetative resemblance, after severe grazing, to other locally widespread plants such as *Satureja intricata* Lange subsp. *intricata*.

In the present paper, affinities and differences of the new taxon with regard to other Betic and Iberian orophilous taxa of *Sideritis* are presented, and data on its ecology, biogeography, phytosociology and conservation status are reported.

MATERIAL AND METHODS

Morphological features and anatomical characters were studied according to Obón & Rivera (1994) and Rivera *et al*. (1990, 1999), from fresh materials and from dried specimens. Populations from Sierra Seca were compared with specimens of seven other orophilous taxa (*S. carbonellis*, *S. hyssopifolia* subsp. *eynensis*, *S. pungens* subsp. *javalambrensis*, and four subspecies of *S. glacialis*), held at the herbaria MUB and ABH. The results are presented in Table 1. The accepted systematic arrangement of *Sideritis* follows proposals by Obón & Rivera (1994).

Authorities of plant names follow Brummitt & Powell (1992). Acronyms of herbaria are those in Index Herbariorum and its supplement (Holmgren, Holmgren & Burnett, 1990; Holmgren & Holmgren, 1993). Bioclimatical and biogeographical features are presented according to Rivas-Martínez (1997).

For all cited herbarium sheets, collection sites are referred to the 1 km side network grid of the Universal Transverse Mercator (U.T.M.) system.

RESULTS

Sideritis tugiensis Ríos, M. B. Crespo & D. Rivera **sp. nov.**

(Sect. *Sideritis* subsect. *Hyssopifolia* Obón & D. Rivera)

Planta pulviniformis, basi valde lignosa. Caules erecti, ramosi, indumento pilis holotrichis heterotrichisque, semper quidem antrorsis necnon brevissimis (0.2–0.6 mm), laxe vestiti. Folia virescentia, oblongo-lanceolata, 12–17 × 2–3 mm, 2-4-dentata (raro integra), acuta atque ad apicem breviter mucronato-apiculata, quae per anthesin conspicuos fasciculos axillares saepissime ferunt; duo suprema bracteiformia, itaque quam contigua inferiora latiora magisque dentata. Inflorescentia brevissima (0.7–2.5 cm, raro 4 cm), globosa vel ovoidea, nonnunquam 1–2-verticillastris (rarissime 4-verticillastris) congestis usque ad 3–6(–10) mm tantum distantibus constituta; axis inflorescentiae numerosis glandulis sessilibus atque pilis eglandulosis antrorsis brevibusque (0.25–0.75 mm) obtectus. Bracteae ovato-deltoideae, latitudine maxima e tertio basali, mediae pagina adaxiali glabra, omnes profunde spinoso-dentatae, dentibus marginalibus quidem ad dimidium latitudinis bracteae attingentibus, apicali usque ad 2.5 mm producto. Calyces 6–7 mm longi, glandulis sessilibus atque pilis eglandulosis longis (0.8–1.5 mm) dense vestiti; carpostegium discontinuum, quod cum dentibus alternans. Corolla 8–9 mm longa, saturate flavescens, labio superiore certe bifido, lobulis leviter crenatis. Stamina brevissima, cum antheris fuscis necnon filamentis 0.3 (–0.5) mm tantum longis. Stylus *c.* 3 mm longus. Nuculae *c.* 1.5 mm longae.

Planta similis *Sideritide carbonellis*, a qua indumento pilis antrorsis brevissimis (0.2–0.6 mm longis), inflorescentia congesta brevique convenit, sed ab illa differt inter multos alios characteres indumento caulium heterotricho, foliis minoribus, latioribus et dentatis (in illa multo longioribus, linearibus integerrimisque), axibus inflorescentiarum cum glandulis numerosis sessilibus necnon pilis eglandulosis dimidio brevioribus, bracteis e tertio basali magis profunde dentatis, atque calyces majoribus confertim pilosis.

Habitat. In dumosis pulvinatis, radicibus demissis in solum arenosum dolomiticum, ad colles apricos lapidososque cacuminum oromediterraneorum loco dicto Cerro Laguna-Sierra Seca (e Sierra de Segura), prope Castril, in provincia Granatensi, ex Hispania austro-orientali.

Derivatio. Nomen speciei loco dicto "Saltus Tugiensis" spectat, qui Romani donaverunt ad terram ubi fontes fluminum Taderis (nunc Segura) et Baetis (nunc Guadalquivir) dictorum sunt.

Holotype. Hispania, GRANADA: Castril, loco dicto Cerro Laguna-Sierra Seca (Sierra de Segura), U.T.M.: 30SWG2799, ad 1980 m alt., ubi die 27.vii.1998 legerunt *S. Ríos, M. B. Crespo, J. L. Solanas* & *E. Camuñas, s.n.* Asservatus est in Herbario Universitatis Lucentinae (ABH num. 43003).

Table 1. Comparison of *Sideritis tugiensis* sp. nov. with other closely related taxa, showing similar features and habitats. Other data from Obón & Rivera (1994) and Rivera *et al.* (1999)

Characters	*S. tugiensis* sp. nov.	*S. carbonellis* O. Socorro	*S. pungens* Benth. subsp. *javalambrensis* (Pau) Obón & D. Rivera	*S. hyssopifolia* L. subsp. *eynensis* (Sennen) Malag.	*S. glacialis* Boss. subsp. *glacialis*	*S. glacialis* Boiss. subsp. *virens* (Boiss.) (Obón & D. Rivera	*S. glacialis* Boiss. subsp. *vestita* Obón & D. Rivera	*S. glacialis* Boiss. subsp. *fontqueriana* Obón & D. Rivera
Arrangement of hair covering at base of branchlets	Holotrichous	Holotrichous	Goniotrichous to holotrichous	Goniotrichous to holotrichous	Holotrichous	Holotrichous	Holotrichous	Holotrichous
Type of hair covering at base of branchlets	Heterotrichous	Heterotrichous	Heterotrichous	Homotrichous	Homotrichous	Heterotrichous	Heterotrichous	Homotrichous
Hair length	(0.2–) 0.4 (–0.8) mm	(0.4–) 0.6 (–0.8) mm	0.5–1.3 mm	0.8–1.2 mm	1.5–2.0 (–2.5) mm	(0.8–) 1.0–1.2 mm	1.0–1.5 mm	1.0–1.5 mm
Number of cells forming the hairs	2–3 (4)	1–2	2–3	1–3	2	1–2	2–3	1–2
Type of cells forming the hairs	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Band-shaped
Type of apical cell of hairs	Conical	Conical	Conical	Conical	Band-shaped or conical	Band-shaped	Band-shaped or conical	Band-shaped
Lower leaves: size (mm)	12–17 × 2–3	10–25 × 1–1.5	10–20 × 2	8–12 × 2–4	5–10 (15) × 1–2 (3)	10–17 × 2–3 mm	5–15 × 2–4	4–9 × 1–2
Lower leaves: margin	Dentate	Entire	Entire	Entire	Entire	Entire	Dentate	Entire
Lower leaves: arrangement of trichomes at margin	Indistinct, except in the basal part of leaves	Clearly distinct	Clearly distinct	Clearly distinct	Indistinct	Indistinct	Clearly distinct to indistinct	Indistinct
Uppermost leaves	Bract-like, with 0–4 teeth	Similar to the lower, exceptionally with 1 tooth	Similar to the lower or narrower	Similar to the lower	Similar to the lower	Similar to the lower	Similar to the lower or narrower	Similar to the lower
Axillary fascicles during flowering time	Very frequent	Absent	Occasional	Occasional	Absent	Occasional	Occasional or frequent	Absent
Number of verticillasters	1–2 (–4)	1–3 (–5)	3–10	(1–) 2–4	2–3 (–4)	2–4	2–4	1–5
Distance of internode between central verticillaster	3–6 mm	5–6 mm	3–7 mm	2–3 (–4) mm	4—10 mm	7–9 mm	(4–) 6–8 (–9) mm	2 mm
Shape of the inflorescence	Ovoid or globose	Ovoid or globose	Cylindrical	Ovoid or globose	Ovoid or globose	Cylindrical	Cylindrical	Ovoid or globose
Inflorescence length (cm)	0.7–2.5	0.5–1.5 (–2)	1.0–6.0	1.0–3.0	0.5–2.0 (–3)	1.5–4.5	1.0–4.0	1.5–2.0
Inflorescence axis: density of glands	Very abundant	Absent	Very scarce	Absent	Very scarce	Very scarce	Scarce	Absent
Inflorescence axis: direction of trichomes	Antrorse	Antrorse	Antrorse or patent	Antrorse	Antrorse or patent	Antrorse	Patent, seldom deflexed	Antrorse
Inflorescence axis: trichomes length (mm)	0.25–0.75	1.2–1.4	1.0–2.0	0.8–1.2	0.8–1.0	0.8–1.5	1.0–1.5 (2.0)	1.0
Lower bract size (mm)	4.5–5.5 × 6–8	5–6 × 4–7	7–12 × 9–12	4–6 × 3–5 (7)	4–5 (6) × 5–7 (8)	5–7 × 7–9	7–10 × 7–10	5–7 × 7–8
Teeth on each side of the lower bracts	2–4 (–5)	2–3 (–5)	4–7	0–2 (–5)	3–4	2–3	3–5	2–5
Lower bracts: greatest width	1/3 above the base	1/2 above the base	1/8–1/4 above the base	1/4–1/2 above the base	1/3–1/2 above the base	1/3 above the base	1/3–1/2 above the base	1/3 above the base
Division of lower bracts	1/2	1/4	1/3	0–1/3	1/3	1/3–1/2	1/3–1/2	1/4
Middle bracts size (mm)	4–5 × 6–7	4–5 × 5–6	6–8 × 10–13	5–6 × 7–8	4–7 × 6–8 mm	6–7 × 9–10	5–7 × 8–11	5–6
Number of teeth on each side of middle bracts	3–6	2–3 (5)	4–7	5	3–5	4–6	4–6	3
Adaxial surface of middle bracts	Glabrous	Glabrous	Glabrous	Glabrous	Less densely hairy than abaxial	Less densely hairy than abaxial	Less densely hairy than abaxial	Glabrous
Calyx length (mm)	6–7	7–8	7–8	6–7	6–7	(7) 8– (9)	6–7	5–7
Calyx: density of glands	Abundant	Scarce or abundant	Scarce	Scarce or absent	Scarce or very scarce	Scarce or very scarce	Very scarce	Scarce or abundant
Calyx: density of trichomes	Abundant	Scarce	Very scarce	Scarce	Scarce or abundant	Abundant	Abundant	Abundant
Calyx: length of trichomes (mm)	0.8–1.5	0.9–1.1	0.9–1.1	1.0–1.5	(1.0) 1.5–2.0	1.4–1.6	1.0–1.5	1.0
Corolla length (mm)	8–9	7–10	7–9	10	9	9–11	10–11	6
Corolla: upper lip	Bifid	Emarginate or notched	Emarginate or notched	Entire or emarginate	Emarginate	Emarginate	Emarginate	Emarginate
Stamens: filament length (mm)	0.3 (0.5)	0.8	1	1	0.8	1	1	1
Style length (mm)	3–3.1	1.8–2.2	2–3	3–4	1.8–2.2	3–4	2–3	2–3

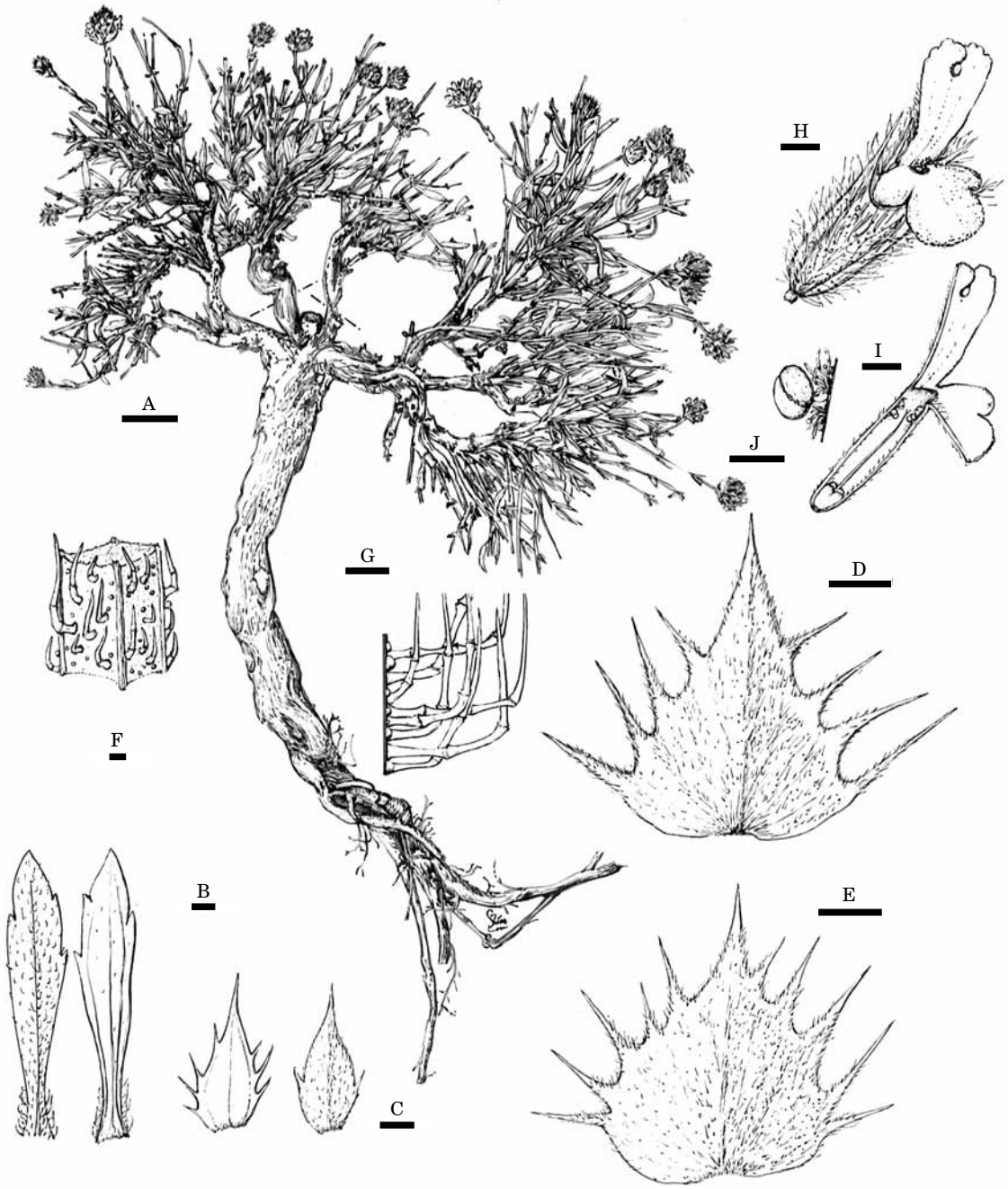

Figure 1. ***Sideritis tugiensis*** **sp. nov.** (holotype): A, habit. B, lower leaves. C, upper leaves. D, lower bract. E, middle bract. F, base of branchlet showing hair covering. G, inflorescence axis showing hair covering. H, calyx and corolla. I, longitudinal section of the corolla. J, stamen. Scale bars, a = 1 cm; b–e, h–j = 1 mm; f, g = 0.1 mm.

Isotypes. ABH (num. 43004, 43005, 43006), MA, MUB.

Illustration. See Fig. 1.

Detailed description

DWARF SHRUB, cushion-shaped. Woody basal parts up to 15 cm including branches. Non-woody branches ascending to 7–10 cm. Branchlets with a holotrichous, heterotrichous hard covering at the base, with glands scarce to abundant and lacking glandular hairs; trichomes scarce, antrorse (exceptionally some trichomes somewhat patent), 0.2–0.6 mm long, with 2–3(4) cells cylindrical, the apical one conical. LEAVES greenish oblong-lanceolate, 12–17 × 2–3 mm, bi- to quadradentate (rarely entire), apiculate or mucronate at the apex, the uppermost bract-like, the lowermost rarely entire; indumentum lax, with eglandular hairs

0.2–0.3 mm long, patent only at the basal part of leaves, always lacking glandular hairs and with scarce sessile glands; axillary fascicles of leaves commonly present at the flowering time. INFLORESCENCE commonly yellowish or greenish, ovoid to globose, 0.7–2.5 cm (rarely up to 4 cm) long, with 1–2 verticillasters (very rarely up to 4), the central 3–6 mm apart (rarely up to 10 mm); axis usually yellow-tinged at the angles, with very abundant sessile glands and antrorse eglandular hairs 0.25–0.75 mm. BRACTS yellowish or greenish, erect-patent, ovate, with the widest part towards its basal third; adaxial surface glabrous, abaxial with abundant sessile glands and eglandular hairs 0.25–0.65 mm long, formed by 3–4 cylindrical cells, the apical one conical; lower bracts 4.5–5.5 × 6–8 mm, with 2–4 teeth on each side reaching half way to midrib; middle bracts 4–5 × 6–7 mm, divided to 1/3–1/2 of its width, with 3–6 teeth on each side. VERTICILLASTERS 6-flowered. CALYX campanulate, 6–7 mm long, with five subequal divergent teeth, 1–2 mm, ending in short spines 0.5–1 mm; the outer surface with abundant sessile glands and eglandular hairs 0.8–1.5 mm long; carpostegium discontinuous, alternate to teeth. COROLLA yellow, 8–9 mm; upper lip bifid up to 1/3–1/2 of its length; STAMENS included in the corolla tube, with short filaments 0.3–0.5 mm long; style up to 3.1 mm long. NUTLETS ovoid, *c.* 1.5 mm.

Phenology. Flowering in late July, and August. Seed maturing in September.

Other specimens examined

Spain, GRANADA: Castril, near Cañada de la Sabina, 30SWH2800, 1800 m, 13.vii.2000, *S. Ríos, J. L. Solanas* & *M. B. Crespo* (ABH 43660). Castril, near Morro del Pocico o de los Cánovas, 30SWG2697, 2030 m, 13.vii.2000, *S. Ríos, J. L. Solanas* & *M. B. Crespo* (ABH 43658). Castril, Morro del Buitre, 30SWG2595, 2130 m, 13.vii.2000, *S. Ríos, J. L. Solanas* & *M. B. Crespo* (ABH 43662). Huéscar, Mojón Alto o Tornajuelos, 30SWG2696, 2100 m, 13.vii.2000, *S. Ríos, J. L. Solanas* & *M. B. Crespo* (ABH 43659). Huéscar, Torca de la Nieve, 30SWG2595, 2060 m, 13.vii.2000, *S. Ríos, J. L. Solanas* & *M. B. Crespo* (ABH 43661).

Habitat and distribution

High mountain screes and slopes, 1800–2130 m altitude, in sites strongly influenced by winds and subject to frequent grazing in summer by goats and sheep. Mean temperatures below 0°C occur at least 4 to 5 months. Snow may lie on the ground at least 60 days of the year.

Sideritis tugiensis grows on dolomitic, stony or sandy soils, sometimes on dune-like formations, to which it is fairly well adapted due to its peculiar root system (Fig. 1). It is confined to the Oromediterranean summits of Sierra Seca, in the Sierra de Segura mountain range, near Castril and Huéscar (Granada province, south-eastern Spain). Sierra Seca is a high plateau about 10 km long by 2 km wide, which includes seven peaks over 2000 m altitude with the highest summit 2141 m. This area is more elevated than other well-known summits of the neighbouring territories, such as Sierra de la Grillimona (2064 m) or the Cazorla-Castril mountains (e.g. Sierra de Empanadas, 2106 m; Sierra de la Cabrilla, 2041 m; Pico Cabañas, 2028 m; Sierra del Buitre, 2020 m). Only the adjacent Sierra de la Sagra (2383 m) is higher. However, Sierra Seca is a very vast territory including low valleys, small meadows, and springs. Erosion of underlying rocks produces red clays which fill up depressions and hollows, as well as white dolomite sands mixed with quartz grains, which accumulate and form dune-like deposits several metres deep. Hitherto, no *Sideritis* populations have been found in the neighbouring localities having similar ecological conditions (e.g. Sierra de la Grillimona, Sierra de Empanadas, Sierra de la Cabrilla, or Sierra del Almorchón). However, references to *Sideritis glacialis* in Sierra de Cazorla (Hervier, 1907), could likely correspond to *S. tugiensis*, though no herbarium materials of those collections have been found.

Phytosociology

Sideritis tugiensis grows in plant communities belonging to the series of the Oromediterranean calcicolous Betic 'pinar-sabinar' (*Daphno hispanicae-Pineto sylvestris Sigmetum pinetoso clusianae Sigmetosum*), together with other shrubs such as *Juniperus sabina* L., *Juniperus communis* L. subsp. *hemisphaerica* (C. Presl) Nyman, *Berberis hispanica* Boiss. & Reut., *Vella spinosa* Boiss., *Genista longipes* Pau subsp. *longipes, Satureja intricata* Lange subsp. *intricata, Helianthemum canum* (L.) Baumg., *H. croceum* (Desf.) Pers. subsp. *cavanillesianum* M. Laínz, or *Teucrium angustifolium* (Willk.) J. B. Peris *et al.*, and some caespitose plants such as *Festuca hystrix* Boiss., *F. segimonsis* Fuente, J. Müller & Ortúñez, Poa ligulata Boiss., *Convolvulus boissieri* Steud., *Hedysarum costae-talensii* López Bernal *et al.* or *Thymelaea granatensis* Pau ex Lacaita. It commonly forms part of open pinewoods (*Daphno hispanicae-Pinetum sylvestris* Rivas Mart. 1964 subass. *pinetosum clusianae* Rivas Goday 1968), cushion-shaped scrubs (*Saturejo intricatae-Velletum spinosae* Rivas Goday 1968 corr. Alcaraz *et al.* 1991) and sometimes dense grasslands (*Minuartio-Poion ligulatae* O. Bolòs 1962). Occasionally, it grows in dolomitic, saxicolous communities belonging to *Platycapno saxicolae-Iberidion granatensis* Rivas Goday & Rivas Mart. 1963).

Conservation

Over 10 000 individuals flowering and fruiting normally were estimated, forming well constituted populations, which are difficult to reach by motor vehicles and are not seriously threatened. However, during summer they endure a severe grazing by wild and domestic herbivores (goats and sheep) that reduces dramatically the biomass produced every year by the population. Consequently, *S. tugiensis* should be labelled as 'vulnerable' (VU) according to the I.U.C.N. categories (1994). Conservation measures should include controlling motor vehicle access, together with the reduction of grazing pressure. Meanwhile, seeds of the new species have been stored at the seed bank of the Centro Iberoamericano de la Biodiversidad (University of Alicante), and living plants are also grown at the teaching gardens of the University of Alicante.

DISCUSSION

TAXONOMIC RELATIONSHIPS

Sideritis tugiensis shares morphological features with other orophilous taxa from subsections *Hyssopifolia* Obón & D. Rivera and *Fruticulosa* Obón & D. Rivera (Table 1). On one hand, it resembles *S. carbonellis* mainly in its general habit, type of inflorescence and indumentum features of the vegetative parts. Both taxa grow in similar habitats in a reduced geographical area. However, they can be clearly separated by more than ten morphological characters, including leaf and bract morphology, flower features, and the hairy covering of the floral parts (Table 1, Fig. 1). On the other hand, it rather closely resembles the group of *S. glacialis* (*s.l.*) in the heterotrichous, holotrichous indumentum, which is more dense on the calyx. *Sideritis tugiensis* is similar to *S. glacialis* subsp. *vestita* in its dentate leaves, short inflorescence and in having axillary fascicles. It resembles subsp. *virens* in its leaf dimensions and short trichomes, that give a general greenish colour to the leaves. It is similar to subsp. *glacialis* in the characters of the deeply toothed lower and middle bracts. It also resembles subsp. *fontqueriana* in the short inflorescence with crowded verticillasters, and the glabrous adaxial surface of the middle bract (unique in the *S. glacialis* aggregate). However, *S. tugiensis* has several unique characters (e.g. uppermost leaves bract-like, filaments of stamens almost absent, and upper lip of corolla deeply bifid), which taken together warrant its recognition at species rank.

Within the current infrasectional arrangement of sect. *Sideritis* (cf. Obón & Rivera, 1994), *S. tugiensis* should be included in subsect. *Hyssopifolia*, because of its indumentum of short, rigid hairs with cylindrical cells. This feature separates it from subsect. *Fruticulosa*, in which the hairs are longer and have the apical cells (and sometimes most of them) band-shaped. However, the new species combines macromorphological characters of taxa from both subsections, as mentioned previously. On the one hand, this fact can be determined by the stressful climatic conditions of its high mountain habitat, which could perhaps explain the existence of analogies, probably due to convergence. On the other hand, *S. tugiensis* can be interpreted as a connecting link between both subsections.

EVOLUTIONARY TRENDS

Section *Sideritis* has a centre of diversity in the southeastern part of the Iberian Peninsula and west North Africa, with 16 subsections and over 60 species (Obón & Rivera, 1994; Rivera & Obón, 1997). Most taxa of the currently accepted subsections grow at low altitudes. Thus, taxa of subsect. *Glauca* D. Rivera & Obón, and subsect. *Leucantha* D. Rivera & Obón, are always found below 1500 m altitude (Rivera & Obón, 1997). Conversely, some subsections (e.g. Subsect. *Borgiae* Obón & D. Rivera, and Subsect. *Lurida* Obón & D. Rivera) group plants growing only on high mountain habitats, whilst others (e.g. Subsect. *Hyssopifolia* and Subsect. *Fruticulosa*) include both high altitude and low altitude taxa.

Adaptation of taxa of sect. *Sideritis* to high mountain habitats is probably polyphyletic, mostly originating from low altitude ancestors (Rivera *et al.*, 1999). The increasing aridity of climate in the Mediterranean Basin during the late Miocene (Bocquet, Wilder & Kiefer, 1978), together with the emergence of newly created high mountain habitats (e.g. Pyrenees, Cordillera Cantábrica, Ibérica and Bética in Spain, and Rif Mountains in Morocco) produced a new scenario for evolutionary radiation. Plants needing more humid conditions were forced to migrate to more favourable habitats. Some groups moved northwards where temperate climatic conditions persisted. Others colonized the new high mountain habitats where the summer drought should be less dramatic due to orographic rains.

In the first case, the sub-Mediterranean or Atlantic conditions of climate combined with the abrupt orography of the territories allowed a rather intense speciation process. This is still active and has resulted in the differentiation of populations at lower taxonomic ranks, currently accepted as subspecies (Fig. 2). This is the case in subsect. *Hyssopifolia*, which is highly diverse (15 taxa) in the northern half of the Iberian Peninsula, and only includes five taxa in the Betic territories. *Sideritis hyssopifolia* is divided into 11 subspecies, of which only one (subsp. *eynensis* Obón & D. Rivera) is exclusively restricted to high mountain

Table 2. Key for identification. The following key includes orophilous taxa of Subsect. *Hyssopifolia* and Subsect. *Fruticulosa* from only high mountain habitats of Spain

1.	Plant whitish. Indumentum of rather soft and long trichomes (up to 2.5 mm). Hairs with at least the apical cells band-shaped 2
1′.	Plant greenish. Indumentum of rather rigid and short trichomes (up to 1.5 mm). Hairs with cells cylindrical, never band-shaped 5
2.	Adaxial surface of bracts glabrous; abaxial surface lacking sessile glands, covered with abundant hairs 0.8–1.2 mm. Internode between central pair of verticillasters 2 mm. Calyx up to 5 mm, covered with hairs up to 1 mm; carpostegium continuous to discontinuous ..... *S. glacialis* subsp. *fontqueriana*
2′.	Adaxial surface of bracts pilose; abaxial surface with some sessile glands and scarce to abundant eglandular hairs 0.7–3 mm. Internode between central pair of verticillasters 4–9 mm. Calyx 6–9 mm, covered with hairs 1–2 mm; carpostegium always discontinuous 3
3.	Leaf hairs 1–1.2 mm. Bract hairs 0.7–1.2 mm long. Calyx 8–9 mm ..... *S. glacialis* subsp. *virens*
3′.	Leaf hairs 1.5–2.3 mm. Bract hairs 1–3 mm long. Calyx 6–7 mm 4
4.	Bract hairs 1–1.4 mm. Corolla 10–11 mm ..... *S. glacialis* subsp. *vestita*
4′.	Bract hairs 2 3 mm. Corolla 9 mm ..... *S. glacialis* subsp. *glacialis*
5.	Base of branchlets holotrichous, covered with very short hairs up to 0.8 mm. Inflorescence usually dense, shortly ovoid to globose, frequently with 1–3 verticillasters 6
5′.	Base of branchlets goniotrichous to holotrichous, covered with hairs 0.8–1.5 mm. Inflorescence usually long, cylindrical, with up to 12 verticillasters 7
6.	Lower leaves entire, 10–25 × 1–1.5 mm, axillary fascicles absent at the flowering time; uppermost leaves similar to the lower, entire. Calyx with scarce trichomes ..... *S. carbonellis*
6′.	Lower leaves dentate, 12–17 × 2–3 mm, axillary fascicles commonly present at flowering time; uppermost leaves bract-like, with 0–4 teeth on each side. Calyx with abundant trichomes ..... ***S. tugiensis* sp. nov.**
7.	Carpostegium discontinuous. Lower leaves lanceolate to oblanceolate, acute and apiculate. Internode between central pair of verticillasters 3–7 mm long ..... *S. pungens* subsp. *javalambrensis*
7′.	Carpostegium generally continuous. Lower leaves spathulate, obtuse not apiculate. Internode between central pair of verticillasters shorter than 3 mm or longer than 7 mm 8
8.	Plants cushion-shaped or decumbent, with short branches up to 15 cm tall 9
8′.	Plants erect or decumbent, with long branches 15–60 cm tall 10
9.	Lower bract 3–6 mm. Middle bract ovate, 3–7 mm long, with 5 teeth on each side ..... *S. hyssopifolia* subsp. *eynensis*
9′.	Lower bract 6–20 mm. Middle bract ovate to trullate, 7–10 mm long, with 3–5 teeth on each side ..... *S. hyssopifolia* subsp. *santanderina*
10.	Plants decumbent, 15–35 cm high. Corolla 10–12 mm. Glandular hairs scarce to very scarce ..... *S. hyssopifolia* subsp. *caureliana*
10′.	Plants erect, 25–60 cm high. Corolla 5–10 mm. Glandular hairs absent 11
11.	Internode between central pair of verticillasters 5–20 mm. Middle bract 5–12 mm. Leaf trichomes 0.5–1.0 mm ..... *S. hyssopifolia* subsp. *hyssopifolia*
11′.	Internode between central pair of verticillasters 1–5 mm. Middle bract 3–6 mm. Leaf trichomes 0.2–0.9 mm ..... *S. hyssopifolia* subsp. *nocedoi*

habitats in the eastern Pyrenees (Obón & Rivera, 1994; Rivera *et al.*, 1999), while the others grow over a wide altitudinal range. *Sideritis hyssopifolia* subsp. *hyssopifolia* is widespread from northern Spain (eastern Pyrenees) to Italy (Alps, Tuscany and Sicily), from 300 to 2000 m. Other morphologically close subspecies that have evolved in mountain areas from north-western Spain (e.g. subsp. *santanderina* Obón & D. Rivera, subsp. *nocedoi* Obón & D. Rivera, and subsp. *caureliana* Obón & D. Rivera) also range from 300 to 2500 m. Introgressive populations can be found commonly in wide contact zones where two of these taxa meet, making identification difficult. This fact supports recognition of all these taxa at the subspecies rank rather than as full species (see Table 2 for key).

The situation in the Betic mountains of south-eastern Spain is quite different. Taxa of *Sideritis* subsect. *Hyssopifolia* are restricted to the summits of the highest mountains. These sites have functioned as islands on which many populations have remained fully isolated from each other and have evolved under peculiar local climates, giving rise to new taxa which are morphologically well defined and exhibit very reduced distributions. In the more arid lowlands, no taxa of subsect. *Hyssopifolia* are currently found. Probably they were replaced by other groups better adapted to endure the Mediterranean climate (e.g. Subsect. *Leucantha*), with which no introgressive forms have been found to date. *Sideritis carbonellis* is endemic to a few localities in the Sierra de Baza and Sierra de la

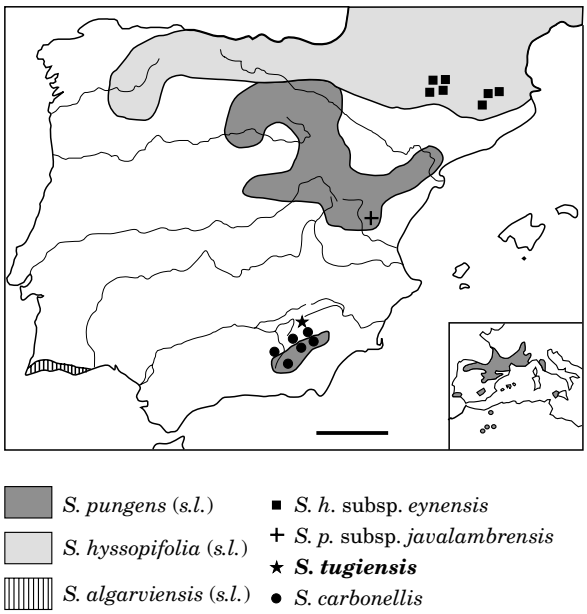

Figure 2. Taxa of subsect. *Hyssopifolia*. Distribution of the Iberian taxa of the subsection (shadowed areas) and details of the exclusively orophilous ones. Inset, distribution of the whole subsection in the west Mediterranean.

Sagra (Fig. 2), always growing on dolomitic stony soils between 1500 and 2200 m altitude. It shows a peculiar combination of morphological characters which allows easy identification. A similar pattern is found in *S. tugiensis*, a plant growing on dolomitic sandy soils above 1800 m, only 10 km away from the classic locality of the former species (Sierra de la Sagra). However, despite the proximity to the range of *S. carbonellis*, ecological and morphological characteristics of *S. tugiensis* support its recognition at species rank (Table 1).

Both Betic taxa, together with those from subsect. *Fruticulosa* (*S. glacialis, s.l.*), are perhaps relictual and are indeed threatened with extinction if changes in land use or an increase of browsing are not controlled. Further research on the highest mountains of southeastern Spain is still needed to achieve a full understanding of the evolutionary patterns followed by these taxa and other related ones still unknown.

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