Botanical Journal of the Linnean Society (1999), *129:* 249–265. With 9 figures
Article ID: bojl.1998.0217, available online at http://www.idealibrary.com on IDEAL

Systematics of the high mountain taxa of the genus *Sideritis* L. section *Sideritis*, subsection *Fruticulosae* Obón & D. Rivera (Lamiaceae)

D. RIVERA* FLS, C. OBON FLS, F. ALCARAZ AND R. LLORACH

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

Received July 1993; accepted for publication October 1998

Section *Sideritis* is an extremely diversified group which is formed mainly by species growing at low altitude. The group of high altitude taxa of this section is polyphyletic and has been taxonomically divided in different subsections in which these taxa appear normally associated with low-lying planitiary ones, the latter being the probable ancestors. The subsections comprising high altitude taxa are: subsect. *Gymnocarpae*, subsect. *Fruticulosae*; subsect. *Hyssopifoliae*, subsect. *Luridae*; subsect. *Borgiae* and subsect. *Aranensis*. Most of the high altitude taxa of section *Sideritis* are endemics with small distribution areas; they are incompletely known and threatened with extinction. The upper altitude limit of this section is attained at over 3000 m in Sierra Nevada (Spain) by *Sideritis glacialis* Boiss., which has been included in subsect. *Fruticulosae* Obón and D. Rivera. The taxonomy of this complex group of high altitude endemic taxa of *Sideritis* subsection *Fruticulosae* is discussed on the basis of macromorphological and micro-morphological characters. These are used in identification keys and for analysis of dissimilarity. The different habitats, allied species and plant communities are described. The following taxa are recognized: *Sideritis glacialis* subsp. *glacialis*, *S. glacialis* subsp. *vestita*, *S. glacialis* subsp. *virens* and *S. glacialis* subsp. *fontquerii*.

ADDITIONAL KEY WORDS:—biogeography – ecology – Gúdar – Labiatae – phylogeny – Sierra Nevada – Spain – taxonomy.

CONTENTS

Introduction 250
Historical background 250
Related taxa 251
Infraspecific variability 252
Role and place in montane and alpine vegetation 252
Discussion 253
Keys 257
Hair covering 257
Macromorphology 257

* Corresponding author. Email: drivera@fcu.um.cs

0024–4074/99/030249+17 $30.00/0

Descriptions of taxa 257
Acknowledgements 264
References 265

INTRODUCTION

The present paper is a part of a general taxonomic revision of *Sideritis* L. section *Sideritis*, undertaken by Obón and Rivera since 1985, and treated in depth by Obón & Rivera (1994). The presence of *Sideritis* species in high altitude habitats of the western Europe and North Africa is relatively uncommon. Several species of subsection *Gymnocarpae* Font Quer, are found at over 3000 m in the Atlas Mountains of Morocco. In Spain subalpine habitats, or their Mediterranean counterparts (crioro – Mediterranean), are colonized by several species of subsections *Fruticulosae* Obón & D. Rivera, *Hyssopifoliae* Obón & D. Rivera; *Borgiae* Obón & D. Rivera, *Luridae* Obón & D. Rivera and *Aranensis* Obón & D. Rivera. Subsection *Fruticulosae* includes the species reaching the highest altitude of subgenus *Sideritis: S. glacialis*, with 3300 m in Sierra Nevada (Spain).

Historical background

The shepherds of the Spanish Sierra Nevada were well acquainted with the '*samarrilla blanca*' a long time before botanists reached the area. This common name was recorded by Boissier (1841) as being used for *Sideritis glacialis*, although González-Tejero (1992) recently recorded '*zahareña*' for the same species. This group of montane taxa remained unknown to science until the exploration of the Spanish mountains during the nineteenth century. *Sideritis glacialis* was found by Edmond Boissier during his first voyage in Spain in August 1837; he collected it in several localities in the Sierra Nevada (Loma del Panderón) and Sierra de Tejeda and the specimens are kept in the Boissier Herbarium in Geneva (G-BOISS). In our opinion the collections of Boissier were mixed gatherings, with specimens of three different subspecies (according to Boissier, 1841): subsp. *virens*, subsp. *glacialis* and subsp. *vestita*. However, at G-BOISS only intermediate specimens of the type subspecies are extant. The lectotype chosen by Burdet, Charpin & Jacquemoud (1987) attached the name to the cushion-shaped variants of the species, which appear almost silvery because of their abundant covering of long hairs. It could seem that the choice of lectotype made by Burdet, Charpin & Jacquemoud (1987) was not appropriate, because Boissier (1841), recognizing a true gradient of forms and indumenta between subsp. *virens–vestita–glacialis*, explicitly said his name *S. glacialis* was reserved for the extremely silvery forms: "et la variété *vestita* qui est d'autant plus velue qu'elle habite des stations plus élevées. Lorsqu'elle est toute couverte d'un épais duvet de poils argentés on la prendrait pour une espèce distincte, et c'est en cet état que je l'avais d'abord décrite sous le nom de *S. glacialis*". In this case, a more extreme specimen among the syntypes would have been a better choice; but a careful examination of the syntypes reveals that the extreme forms, which are relatively scarce in the Sierra Nevada (restricted to the highest summits, such as Mulhacén) are not represented among his extant herbarium specimens.

Subspecies *virens* was collected for the first time also by Boissier, on limestone, in

TABLE 1. Comparison of *Sideritis glacialis* with other species of mountain habitats showing similar features. Data from Obón & Rivera (1994)

Characters	*Sideritis glacialis* Boiss.	*S. carbonellis* O. Socorro	*S. jahandiezii* Font Quer	*S. pungens* Benth. subsp. *javalambrensis* (Pau) Obón & D. Rivera	*S. hyssopifolia* L, subsp. *eynensis* (Sennen) Malag.
Hair covering in the base of branchlets	Holotrichous	Holotrichous	Holotrichous	Goniotrichous to holotrichous	Goniotrichous to holotrichous
Hair length	1000–2500 μm	400–800 μm	1500–2300 μm	500–1300 μm	800–1200 μm
Leaves	4–17 × 1–4 mm	10–25 × 1–1.5 mm	20–30 × 3–4 mm	10–12 × 2 mm	8–12 × 2–4 mm
Infl. axis length	800–2000 μm	1200–1400 μm	1800–2300 μm	1000–2000 μm	800–1200 μm
Lower bracts	4–10 × 5–10 mm	5–6 × 4–7 mm	10–14 × 6–9 mm	7–12 × 9–12 mm	4–6 × 3–7 mm
Teeth on each side of the lower bracts	2–5	2–3(5)	6–8	4–7	0–2(5)
Middle bracts	4–7 × 6–11 mm	4–5 × 5–6 mm	11–14 × 12–16 mm	6–8 × 10–13 mm	5–6 × 7–8 mm
Teeth on each side of the middle bracts	2–6	0–5	8–9	4–7	5
Calyces	5–9 mm	7–8 mm	6–11 mm	7–8 mm	6–7 mm

August 1837, but only after Bourgeau's collections of July 1851, made at the Monte Verde near La Cortijuela, were specimens of it distributed. Boissier (1859) recognized this as a new taxon, *S. vestita* var. *virens*.

The fourth taxon (subsp. *fontqueriana*) remained unknown for about another century, until the exploration made by Font Quer of the Sierra de Gúdar (Province of Teruel), in July 1946, discovered these plants on El Collado de la Gitana at 2000 m. The epithet *pulvinata* was given to the specimens distributed under *no. 268*, but, unfortunately, the diagnosis was left for Font Quer to undertake in a future paper that was never published. This subspecies appears similar to the type subspecies in the main structure corresponding to similar habitats, but in the type of hair covering it is more similar to subspecies *virens*.

Related taxa

Some taxa endemic to the oromediterranean belt of the high Spanish mountains have sometimes been referred to as being linked to *S. glacialis*. For instance, some authors have confused or synonymized *S. carbonellis* Socorro (Boucher, 1982), *S. javalambrensis* Pau (Rivas-Goday & Borja, 1961), or *S. hyssopifolia* L. subsp. *eynensis* (Sennen) Malag. (*S. pyrenaica* Poiret) (Rivas-Goday & Borja, 1961) with *S. glacialis*, but the very few similarities found in their macromorphology are mainly due to convergent adaptations to the high altitude environment (Table 1). The aforesaid three species belong to the subsection *Hyssopifolia* Obón & D. Rivera (Rivera *et al.*, 1990, Obón & Rivera, 1994), because of the nature of the hair covering at the base of their shoots, which is fundamentally goniotrichous with only a slight tendency to become holotrichous and composed of shorter and more robust trichomes. Specimens from El Almadén (Sierra Mágina, Jaén Province), collected at 1800 m, have been named by Cuatrecasas (1930) *S. glacialis* forma *hispanica* (Font Quer) Cuatrecasas,

but properly also belong to subsection *Hyssopifolia* (Rivera *et al.*, 1990, Obón & Rivera, 1994).

Sideritis glacialis is included in subsection *Fruticulosae* Obón & D. Rivera because of its hair covering at the base of the branchlet, always typically holotrichous and composed of extremely long and thin trichomes. The type of hairs is also different. Subsection *Hyssopifolia* is characterized by broadly antrorse cylindrical hairs, with the apical cell conical, whereas subsection *Fruticulosae* shows characteristic adpressed hairs with an apical cell longer and band-shaped.

Other taxa, like *S. fruticulosae* Pourret, *S. subspinosa* Cav., *S. spinulosa* Barnadés ex Asso, and *S. jahandiezii* Font Quer are included within subsection *Fruticulosae* because of their common type of hair covering. The macromorphology also reveals similarities with *S. glacialis*, but their floral morphology and inflorescences are quite different.

Infraspecific variability

Within *Sideritis glacialis* has been found a complex of variants showing a geographically or ecologically directed pattern. Obón & Rivera (1994) interpreted this complex in the sense of four subspecies belonging to a single species. Other authors, such as Prof. Rivas Martinez (pers. comm.), have suggested a more analytical approach concerning far distant populations geographically or ecologically isolated from the main group of the top of Sierra Nevada mountains (e.g. plants living in Gúdar (Teruel) or plants growing on dolomite in the lower mountain range of Sierra Nevada). A similar approach was adopted by Peris *et al.* (1994) for their *Sideritis boissieriana*.

Herbarium specimens covering the whole range of described variability were examined and analysed for 101 characters. In total, 56 different cluster analyses were performed using program NCLAS (Podani, 1990). The operative units adopted for this analysis were the four subspecies recognized by Obón & Rivera (1994) and the closely related taxa *S. jahandiezii* and *S. carbonellis*.

Role and place in montane and alpine vegetation

Sideritis glacialis reaches the highest altitudes of any species in the section *Sideritis*, growing at an altitude of over 3000 m. It is an alpine plant in the sense of Polunin & Walters (1985), although, when strictly defined, the vegetation of Sierra Nevada must properly be included within the range of the Mediterranean region (Martínez-Parras, Peinado & Alcaraz, 1987a, b; Pérez-Raya *et al.*, 1990). Amongst the four subspecies recognized, two are calcicole (subsp. *fontqueriana* and subsp. *virens*). The two other subspecies (subsp. *glacialis* and subsp. *vestita*) colonize siliceous substrates. The plant communities in which the different subspecies have been found are discussed in the following paragraphs organized into the main distribution areas.

Sierra Nevada and neighbouring mountain ranges of eastern Andalusia

(a) *Sideritido–Arenarietum pungentis* (Quezel, 1953) (viz. Losa *et al.*, 1986) which is a plant community dominated by thorny cushion-shaped species such as *Arenaria pungens* Clemente ex Lag., *Astragalus sempervirens* subsp. *nevadensis* (Boiss.) P. Monts. or

Hormathophylla spinosa (L.) Küpfer, living in the stony places of the upper oro-mediterranean and lower crioromediterranean belts. The presence of bases in the soil is taken as a characteristic for this community. These bases are derived from the underlying ultrabasic schists, or also are imported by the winds from the neighbouring limestone and dolomite (Losa *et al.*, 1986). The influence of strong winds is another factor which has been invoked to explain the dominant shape of this community, which is also influenced by grazing pressure.

(b) *Astragalo boissierii–Festucetum hystricis* (Quézel, 1953). Colonizes calcareous and dolomitic stony places in upper levels of the supramediterranean belt and the lower horizon of the oromediterranean belt, which is an open community rich in thorny cushion-shaped plants e.g. *Vella spinosa* Boiss., *Erinacea anthyllis* Link, *Bupleurum spinosum* Gouan, *Hormathophylla spinosa* (L.) Küpfer, etc. (Table 2, columns 3 and 4) (also Molero & Pérez-Raya, 1987, Pérez-Raya *et al.*, 1990).

(c) *Arenario imbricatae–Festucetum indigestae* (Rivas Martínez, 1965) (viz. also Losa *et al.*, 1986), which is a secondary sclerophyllous discontinuous 'tomillar'-grassland community developed in Sierra Nevada after clearance of the procumbent xerophytic 'piornal-enebral'. This widespread in burned zones. This grassland is characterized by the presence of *Festuca indigesta* Boiss. and *Thymus serpylloides* Bory, on siliceous substrates of the oromediterranean belt (Table 2, columns 5 and 6).

(d) *Festucetum pseudoeskio–baeticae* (Quézel, 1953). Grasslands of the upper oro-mediterranean and crioromediterranean belts which colonize sunny pronounced slopes exposed to very strong winds, on stony siliceous substrates (Table 2, column 8).

(e) *Festucetum clementei–Erigerontetum frigidi* (Quézel, 1953). Open grassland with a coverage of below 25% which is the potential plant community of the crioro-mediterranean belt in Sierra Nevada. It is hardy, enduring being submerged in snow for a long time and being buffetted by strong winds (Table 2, column 7).

Mountains of Gúdar (Teruel)

(a) *Sideritido glacialis–Arenarietum erinaceae* (Rivas Goday & Borja, 1961), which is a plant community vicariant of the Andalusian *Astragalo boissieri–Festucetum hystricis* Quézel, colonizing calcareous substrates in Gúdar and Javalambre (Teruel), between 1900 and 2000 m, in which the strong winds determine the pulvinate form of the plants. Characteristic species: *Arenaria erinacea* Boiss., *Dianthus brachyanthus* Boiss., *Festuca indigesta* subsp. *aragonensis* (Willk.) Kerguélen, *Festuca hystrix* Boiss., *Thymus zapateri* Pau ex Willk., etc. (Table 2, columns 1 and 2).

(b) *Paronychio capitatae–Artemisietum lanatae* (Rivas Goday & Borja, 1961), which is a grassland community developed under extreme anthropo-zoogenic pressure, after destruction of the thorny cushion garrigue in Gúdar, between 1600 and 1800 m. It is characterized by *Artemisia assoana* Willk., *Paronychia capitata* (L.) Lam., *Festuca indigesta* subsp. *aragonensis* (Willk.) Kerguélen and *Festuca hystrix* Boiss.

DISCUSSION

The variation within *S. glacialis* is extremely gradual, as clearly demonstrated by Boissier (1841). The subspecies recognized here can be understood as groups of

TABLE 2. Eight relevés of vegetation from the habitats of the four subspecies of *Sideritis glacialis* with the most relevant accompanying species. Localities: 1 and 2, Sierra de Gúdar; 3 and 4, Collado de la Sabina, Sierra Nevada (Granada); 5, Parador Universitario, Sierra Nevada, VH6705 (Granada); 6, between El Veleta and Peñones de San Francisco, Sierra Nevada, VH5441 (Granada). 7, Mulhacén, Sierra Nevada, VH4741 (Granada); 8, northern slope of El Veleta, Sierra Nevada, VH5441 (Granada). Numbers follow the scale of abundance–dominance by the Zürich–Montpellier system

N° Order	1	2	3	4	5	6	7	8
Altitude (m × 10)	200	200	207	213	260	278	306	285
Exposure	E	E	NW	W	N	N	W	W
Inclination (°)	15	10	15	10	15	30	30	40
Area (m^2)	80	90	80	150	100	60	80	70
Sideritis glacialis Boiss. subsp. *fontqueriana* Obón & D. Rivera	2	2	–	–	–	–	–	–
Thymus zapateri Pau ex Willk.	3	2	–	–	–	–	–	–
Festuca hystrix Boiss.	2	2	1	+	–	–	–	–
Koeleria vallesiana (Honcheny) Gaudin subsp. *humilis* Braun-Blaq.	1	2	+	–	–	–	–	–
Potentilla cinerea Chaix ex Vill.	1	1	–	–	–	–	–	–
Carduncellus monspelliensium All.	1	+	–	–	–	–	–	–
Helianthemum canum (L.) Baumbg.	–	2	1	–	–	–	–	–
Sideritis glacialis Boiss. subsp. *virens* (Boiss.) Obón & D. Rivera	–	–	1	+	–	–	–	–
Erinacea anthyllis Link	–	–	3	2	–	–	–	–
Vella spinosa Boiss.	–	–	3	2	–	–	–	–
Ononis aragonensis Asso	–	–	2	1	–	–	–	–
Erysimum baeticum (Heywood) Polatschek subsp. *baeticum*	–	–	1	1	–	–	–	–
Astragalus granatensis Lamk.	–	–	+	1	–	–	–	–
Teucrium polium L.	–	–	+	1	–	–	–	–
Helianthemum croceum (Desf.) Pers. subsp. *cavanillesianum* Lainz	–	–	+	1	–	–	–	–
Acinos alpinus (L.) Moench subsp. *meridionalis* (Nyman) P.W. Ball	–	–	1	–	–	–	–	–
Festuca nevadensis (Hackel) Markgr.–Dannenb.	–	–	1	–	–	–	–	–
Juniperus sabina L.	–	–	1	–	–	–	–	–
Prunus prostrata Labill.	–	–	–	1	–	–	–	–
Sideritis glacialis Boiss. subsp. *vestita* Obón & D. Rivera	–	–	–	–	2	2	–	–
Festuca indigesta Boiss.	–	–	1	–	4	3	–	–
Thymus serpylloides Bory	–	–	–	–	2	2	+	–
Galium pyrenaicum Gouan	–	–	–	–	1	1	2	–
Draba hispanica Boiss. subsp. *laderoi* Rivas Mart., M.E. García & Penas	–	–	–	–	1	+	+	–
Poa ligulata Boiss.					1	1	–	–
Silene boryi Boiss.	–	–	–	–	1	1	–	–
Anthyllis vulneraria L. subsp. *argyrophylla* (Rothm.) Cullen	–	–	–	–	2	–	–	–
Tulipa sylvestris L. subsp. *australis* (Link) Sampaio	–	–	–	1	–	–	–	–
Sedum forsteranum Sm.	–	–	–	–	1	–	–	–
Sideritis glacialis Boiss. subsp. *glacialis*	–	–	–	–	–	–	2	2
Arenaria imbricata Lag. & Rodr.	–	–	–	–	+	2	2	2
Festuca pseudoeskia Boiss.	–	–	–	–	–	–	–	3
Festuca clementei Boiss.	–	–	–	–	–	–	2	–
Eryngium glaciale Boiss.	–	–	–	–	–	–	+	1
Leontodon boryi Boiss.	–	–	–	–	–	–	1	+
Ptilotrichum spinosum (L.) Boiss.	–	–	–	–	–	+	1	1
Jasione amethystina Lag. & Rodr.	–	–	–	–	1	+	1	1
Holcus caespitosus Boiss.	–	–	–	–	1	–	–	1
Dactylis glomerata L. subsp. *juncinella* (Bory) Stebbins & Zohary	–	–	–	–	–	–	–	1
Erigeron frigidus Boiss. ex DC.	–	–	–	–	–	–	1	–
Erodium cheilanthifolium Boiss.	–	–	–	–	–	–	–	1
Hormatophylla purpurea (Lag. & Rodr.) P. Küpfer in Castrov. & al.	–	–	–	–	–	–	1	–
Sempervivum minutum (Willk.) Pau	–	–	–	–	–	–	1	–
Trisetum glaciale (Bory) Boiss.	–	–	–	–	–	–	1	–

variants relatively coherent within each one, and separated from each other by gaps, defined here in the sense not of an absolute lack of intermediate individuals but in terms of a lower frequency of these. In their neighbouring zones, the subspecies growing on the Sierra Nevada overlap in their distribution, and can be found relatively close also to each other. The synthetic viewpoint appeals to us as an alternative approach to the taxonomy of this group but, following this second path, new problems have arisen because of the high morphological and ecological heterogeneity within the *S. glacialis* aggregate.

How long the variants respond to environmental factors or grazing pressures acting on the phenotype is probably a nontaxonomic question, because these factors have been constant and uniformly acting over these populations in a differentiating way. These forms are more or less fixed, ecologically, if not genetically, and the taxa are then described on a factual basis over in state of balance.

According to Fernández-Peralta (1981) the chromosome number characteristic of *S. glacialis* subsp. *glacialis*, $n = 17$, is the upper disploid level of the series composed by the Section *Sideritis*. This level corresponds to taxa living in high mountain habitats like *S. glacialis*, *S. stachydioides* Willk., or *S. pyrenaica* Poiret and to others living at a low altitude but extremely isolated within the systematics of this section, like *S. glauca* Cav. or *S. lacaitae* Font Quer.

The similarities in the type of hair covering between subspecies *virens* and *fontqueriana* could be interpreted in the sense of a common ancestor. The influence of the strong winds, drought, etc. could have conditioned the actual cushion-shape of subsp. *fontqueriana* while subsp. *virens* remained tall and erect under less severe environmental restrictions; both subspecies are calcicole. Within the *Sideritis glacialis* complex found in Sierra Nevada, subsp. *virens* with a less specialized type of hair covering and structure could be interpreted as more primitive than subsp. *vestita* and subsp. *glacialis*, which evolved colonizing the high mountain habitats after the uplift of the Sierra Nevada.

Most of the taxa included in section *Sideritis* are calcicoles; only some, supposedly highly evolved (according to their chromosome number and morphology), can grow on siliceous soils. The ability to colonize this kind of soil can be interpreted as an evolved state, and hence invoked for sustaining the evolved character of subsp. *vestita* and subsp. *glacialis* in relation to the primitiveness of subspecies *virens* growing on dolomite. Subsp. *vestita* can be found both on calcareous or siliceous substrates, while subsp. *glacialis* exclusively occurs on siliceous soils.

Alternatively this variability may be interpreted in the sense of an ecologically determined clinal variation between two extreme forms: *Sideritis carbonellis* (calcicole, lower altitude) and *Sideritis glacialis* subsp. *glacialis* (silicicole, higher altitude). Figure 1 displays a summary of the results of 56 different cluster analyses performed by the program NCLAS (Podani, 1991) taking into consideration 101 morphological characters (those used in the description of taxa) and six OTUs. The Syn–Tax package, version 5.0, was employed for comparison (Podani, 1991); (UPGMA) average linkage and complete linkage were calculated. Hierarchical classification was generated using combined agglomerative methods characterized by the recurrence formula as follows:

$d_{h,ij} = \alpha_i\, d_{hi} + \alpha_j\, d_{hj} + \beta\, d_{ij} + \gamma \mid d_{hi}\, d_{hj} \mid$, where $d_{h,ij}$ is the new distance value between cluster C_h and cluster C_{ij}, obtained from the fusion of C_i and C_j. As recommended by Podani (1991) the data set was analysed using more than two

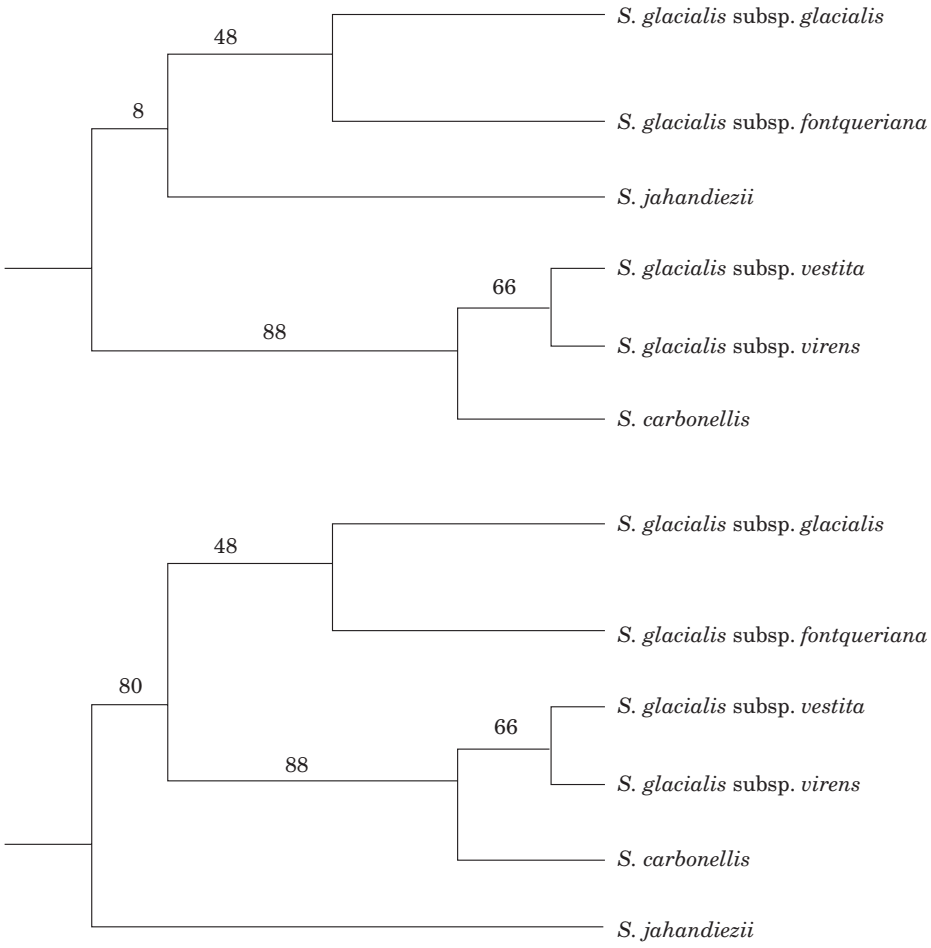

Figure 1. Two synthesis dendrograms of 56 different cluster analysis performed by program NCLAS. With 101 variables and 6 OTUs. Numbers refers to the percentage of dendrograms supporting each branch.

options. These included calculated complete linkage (farthest neighbour, euclidean distance) (CL) and unweighted group average (average, euclidean distance) (UPGMA).

The cluster showing the close relation between *S. carbonellis* to *S. glacialis* subspecies may point towards the hybrid origin of subps. *virens* and subsp. *vestita*. This hybrid swarm thus may be relatively old. In this case the parent species are at present becoming diffuse and scarce. *S. carbonellis* is actually absent from Sierra Nevada (restricted to Sierra de la Sagra). It was displaced from the calcareous zones there by the intermediate and presumably hybrid *S. glacialis* subsp. *virens*. The type of *S. glacialis* is restricted to the upper part of the mountain range, above 3000 m, being substituted below by the intermediate *S. glacialis* subsp. *vestita*, which in fact colonized most of the siliceous habitats available there for the species.

KEYS

Hair covering

1. Abaxial surface of bracts lacking glands, and glandular hairs, covered with abundant tricellular uniseriate hairs, 0.8–1.2 mm, apical cell conical; carpostegium continuous to discontinuous; spine of the calycinal teeth up to 0.1 mm long; hairs on the calyces up to 1 mm . . . . . 4. *S. glacialis* subsp. *fontqueriana*
1. Abaxial surface of bracts with some glands and long glandular hairs, also with scarce to abundant covering tricellular uniseriate hairs, 0.7–3 mm, apical cell band-shaped to conical; carpostegium discontinuous; spine of the calycinal teeth 0.5–1 mm; hairs on the calyces 1–2 mm 2
2. Leaf hairs 1–1.2 mm; bract hairs 0.7–1.2 mm long . . 3. *S. glacialis* subsp. *virens*
2. Leaf hairs 1.5–2.3 mm; bract hairs 1–3 mm 3
3. Bract hairs 1–1.4 mm . . . . . 2. *S. glacialis* subsp. *vestita*
3. Bract hairs 2–3 mm . . . . . 1. *S. glacialis* subsp. *glacialis*

Macromorphology

1. Plants with lower woody portion erect to decumbent; lower leaves 5–17 × 2–4 mm; inflorescences cylindrical to attenuate, 10–45 mm; lower bracts 5–10 × 7–9 mm, 1/2 to 1/3 divided; middle bracts 5–7 × 8–11 mm, with 4–6 teeth on each side 2
1. Plants with lower woody portion cushion shaped; lower leaves 5–10 × 1–2(3) mm; inflorescences ovoid to globose, 5–20 mm; lower bracts 4–7 × 5–8 mm, 1/4 divided; middle bracts 4–7 × 6–8 mm, with 3–5 teeth on each side 3
2. Non woody branches up to 20 cm long; lower leaves 5–15 × 2–4 mm; lower bracts bent downward, sometimes patent to erecto-patent, with 3–5 teeth on each side; calyces 6–7 mm, teeth 1–2 mm . . . . . 2. *S. glacialis* subsp. *vestita*
2. Non woody branches up to 40 cm long; lower leaves 10–17 × 2–3 mm; lower bracts patent to erecto-patent, with 2–3 teeth on each side; calyces 8–9 mm, teeth 2–3 mm . . . . . 3. *S. glacialis* subsp. *virens*
3. Central pair of verticillasters 4–10 mm apart; calyces 6–7 mm, corolla 9 mm long . . . . . 1. *S. glacialis* subsp. *glacialis*
3. Central pair of verticillasters 2 mm apart; calyces up to 5 mm, corolla 6 mm long . . . . . 4. *S. glacialis* subsp. *fontqueriana*

DESCRIPTIONS OF TAXA

Sideritis glacialis Boiss. *Notice sur l'Abies pinsapo*: 12, (February, 1838). (Emendavit Boiss, *Voyage Botanique dans le Midi de l'Espagne, Livraison 16, Vol. 2.*: 508, 1841). subsp. *glacialis*. Figs 2, 3.

Type locality. Sous-arbrisseau tortueux et appliqué contre le sol, s'élevant jusqu'à plus de 9000′ (feet = 3000 m) sur les pentes stériles de la Sierra-Nevada.

Typification. Lectotypified by Burdet, H.M., A. Charpin, & F. Jacquemoud, *Candollea*, *42*: 118 (1987) in the herbarium G-BOISS. by the specimen on the left lower corner

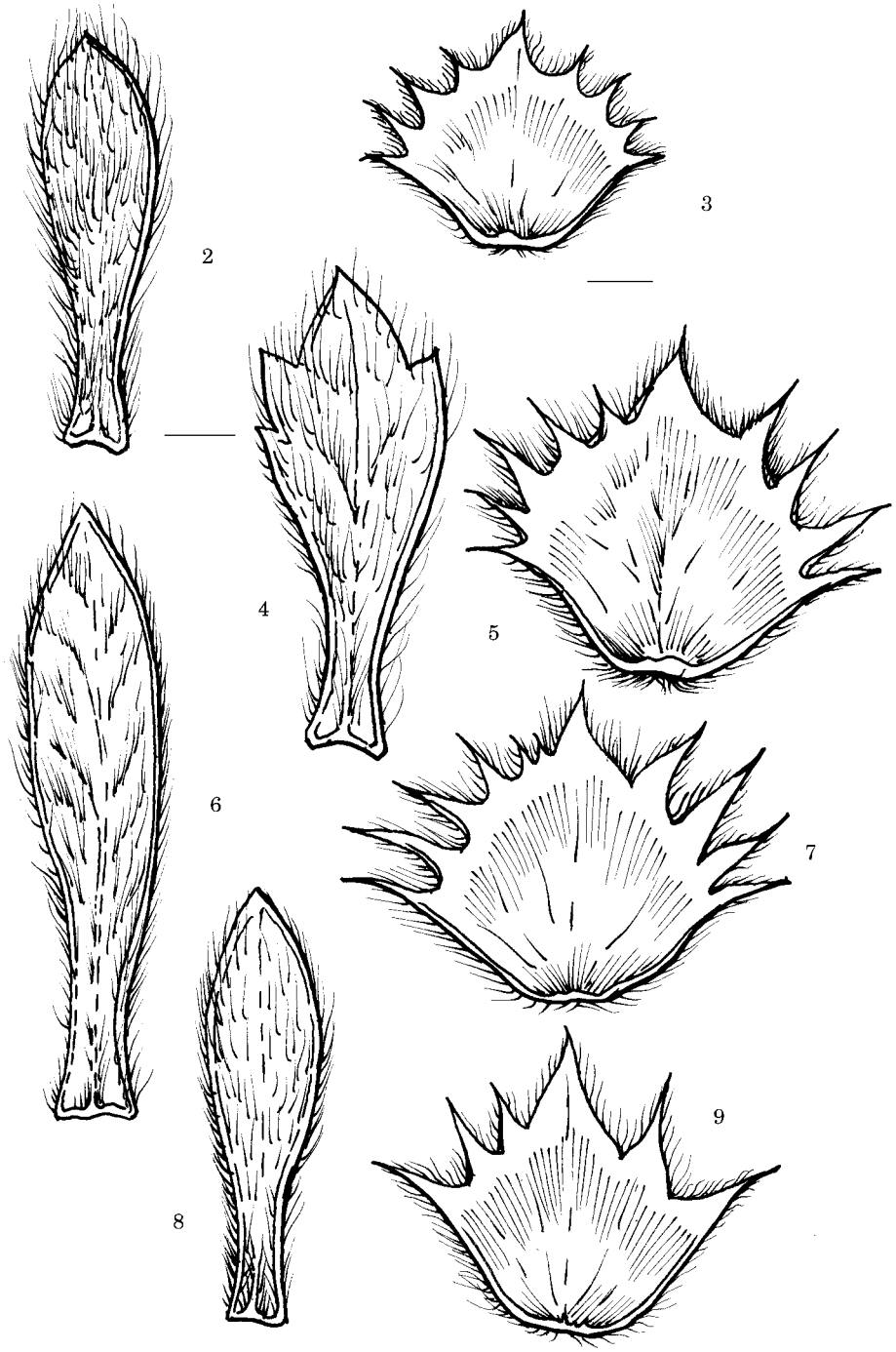

Figure 2–9. *Sideritis glacialis* Boiss. *Sideritis glacialis* Boiss. subsp. *glacialis*. 2. Lower leaf. 3. Middle bract. *Sideritis glacialis* Boiss. subsp. *vestita* Obón & D. Rivera. 4. Lower leaf. 5. Middle bract. *Sideritis glacialis* Boiss. subsp. *virens* (Boiss.) Obón & D. Rivera. 6. Lower leaf. 7. Middle bract. *Sideritis glacialis* Boiss. subsp. *fontqueriana* Obón & D. Rivera. 8. Lower leaf. 9. Middle bract.

of the first sheet with the following label attached: HERB. E. BOISSIER.//Sierra Nevada loma de Panderon/aug. 1837 (m. Boissier).

Synonyms. ≡ *S. hyssopifolia* var. *glacialis* (Boiss.) Pau, *Bol. Soc. Aragon. Ci. Nat. 8*: 126(23), (v.1909).
≡ *S. hyssopifolia* var. *glacialis* (Boiss.) Pau, *Bol. Soc. Aragon Ci. Nat., 8*: 132(24), (vi. July 1909).
≡ *S. scordioides* var. *glacialis* (Boiss.) Font Quer, *Trab. Mus. Ci. Nat. Barcelona, 5/4:* 24, (v.1924).
≡ *S. scordioides* var. *boissieri* Webb, *Iter hispan*: 22, 1838. Based on *S. glacialis* Boiss. *Notice sur l'Abies pinsapo:* 12 (1838).

Type: as *S. glacialis* Boiss.
≡ *S. scordioides* var. *vestita* Boiss., *Elench. pl. nov.*: 76, (vii.1838).
= *S. vestita* (Boiss.) Boiss. *Diagn. pl. orient. ser II, N°4:* 33–34, 1859 (pro parte).
= *S. glacialis* forma *incana* Willk., *Bot. Zeit., 33:* 284, 1859.
– *S. glacialis* forma *cinerascens* Sennen, in sched., Plantes d'Espagne-F. Sennen, n°9848. 1934. (*Nomen nudum*, Art. 32.1. ICBN).
– *S. glacialis* var. *incana* Amo, *Fl. fan. Penins. Iberica, 3:* 191, 1872. (Superfluous, Art. 63.1 ICBN).

BASAL PARTS woody, persistent, cushion-shaped; to 15 cm, including branches. Non-woody branches ascending to 10 cm. Hair covering at the base of branchlets holotrichous and heterotrichous. Glands very scarce, glandular hairs lacking. Trichomes abundant, antrorse, 1.5–2 mm, with three cells cylindrical, apical cell band-shaped to conical. LOWER LEAVES, 5–10 × 1–2 mm, entire (sometimes with scarce minute teeth concealed by the hair covering), lanceolate to spathulate, apiculate. Glands very scarce, glandular hairs absent, trichomes abundant, not differentiated at the margin, 1.8–2.2 mm; upper leaves similar to lower. INFLORESCENCES yellow–whitish at the corners of axis, bracts and calyces; ovoid to globose, 5–20 mm, with 2–4 verticillasters, the central 4–10 mm apart. LOWER BRACTS erecto-patent to patent, ovate, widest zone 1/2–1/3 from the base, divided to 1/4, 4–6 × 5–7 mm, with 3–4 teeth at each side; middle bracts erecto-patent to patent, ovate, widest zone 1/2–1/3 from the base, 1/3 divided, 4–5 × 6 mm, 3–5 teeth on each side. Abaxial surface with glands, scarce to very scarce, glandular hairs scarce, long with tiny glands, trichomes abundant, 2–3 mm, with 3–4 cylindrical cells, apical cell conical to band-shaped. VERTICILLASTERS with six flowers. CALYCES campanulate, 6–7 mm, with five subequal divergent teeth, 1–2 mm, ending in spines 1 mm. Carpostegium discontinuous. Outer surface of calyx: glands scarce to very scarce, glandular hairs absent to very scarce, with tiny glands, trichomes scarce to abundant, 1–2 mm. COROLLAS 8–10 mm, 2-lipped for 1/2–1/3 of their length, yellow. Stamens included in the corolla tube, filaments 0.8–1 mm. Style up to 2 mm. FRUITS ovoid, 1–1.5 mm.

Distribution. Upper zones of Sierra Nevada (Granada, Spain), 2700–3100 m. Oro-mediterranean and crioromediterranean belts.

Phenology. Flowering in late July and August. Seeds maturing in August.

Habitat. High mountain rocks, screes. In *Sideritido–Arenarietum pungentis* Quézel, 1953; also in the grasslands of *Festucetum pseudoeskio–baeticae* Quézel, 1953 and *Festucetum clementei–Erigerontetum frigidi* Quézel, 1953. Extremely silvery specimens of the type

subspecies have been found living in *Violo nevadensis–Linarietum glacialis* Quézel (1953) (Pérez-Raya, pers. comm.). This is a crioromediterranean pioneering community living on mobile stony substrates at the summits of the Veleta and Mulhacén (Losa *et al.*, 1986).

Specimens studied. GRANADA: Sierra Nevada, sine dat. *Boissier* (K); Sierra Nevada, sine dat., sine collect. (MA 1613); sine loc., sine dat., sine collect. G-BOISS (5674); Sierra Nevada, Loma de Panderón c. Vacares, sine dat., *Boissier* (G-BOISS 7505–4); Sierra Nevada, Loma del Panderón, 1834, *Boissier* (G-BOISS 7505–2); Sierra Nevada, viii. 1837, *Boissier* (BM, CGE-Lindley, GH, LY, MA 1608, P); Sierra Nevada, 1840, *Colmeiro* (LY); Sierra Nevada, 23.viii.1841, *Willkomm* 705 (K); Sierra Nevada, Camino de la Nieve, 26.vii.1844, *Wilkomm* (COI); Sierra Nevada (Puerto de Vacares), 23.viii.1844, *Willkomm* (COI); Sierra Nevada (Corral del Veleta), 4.viii.1845, *Willkomm* (COI); Sierra Nevada (Las Lagunillas), viii.1848, *Munby* (K); Sierra Nevada (Mulhacen), viii.1848, *Funk* (BM, COI); Sierra Nevada (Picacho del Veleta), 24.vii.1851, *Bourgeau 1422* (CGE, COI, K, LY); Cueva de los Panderones, 21.vii.1852, *Del Campo* (*Bourgeau 82)* (CGE, COI, K, LY); Sierra Nevada, Cueva de los Panderones, 4.viii.1853, *Sainz* (LY; MA 1606); Sierra Nevada, Panderones, 21.vii.1852, *Del Campo 52* (BM); Sierra Nevada, Panderones, 2.viii.1859, *Del Campo* (BM, LY); Sierra Nevada (Picacho Veleta), 30.vii.1873, *Winkler* (K, TL); Sierra Nevada, 1876, *Hackel* (TL); Sierra Nevada, Panderón, 28.vii.1879, *Huter Porta & Rigo 1058* (K, LY, TL); Sierra Nevada, Panderones, 27.vii.1883, *Nilson* (BM); Sierra Nevada (Picacho del Veleta), viii.1891, *Porta & Rigo 486* (BM, K, LY, MA 1609); Sierra Nevada (Picón de Jerez), viii.1908, *Pau* (MA 1611); Sierra Nevada (Mulhacen), 13.viii.1923, *Font Quer, Cuatrecasas & Gros* (MA 1610); Sierra Nevada, (Carretera al Veleta), 3.vii.1926, *Lacaita* (K); Sierra Nevada (Vertiente del Genil), 15.viii.1928, *Huguet del Villar* (MAF 59862); Sierra Nevada (valle del rio Lanjarón, Peñón Colorado), 5.viii.1930, *Ceballos & Vicioso* (MA 1607); Sierra Nevada (Estribaciones del Veleta), 10.viii.1946, *Muñoz Medina 476* (ALMERIA 5526, MA 140429, MA 344898, MAF 32410); Sierra Nevada, Canchiles, vii.1965, *Varo* (GDA 1248); Sierra Nevada (Veleta), 28.viii.1966, *R.M. & A.M. Harley* (BM); Sierra Nevada (Subida al Veleta), 4. vii. 1969, *Sattler & Carter* (BM); Sierra Nevada, Carretera al Veleta, 19.vii.1970, *Fernández Casas* (MA 332522); Sierra Nevada, Barranco del Guarnon, 7.ix.1970, *Espinosa & Morales* (GDA 1247); Carrihuela del Veleta, 25.vii.1973, *Fernández Casas* (MA 332521); Sierra Nevada carretera al Veleta, 19.vii.1975, *Halliwell, Mason & Smallcombe 1671* (K); Sierra Nevada (Güejar, hoya de la Laguna Larga), 5.x.1975, *Fernández Casas & Garcia Guardia* (MA 393997); Sierra Nevada (Pico Veleta), 17.vii.1976, *A. Barra, Castroviejo, Cirujano & Valdés Bermejo* (MA 435323); Sierra Nevada, Barranco Valdeinfierno, 13.viii.1976, *Blanca & Gill* (GDA 2434); Sierra Nevada (El Chorrillo), 15.vii.1981, *Nieto* (MGC 8631); Sierra Nevada (Mulhacen), 15.vii.1981, *Nieto* (MGC 8632); Sierra Nevada (El Mulhacén), 25.vii.1983, *Alcaraz* (MUB 10196); Sierra Nevada, near pico Veleta, 22.vii.1984, *Luceño* (MA 435941); Sierra Nevada (Veleta), 3.viii.1984, *Cabezudo, Guerra & Pérez-Raya* (MGC 14469); Sierra Nevada, 4.viii.1984, *Cabezudo, Guerra & Pérez-Raya* (MGC 14474); Sierra Nevada (Falda del Pico Veleta), 6.vii.1987, *Losa* (MA 464758); Sierra Nevada (above Rio Seco), 23.viii.1982, *Auriault* (AURIAULT); Sierra Nevada (solana del Mulhacén), 25.vii.1983, *Alcaraz* (MUB 10197); Sierra Nevada (Veleta), 18.vii.1986, *Rivera & Obón* (MUB 37085); Sierra Nevada (Subida al Mulhacen, Capileira), 22.vii.1987, *Cabezudo, Nieto & Flores* (MGC 20638).

Note. Under No. 1058 of Huter, Porta & Rigo's exsiccata, specimens belonging

to three of the four subspecies recognized here are included, although they were probably collected from various localities in the Sierra Nevada, and were labelled with the sole locality name of 'Panderón, etc.'. Each specimen should be examined separately and a final ascription carefully checked against the keys given here.

Sideritis glacialis subsp. *vestita* Obón & D. Rivera. Phanerogamarum Monographiae, 21: 201 (ix. 1994). Figs 4, 5.

Type. Holotype: Spain, prov. Granada, Sierra Nevada, on the side of the road to Veleta, near the Albergue Universitario, 2.vii.1982, *Raoul Auriault* (holo. MUB 37335). Isotypes: several specimens of the same collection *herb. Auriault.*

= *S. vestita* Boiss., *Diagn. pl. orient. ser II, N°4*: 33–34, 1859, (pro parte, excluding type of *S. glacialis*).

= *S. boissierana* Peris, Stübing, Olivares & Martin, *Fontqueria 39*: 59–63, 1994.

Type. Holotype: Spain, prov. Granada, Sierra Nevada, Horcajo de Trévelez, 15.vii.1923, *Font Quer* (BC 73554).

– *S. nevadensis* Gand., *Fl. Eur. 17*: 284, 1889. (Invalid, Art. 33.4, Ex. 12).

– *S. deflexicaulis* Gand., *Fl. Eur. 17*: 284, 1889. (Invalid, Art. 33.4, Ex. 12).

BASAL PARTS woody, persistent and decumbent to erect; to 25 cm, including branches. Non woody branches ascending to 20 cm. Hair covering at the base of branchlets holotrichous and heterotrichous; glands scarce to very scarce, glandular hairs very scarce, with tiny glands, trichomes scarce to very scarce, antrorse, 10–15 mm, with 3–4 cells cylindrical, apical cell conical to band-shaped. LOWER LEAVES, 5–15 × 2–4 mm, toothed or serrulate, lanceolate to linear spathulate, sometimes ovate, apiculate or spinescent; glands very scarce, glandular hairs very scarce, with tiny glands, trichomes scarce, more or less differentiated in the margin, 1.5–2 mm; upper leaves similar or narrower than lower. INFLORESCENCES yellowish-green at the corners of the axis, bracts and calyces, cylindrical, 1–4 cm, with 2–4 verticillasters, the central 4–9 mm apart. LOWER BRACTS bent downward, ovate, widest zone 1/2–1/3 from the base, divided to 1/2–1/3, 7–10 mm × 7–10 mm, 3–5 teeth on each side; middle bracts patent, ovate, widest zone 1/2–1/3 from the base, divided to 1/2–1/3, 5–6 mm × 8–11 mm, 3–5 teeth on each side. Abaxial surface with extremely scarce glands; glandular hairs scarce, with tiny glands, trichomes scarce, 10–14 mm, with three cylindrical cells, apical cell band-shaped to conical. VERTICILLASTERS with six flowers. CALYCES campanulate, 6–7 mm, with five subequal divergent teeth, 1–2 mm, ending in spines 0.5–1 mm. Carpostegium discontinuous. In the external surface of calyx: glands very scarce, glandular hairs very scarce, with tiny glands and abundant trichomes, 1–1.5 mm. COROLLAS 10–11 mm, 2-lipped for 1/3–1/4 of their length, yellow. Stamens included in the corolla tube, filaments 3 mm. Style up to 1 mm. FRUITS ovoid, 1.5 mm.

Distribution. Mountains of southern Spain (Provinces of Málaga, Granada, Almería): Sierra de Tejeda, Sierra Nevada, Sierra de Baza, Sierra de Gádor. 2000–2800 m. Oromediterranean.

Phenology. Flowering in July and early August. Seeds maturing in early August.

Habitat. High mountain rocks, screes. In the lower limit of *Sideritido–Arenarietum pungentis* Quézel, 1753. High mountain grasslands. In *Arenario imbricatae–Festucetum indigestae* Rivas-Martínez (1965). Also in *Astragalo boissierii–Festucetum hystricis* Quézel,

1953 in the mountains of Gádor and Tejeda, but not in Sierra Nevada where it is replaced by the subsp. *virens* (viz. Molero & Pérez-Raya, 1987, Pérez-Raya *et al.*, 1990).

Specimens studied. ALMERÍA: Sierra Nevada (above Minas de Beire near Cerro Almirez), 30.vi.1926, *Willmott & Lofthouse* (BM); Sierra Nevada (above Minas de Beire near Cerro Rayo), 22.vi.1926, *Willmott & Lofthouse* (BM); Sierra de Abrucena, 2.vii.1929, *Gros* (MA 1616); Sierra Nevada (Cerros del Almirez, 19.vii.1935, *Jerónimo (Sennen 9848)* (MA 1617, MA 162713, MAF 9848); El Almirez, 29.vii.1960, *Rivas Goday* (MAF 78222); Sierra de Gádor (Subida desde Castala), 19.vii.1980, *Morales & López* (MA 256259); El Almirez, 9.viii.1984, *Robledo* (MUB 37089); Sierra de Gádor (Morrón), 20.vii.1984, *Pallarés* (MA 476727); Sierra Nevada (Cerro Almirez), 9.viii.1984, *Alcaraz & Robledo* (MUB).

GRANADA: Sierra Nevada, Panderones, 28.vii.1879, *Huter, Porta & Rigo 1058* (BM) (sic.!, collection mixed involving several localities); Sierra Nevada, viii.1893, *Sainz Gutierrez* (MAF 32411); Sierra Nevada (Peñón de San Francisco), viii.1913, *Beltran* (MA 1612, MA 438576); Sierra Nevada (Peñón de San Francisco), 3.vii.1926, *Lacaita* 259–26 (BM); Sierra Nevada (Barranco del Lori), 10.vii.1951, *Jerónimo* (ALMERIA 5527); Albergue Universitario (Vertiente Norte del Veleta), 29.ix.1952, *Gaussen 7660* (TL); Sierra Nevada (Jerez del Marquesado), 7.viii.1953, *Jerónimo* (ALMERIA 5528); Sierra Nevada, 28.vii.1954, *Muñoz Medina* (GDA 33905); Sierra Nevada, Borreguiles del Monachil, 17.vii.1969, *Varo* (GDA 1245, 1249); Above Puerto de la Ragua, 17.vii.1973, *Ladero & Valdés* (MA 256260, MAF 94433); Sierra Nevada, 6.viii.1978, *Fuertes* (MA 256258); Sierra de Baza (Cerro de Santa Bárbara), 4.vii.1979, *Cannon, Crane, Jury & Moore* (RNG); Albergue Universitario, 2.vii.1982, *Auriault (herb*. AURIAULT, Isotype); Albergue Universitario, 2.vii.1982, *Auriault* (MUB 37335); Sierra Nevada (Road to Veleta, 1 km from the Albergue Universitario), 13.viii.1982, *Goyder & Jury* (BM 1045).

MÁLAGA: Sierra Tejeda, viii.1837, *Boissier* (K); Sierra Tejeda, 29.vii.1919, *Font Quer* (MA 1614); Sierra Tejeda, 5.viii.1934, *Laza* (MAF 32408); Cumbres de Sierra Tejeda, 7.vii.1935, *Laza* (COI, MA 1615); Sierra Tejeda (Maroma), sine dat., *Cabezudo & Nieto* (MGC 224).

Sideritis glacialis subsp. *virens* (Boiss.) Obón & D. Rivera Phanerogamarum Monographiae, 21: 205 (ix. 1994). Figs 6, 7.
≡ *Sideritis vestita* var. *virens* Boiss. *Diagn. pl. orient. ser II, N° 4*: 34, 1859.

Type. Hab. in parte calcarea Sierra Nevada Boiss! Bourg. exs. 1851, N° 1425 a. (G-BOISS.).

Typification. Lectotypified by Burdet, H.M., A. Charpin & F. Jacquemoud in Candollea 42/1: 119, 1987 by the specimen on the sheet with the following label attached: E. Bourgeau, Pl. d'Espagne, 1851//1425 a. *Sideritis scordioides* L. var. *alpina*, Boiss. (Coss.) /Sierra Nevada, région alpine, au/Monte verde près de la Castijuela./ 22 juillet. Syntype: Specimen on the sheet with the label: HERB. E. BOISSIER.// Sideritis scordioides L. var. vestita Boiss. El. n° 164 7 in summis Sierra Nevada./ viii. 1837. Alt. 6000–9000′/*SA Nevada pars calcarea* (m. Boissier).

Synonyms
– *S. scordioides* var. *alpina* Boiss., Voy. Bot. Espagne: 508, 1841 non (Villars) Bentham.
– *S. scordioides* var. *alpina* (Boiss.) Cosson in E. Bourgeau, Plantes d'Espagne, n° 1425, 1851.

– *S. glacialis* forma. *virens* Willk., *Bot. Zeit., 33*: 284, 1859. *Type: S. scordioides* var. *alpina* Boiss., planta in Sierrae Nevadae parte calcarea ad 6500–7000′ crescens, mihi ignota (sic. !).
– *S. glacialis* var. *virens* Amo, *Fl. fan. Penins. Iberica, 3*: 191, 1872. (= *S. scordioides* var. *alpina* Boiss.?) (Invalid Art 34.1a).

BASAL PARTS woody, persistent, erect; to 40 cm, including branches. Non woody branches erect to 25 cm. Hair covering at the base of branchlets holotrichous and heterotrichous. Glands extremely scarce, glandular hairs scarce to extremely scarce, with tiny glands, trichomes scarce to extremely scarce, antrorse, 1–1.2 mm, with 2–3 cells cylindrical, the apical cell is band-shaped. LOWER LEAVES 10–17 × 2–3 mm, entire to toothed, linear-spathulate to lanceolate, obtuse; glands extremely scarce, glandular hairs extremely scarce, with tiny glands, trichomes scarce to extremely scarce, neatly differentiated in the margin, 1–1.2 mm. Upper leaves narrower than lower. INFLORESCENCES greenish to yellowish at the corners of the axis, bracts & calyces, attenuate, 1.5–4.5 cm, with 2–4 verticillasters, the central pair 7–9 mm distant. LOWER BRACTS patent, ovate, widest zone 1/3 from the base, divided for 1/2–1/3, 5–7 × 7–9 mm, 2–3 teeth on each side; middle bracts patent, ovate, widest zone 1/3 from the base, divided to 1/3, 6–7 × 9–10 mm, 4–6 teeth on each side. Abaxial surface with: glands extremely scarce, glandular hairs extremely scarce, with tiny glands, trichomes scarce, 7–12 mm, with three cylindrical cells, apical cell band-shaped to conical. VERTICILLASTERS with six flowers. Bracteoles absent. CALYCES campanulate, 8–9 mm, with five subequal divergent teeth, 2–3 mm, ending in spines 1 mm. Carpostegium discontinuous. Outer surface of calyx: glands scarce to extremely scarce; glandular hairs scarce to extremely scarce, with tiny glands; trichomes abundant, 1.5 mm. COROLLAS 9–11 mm, 2-lipped for 1/2–1/3 of their length, yellow. Stamens included in the corolla tube, filaments 1 mm. Style up to 4 mm. FRUITS ovoid, 1.5 mm.

Distribution. Northern slopes of the Sierra Nevada (Granada, Spain). 1700–2400 m. Supramediterranean and oromediterranean.

Phenology. Flowering in July. Seeds maturing in July and early August.

Habitat. In stony places in summit zones of the supramediterranean belt and the lower horizon of the oromediterranean belt within *Astragalo boissierii–Festucetum hystricis* Quézel, 1953 of Sierra Nevada.

Specimens studied. GRANADA: Sierra Nevada (Monte Verde near La Cortijuela), 22.vii.1851, *Bourgeau 1425 a* (BM, G 7505–12, LY, P); Sierra Nevada (Panderona), 28.vii.1879, *Huter, Porta & Rigo 1058* (GH); Sierra Nevada (Jerez del Marquesado), 7.viii.1953, *Jerónimo* (ALMERIA 5529); Sierra Nevada (Dornajo), 22.viii.1979, *Pérez-Raya & Molero Mesa* (MA 436771); Sierra Nevada (E1 Dornajo), 1985, *Alcaraz* (MUB 14170); Sierra Nevada (E1 Dornajo), 17.vii.1986, *Rivera, Obón, Asencio et als.* (MUB 37088); Sierra Nevada (El Dornajo), 19.vii.1986, *Alcaraz* (MUB 29927); Sierra Nevada, Panderón, 28.vii.1879, *Huter Porta & Rigo 1058* (K).

Sideritis glacialis subsp. *fontqueriana* Obón & D. Rivera Phanerogamarum Monographiae, 21: 209 (ix.1994). Figs 8, 9.

Holotype. SPAIN, prov. Teruel, near la Virgen de la Vega in Alcalá de la Selva (valley below the Collado de la Gitana), 10.vii.1946, *Font-Quer, Sierra and Torres* (HAH

18878; holotype is the specimen contained within a cellophane envelope). Isotypes in MA (MA 1618, MA 364902).

Synonyms

– *S. glacialis* var. *pulvinata* Font Quer, *Fl. Hispan. Tercera Cent.*: 7–8, 1947. (Nomen nudum, Art. 32.1).
– *S. glacialis* subsp. *pulvinata* (Font Quer) Mateo, *Claves para la Flora de la Provincia de Teruel*: 390, 1992. (Comb. inval.).
– *S. javalambrensis* Rivas Goday & Borja (1961), non Pau.

BASAL PARTS woody, persistent and cushion-shaped; to 15 cm, including branches. Non woody branches erect and ascending to 8–10 cm. Hair covering at the base of branchlets holotrichous and homotrichous; glands absent, glandular hairs absent. Trichomes abundant, antrorse, 10–15 mm, with 2–3 cells band-shaped, the apical cell band-shaped. LOWER LEAVES, 4–9 × 1–2 mm, entire, lanceolate, acute; glands extremely scarce, glandular hairs absent, trichomes scarce to abundant, neatly differentiated in the margin, 0.8–1.2 mm; upper leaves similar to the lower. INFLORESCENCES yellowish-green at the corners of the axis, bracts and calyces; ovoid to globose, 0.5–2 cm, with 1–5 verticillasters, the central 2 mm apart. LOWER BRACTS erecto-patent, trullate, widest zone 3/7 from the base, divided to 1/4, 5–7 × 8 mm, 2–5 teeth on each side; middle bracts erecto-patent, trullate, widest zone 3/5 from the base, divided to 1/4, 5 × 6 mm, three teeth on each side. Abaxial surface: glands absent, glandular hairs absent, trichomes abundant, 8–12 mm, with three cylindrical cells, apical cell conical. VERTICILLASTERS with 6 flowers. CALYCES campanulate, 5 mm, with five subequal divergent teeth, 1 mm, ending in spines 0.1 mm. Carpostegium continuous or discontinuous. Outer surface of calyx: glands scarce to abundant, glandular hairs absent, trichomes abundant, 1 mm. COROLLAS 5–7 mm, 2-lipped for 1/3 of their length, yellow. Stamens included in the corolla tube, filaments 0.9–1.2 mm. Style up to 3 mm. FRUITS ovoid, 1–1.2 mm.

Distribution. Endemic to Gúdar mountains (Teruel, Spain). 1800–2000 m. Supramediterranean and oromediterranean.

Phenology. Flowering from late July to early August. Seeds maturing in August.

Habitat. High mountain rocks, screes. In *Sideritido pulvinatae–Arenarietum erinaceae* (Rivas Goday & Borja) and in high mountain grasslands of *Paronychio capitatae–Artemisietum lanatae* (Rivas Goday & Borja, 1961).

Specimens studied. TERUEL: Sierra de Gúdar, 24.vi.1946, *Rivas Goday* (MAF 77086); Near la Virgen de la Vega in Alcalá de la Selva (valley below the collado de la Gitana), 10.vii.1946, *Font Quer, Sierra & Torres* (HAH 18878, holotype; MA 1618 & MA 344902, isotypes); Altiplano de los Monegros (Gúdar), 5.vii.1957, *Esteve* (HAH 18877); Pine forest of la Cespedosa in Linares (Sierra de Gúdar), 30.vii.1957, *Borja* (MAF 65725); Sierra de Gúdar, 5.viii.1974, *G. López & Valdés Bermejo* (MA 435326); Puerto de Valdelinares, 5.viii.1982, *Molina* (MAF 120116).

ACKNOWLEDGEMENTS

The authors wish to express their thanks to Dr A. Charpin, curator of the Boissier Herbarium at Geneva, for kindly allowing us the loan of the type specimens for

study. Acknowledgement is also made to the curators of the herbaria BM, CGE, COI, G, GH, GDA, HAH, K, LY, MA, MAF, MGC, MUB, P, TL, and to Mr R. Auriault for similar help. We are indebted to the referees and editors for their comments and detailed revision of our manuscript.

REFERENCES

Boissier E. 1841. *Voyage botanique dans le midi de l'Espagne, Livraison 16, Vol. 2*. Paris: Gide & Cie.

Boissier E. 1859. *Diagnoses plantarum orientalium novarum. Ser. 2, Vol. 3/4*. Leipzig: B. Hermann.

Boucher C. 1982. Contribution à l'étude de la végétation orophile des sierras d'Andalousie calcaire (Espagne). *Ecologia Mediterranea* **8**(3)**:** 69–83.

Burdet H, Charpin A, Jacquemoud F. 1987. Types nomenclaturaux des taxa ibériques décrits par Boissier ou Reuter. vii. Labiées. *Candollea* **42:** 111–127.

Cuatrecasas J. 1930. Adiciones y correcciones a mis estudios sobre Mágina. *Cavanillesia* **3:** 8–19.

Fernández-Peralta MD. 1981. Estudios citogenéticos y evolutivos en el género *Sideritis*. Unpublished Ph. D. thesis. Universidad Autónoma de Madrid. Madrid.

Gonzalez-Tejero R. 1992. Estudio etnobotánico en la provincia de Granada. Granada: Universidad de Granada (Microfiche).

Losa JM, Molero J, Casares M. 1986. *El paisaje vegetal de Sierra Nevada. La cuenca alta del rio Genil*. Granada: Universidad de Granada.

Martínez-Parras JM, Peinado M, Alcaraz F. 1987a. Datos sobre la vegetación de Sierra Nevada. *Lazaroa* **7:** 515–533.

Martínez-Parras JM, Peinado M, Alcaraz F. 1987b. *Comunidades vegetales de Sierra Nevada (España)*. Granada: Universidad de Granada.

Molero J, Perez-Raya J. 1987. *La flora de Sierra Nevada*. Granada: Universidad de Granada.

Obón C, Rivera D. 1994. *A taxonomic revision of Section Sideritis, Genus Sideritis (Labiatae)*. Berlin. J. Cramer.

Pérez-Raya F, López J, Molero J, Valle F. 1990. *Vegetación de Sierra Nevada*. Granada: Ayuntamiento & Universidad de Granada.

Peris JB, Stübing G, Olivares A, Marti J. 1994. *Sideritis boissierana*, especie nueva de Sierra Nevada. *Fontqueria* **39:** 59–63.

Podani J. 1991. *Syn-Tax IV. Computer Programs for Data Analysis in Ecology and Systematics on IBM-PC and Macintosh Computers. User's Manual*. Trieste: International Centre for Science and High Technology.

Polunin O, Walters M. 1985. *A guide to the vegetation of Britain and Europe*. Oxford: Oxford University Press.

Quézel P. 1953. Contribution à l'étude phytosociologique de la Sierra Nevada. *Memórias da Sociedade Broteriana* **9:** 5–77.

Rivas-Goday S. 1969. Algunas novedades fitosociológicas de España Meridional. *Collectanea Botanica (Barcelona)* **7**(2): 997–1031.

Rivas-Goday S, Borja J. 1961. Estudio de vegetación y flórula del Macizo de Gúdar y Jabalambre. *Anales del Jardín Botánico de Madrid* **19:** 3–550.

Rivas-Martínez S. 1965. Esquema de la vegetación potencial y su correspondencia con los suelos en la España Peninsular. *Anales del Jardín Botánico de Madrid* **22:** 341–405.

Rivera D, Obón C, Tomás-Lorente F, Ferreres F, Tomás-Barberán F. 1990. Infrasectional systematics of the genus *Sideritis* L. Section *Sideritis* (Lamiaceae). *Botanical Journal of the Linnaean Society* **103:** 325–349.