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Research article

Linaria sagrensis (Plantaginaceae), a new high mountain species from the SE Iberian Peninsula

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Linaria sagrensis, from the south-eastern Iberian Peninsula, is here newly described, illustrated, and compared with its morphologically closest relatives from *L.* sect. *Supinae*: *L. pruinosa*, *L. nevadensis*, *L. glacialis* and *L. alpina* subsp. *alpina*. The species is characterized by being perennial, entirely glandular-hairy, with inflorescence dense and corymbiform, and calyx lobes unequal; corolla small, pinkish-violet, with conspicuous dark veins and yellow to orangish palate, and spur shorter than the rest of the corolla; capsule globose, glandular-hairy at apex; seeds large, black to dark greyish, with apparently smooth disc, though with very few and scattered small tubercles, and light-grey wing. *Linaria sagrensis* is endemic to Sierra de la Sagra (N Granada province, Spain), growing in calcareous screes of the Mediterranean high mountain. Additionally, *L. aeruginea* subsp. *pruinosa* is here raised to species rank, *L. pruinosa*, and therefore a new combination is proposed. The value of seed characters in *Linaria* taxonomy is discussed based on newly discovered infraspecific variability in several taxa.

Keywords: Antirrhineae, Betic Massif, endemic plants, Granada province, *Linaria* sect. *Supinae*, seed micromorphology, Sierra de la Sagra, Spain, taxonomy

Introduction

Linaria Mill. is the largest genus of the tribe Antirrhineae Dumort. (Plantaginaceae *sensu* APG IV 2016), including nearly 150 species, distributed mainly in Europe, North Africa, and western as well as central Asia, with some taxa being introduced or naturalized in other areas (Sutton 1988). This genus ranks fifth among the vascular plant genera with the highest numbers of endemic species in the Iberian Peninsula

(Buira et al. 2016). Recent phylogenetic studies have pointed out the monophyly of this genus (Blanco-Pastor et al. 2012, Fernández-Mazuecos et al. 2013).

Among the seven sections of the genus recognized by botanists (cf. Sutton 1988), *Linaria* sect. *Supinae* (Benth.) Wettst. is the most complex taxonomic section, including approximately a third of the species of the genus, and its main centre of diversity is found in the Iberian Peninsula and the Maghreb (Valdés 1970, Hong 1983, Sutton 1988, Sáez et al. 2004, Sáez and Bernal 2009, Blanco-Pastor et al. 2012, Fernández-Mazuecos et al. 2013, Vigalondo et al. 2015). This section comprises hermaphroditic annual and perennial herbs, mostly with heteromorphic stems, characterised by flowers arranged in bracteate racemes, with calcarate personate corollas having a well-developed palate that closes the entry to the tube, bilocular ovary, with a simple style and entire stigma, oblong to globose capsule, truncate to slightly emarginated, with locules dehiscing by three valves, and differentiated from species of other sections by having laterally compressed discoid winged seeds in a horizontal arrangement (Valdés 1970, Sutton 1988, Sáez and Bernal 2009, Juan et al. 2018).

Among the three subsections recognized by Blanco-Pastor et al. (2012), *L.* sect. *Supinae* subsect. *Supinae* includes perennial to annual herbs, with globose capsule and membranous seed wings. Sáez and Bernal (2009) assigned 26 species or 46 taxa (including subspecies) from the Iberian Peninsula and Balearic Islands to this subsection. Many of these taxa are endemic to relatively small areas and often show specialized ecological behaviour, with narrow southern Iberian distributions (Valdés 1970, Sutton 1988, Sáez et al. 2004, 2009, Sáez and Sainz 2011, Blanca et al. 2023).

Within the framework of our studies on the vascular flora of Andalusia (Fuentes et al. 2017, 2018, 2019, 2020, 2021, 2022) and more particularly on the genus *Linaria* (Blanca et al. 2017, 2018, 2022, 2023, Juan et al. 2018), we found in Sierra de la Sagra (municipality of Huéscar, N Granada province, Spain) some plants belonging to the aforementioned genus that at first appeared to belong to *L. aeruginea* (Gouan) Cav. s.l., or even more particularly to the subsp. *pruinosa* (Sennen and Pau in Pau) Chater and Valdés, but they had high glandulosity, very small flowers, and, contrarily, large and additionally smooth seeds with a few widely spaced small tubercles on the disk, and a biotype specially adapted to the high-mountain scree in which they grow.

A preliminary identification, based on 'Flora iberica' (Sáez and Bernal 2009), led us to the couplet no. 16, that leads to *L. verticillata* Boiss. or *L. diffusa* Hoffmanns. and Link. Compared to the first of these two species, the plant from Sierra de la Sagra also has much smaller flowers, while *L. diffusa* is a notably different annual species that inhabits the N and C Portugal and León province (NW Spain).

Another possibility that we also took into account is that, due to its practically smooth seeds, it could be *L. accitensis* L. Sáez et al., a species recently described from relatively nearby localities (NW Granada province); but this species has a markedly different morphology in its glabrous inflorescence axis (sometimes with short glanduliferous hairs), longer racemes, glabrous calyx lobes, a larger, white corolla, a glabrous capsule, and smaller seeds, and inhabits volcanic soils (andesites and alkaline basalts) at lower elevations (800–1000 m a.s.l.).

Subsequently, we carried out a field study of the populations detected, verifying that the individuals analyzed invariably inhabit calcareous screes. Finally, we also compared the species from Sierra de la Sagra, which lives above 2200 m a.s.l., with other high-mountain species, specifically with *L. glacialis* Boiss., *L. nevadensis* (Boiss.) Boiss. and Reut. and *L. alpina* (L.) Mill., from which we also noted great differences, thus supporting the taxonomic distinctiveness of the species which is here described as new.

Material and methods

Morphological observations and measurements of vegetative and reproductive parameters were undertaken on plant material kept at the herbaria BC, G, GDA, GDAC, HUAL, MA, MGC and SEV. Seeds were gold-coated for micrographs to be taken with a Field Emission Scanning Electron Microscope (FE-SEM, GEMINI, SIGMA 300 VP, ZEISS). For taxonomic identification, Spanish floras and specific scientific works (Sutton 1988, Sáez and Bernal 2009, Sáez and Sainz 2011) were used. Diagnostic characters reported by Sutton (1988) and Sáez and Bernal (2009) and other key features based on our field experience were included. The descriptive terminology follows Sutton (1988) and Simpson (2006). To evaluate the conservation status of the new species, the IUCN (2012, 2017) Red List categories and criteria were used. The distribution map of the species and localities studied was drawn with free and open source QGIS with the coordinate reference system WGS 84 / UTM zone 30S.

Taxonomic results

The combination of characters with diagnostic value, the ecological specificity, and a review of the foremost regional floras and taxonomic revisions (Willkomm and Lange 1865–1870, Willkomm 1893, Coutinho 1939, Tutin et al. 1972, Franco 1984, Valdés et al. 1987, Sutton 1988, Castroviejo et al. 2009, Blanca et al. 2011) supported that the assignment of the individuals from Sierra de la Sagra (Granada, Spain) belong to a new species, described below.

Linaria sagrensis Blanca, Cueto, J.Fuentes, L. Gutiérrez and F.B.Navarro sp. nov. (Fig. 1–3, Table 1)

A species differing from *L. pruinosa* (Sennen and Pau) L. Sáez et al., *L. nevadensis* (Boiss.) Boiss. and Reut., *L. glacialis* Boiss. and *L. alpina* Mill. subsp. *alpina* in being entirely glandular-hairy, having dense and corymbiform racemes to 1.5 cm long, short pedicels only (0.1–)0.2–0.5 mm in flower, and smaller corolla (12–14 mm long, with spur 4.0–5.5 mm

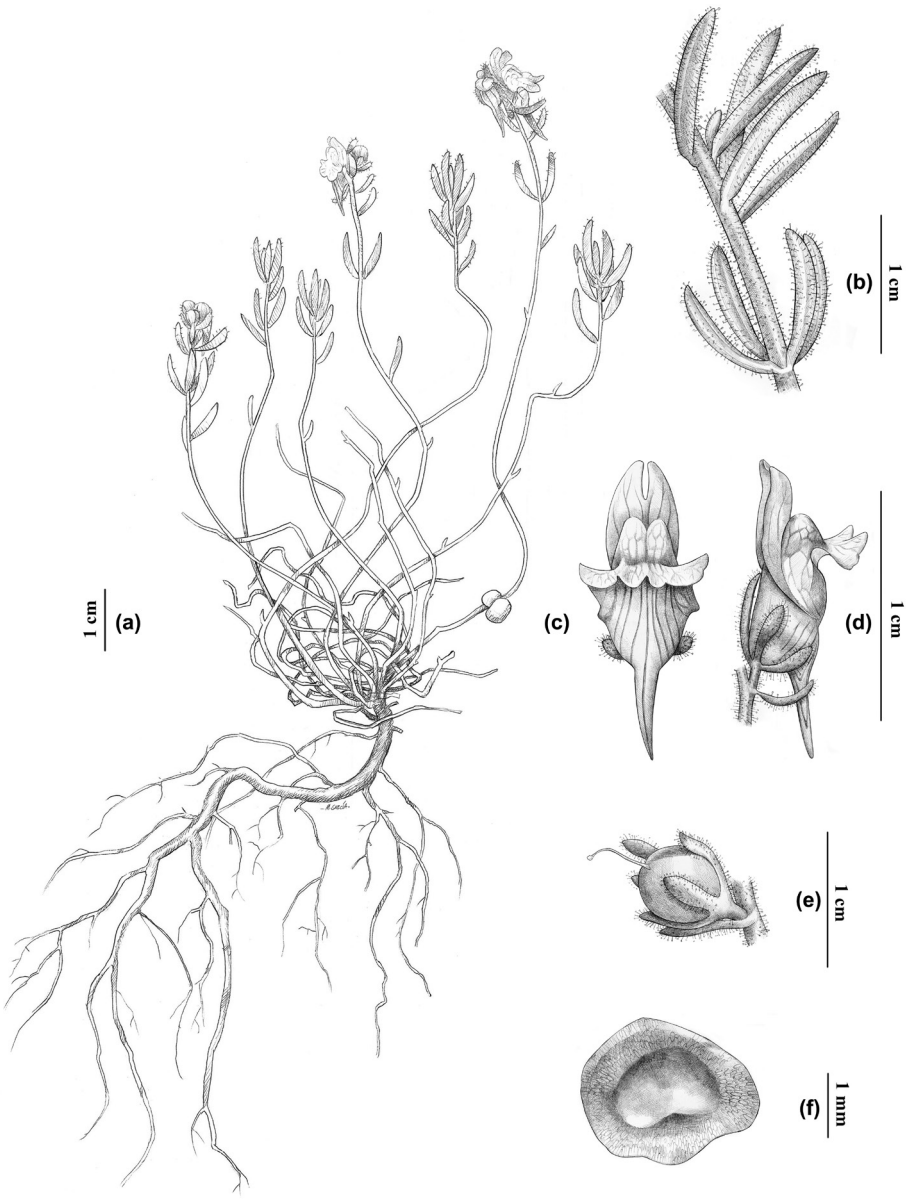

Figure 1. *Linaria sagrensis* sp. nov. (from holotype). (a) Habit, (b) detail of leaves (fertile stems), (c) flower front view, (d) flower lateral view, (e) capsule, (f) seed front view.

long) (versus glabrous to glandular-hairy in the inflorescence or rarely in the upper half, usually longer racemes 0.8–12.0 cm long, pedicel (0–)0.5–12.0 mm long in flower, corolla (11–)12–31 mm long, and spur 5–15 mm long). It also differs from *L. pruinosa* in having a pinkish-violet corolla and light-grey seed-wing colour (versus greyish-rose to pinkish-purple corolla and black or greyish seed-wing colour). It also differs from *L. nevadensis* in having a pinkish-violet corolla, and seeds 2.4–3.0 × 2.5–3.5 mm with smooth disc surface (versus yellow corolla, and smaller seeds with smooth or tuberculate disc surface, sometimes with anastomosed tubercles forming ± sinuose ridges). It also differs from *L. glacialis* in having leaves 3–5-verticillate, linear, bracts 2.0–5.0 × 0.3–0.9 mm, and smaller capsule of 4–6 × 4–6 mm (versus leaves four-verticillate, elliptic to linear-lanceolate, bracts 12.0–20.0 × 1.2–3.0 mm, and capsule (5–)7–8(–10) × 7–8(–10) mm). Finally, the new species is distinct from *L. alpina* subsp. *alpina* in having leaves 4.0–12.0 × 0.5–1.2 mm, corolla pinkish-violet, capsule glandular-hairy at apex, and light-grey seed-wing colour (versus leaves 2.5–25.0 × 0.6–5.0 mm, blue-violet, pink or yellow corolla, glabrous capsule and grey or black seed-wing colour).

Type: Spain, Granada province: Huéscar, Sierra de la Sagra, orientación NE, gleras de naturaleza caliza, localmente abundante, cohabita con *Crepis granatensis*, UTM 30S WH3800, 2250 m, 23 June 2022, J. Fuentes and F. B. Navarro (holotype: GDA-Fanero 70256; isotype: HUAL 29711).

Figure 2. *Linaria* taxa studied: (a–d) *Linaria sagrensis* sp. nov. ((a) habit; (b) flower detail; (c) capsules detail; (d) small tubers detail). (e) *Linaria pruinosa,* (f) *Linaria nevadensis,* (g) *Linaria glacialis,* (h) *Linaria alpina* subsp. *alpina.* Photographs: (a–d) Granada, Huéscar, Sierra de la Sagra, by J. Fuentes; (e) Majorca, Puig de Massanella, by L. Sáez; (f–g) Granada, Sierra Nevada, Veleta, by G. Blanca; (h) Huesca, Cerler, by G. Blanca.

Etymology

The specific epithet refers to Sierra de la Sagra, located in Huéscar (north of the Granada province, Andalusia, Spain), which with 2383 m in elevation is the highest mountain in the southern half of the Iberian Peninsula, after Sierra Nevada.

Description

Herbaceous perennial plant, with strong and profusely branched roots; glaucous, entirely glandular-hairy, with very densely set and glandular hairs up to 0.8 mm long in the inflorescence and upper half, short glandular hairs or subsessile glands towards base, more rarely glabrescent at base. Fertile stems 1–10(–15), 5–22(–23) cm long, decumbent, flexuose and fragile, often with small tubers in the leafless part hidden between stones (Fig. 2d), simple or sparsely branched; sterile stems 1–10, shorter, 4–15 cm long. Leaves in whorls of 3–5, the upper opposite to alternate, linear; leaves of fertile stems 4.0–12.0 × 0.5–1.2 mm; leaves of sterile stems

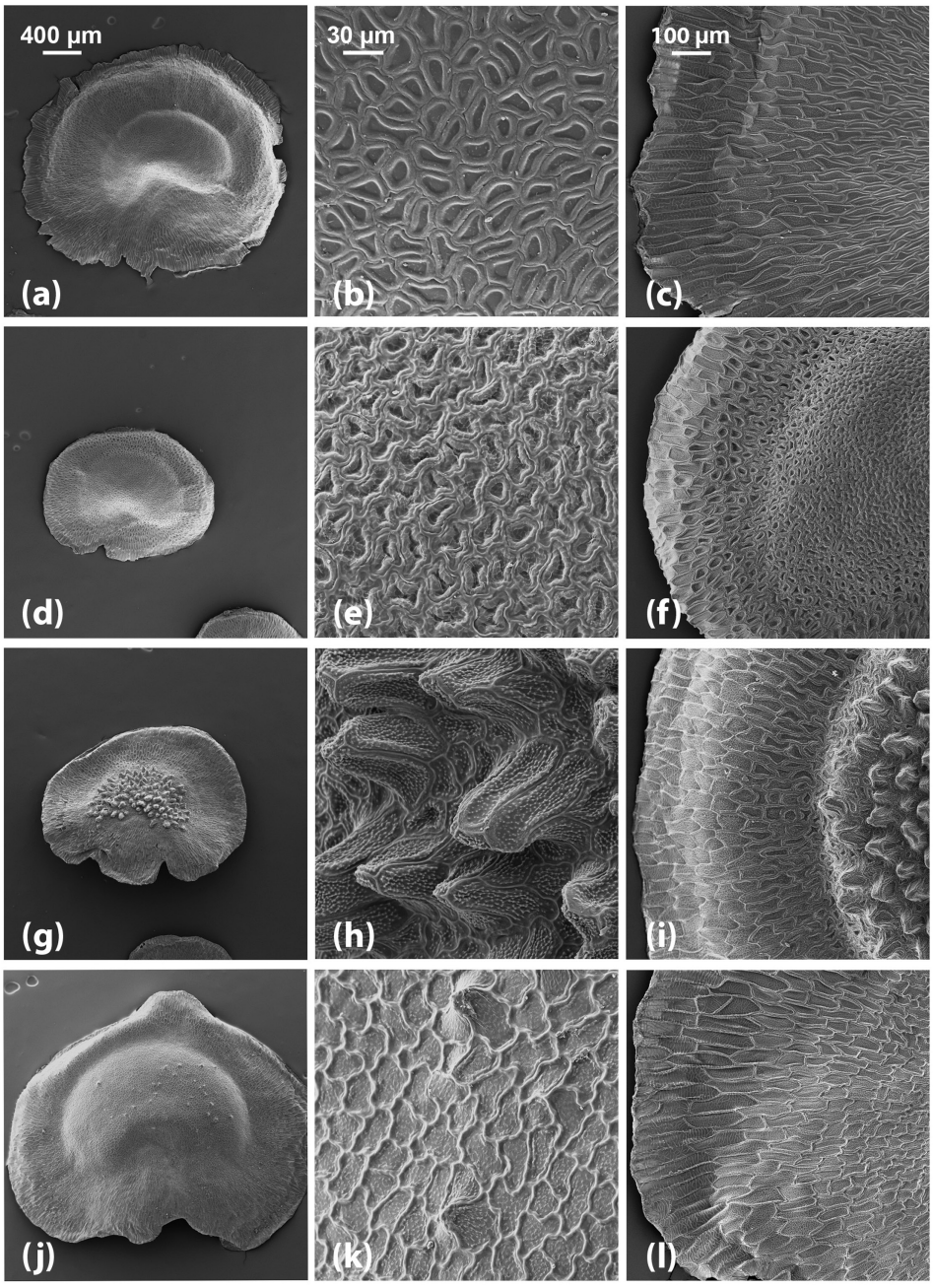

Figure 3. Seeds SEM micrographs of: (a–c) *Linaria pruinosa* (GDA-Fanero 70260), (d–f) *Linaria nevadensis*, smooth seed (GDA-Fanero 70259), (g–i) *Linaria nevadensis*, tuberculated seed (GDAC 2368), (j–l) *Linaria sagrensis* (GDA-Fanero 70256). [Scale bars: (a, d, g, j) overview of the seeds 200 µm; (b, e, h, k) disc detail 30 µm; (c, f, i, l) wing detail 100 µm].

3.5–9.0 × 0.3–0.9 mm. Inflorescence up to 1.5 cm long during anthesis, simple, dense, corymbiform, with 2–7(–8) flowers, remaining dense in fruiting; axis densely glandular-hairy, with hairs 0.2–0.8 mm long. Bracts 2.0–5.0 × 0.3–0.9 mm, linear-oblong to narrowly oblanceolate, glandular-hairy. Pedicels (0.1–)0.2–0.5 mm long in flower, 1.0–1.5 mm long in fruit, erect to ascending. Calyx lobes unequal, oblanceolate, acute to subobtuse, glandular-hairy; adaxial lobe 3.5–4.5 × 0.6–0.9 mm in flower and 4.0–6.0 × 0.6–0.9 mm in fruit; abaxial lobes 2.5–3.0 × 0.6–0.8 mm in flower and 3.0–3.5 × 0.6–0.8 mm in fruit. Corolla 12–14 mm long, pinkish violet, with yellow to orangish palate and conspicuous dark veins; tube (2–)2.5–3.5 mm broad in dorsiventral section, erect; adaxial lip sinus 1.0–1.2 mm; spur 4.0–5.5 × 0.7–1.5 mm (the width measured at the base), straight or slightly curved, shorter than the rest of the corolla, yellowish. Capsule 4–6 × 4–6 mm, globose, glandular-hairy at apex. Seeds 2.4–3.0 × 2.5–3.5 mm, suborbicular–reniform, discoid, slightly concave–convex or flat (Fig. 3j); disc reniform, black to dark greyish, smooth, sometimes with very few and scattered small

Table 1. Comparison of *Linaria sagrensis* with its closest relatives in *L.* sect. *Supinae*. Abbreviations: fl.: flower; fr.: fruit. (data according *to Sáez and Bernal 2009, and own observations).

	*Linaria pruinosa**	*Linaria nevadensis**	*Linaria sagrensis*	*Linaria glacialis**	*Linaria alpina subsp. alpina**
Habit	Perennial	Perennial	Perennial	Perennial	Annual, biannual or perennial
Vestiture	Glandular-hairy in the inflorescence	Glandular-hairy in the inflorescence (sometimes in the upper half)	Entirely glandular-hairy	Glandular-hairy in the inflorescence and upper leaves	Glabrous (see inflorescence)
Fertile stems length (cm)	4.5–28.0	4–15	5–22(–23)	5–20	5–40
Leaves (fertile stems)					
Arrangement	3–4-verticillate, upper alternate	3–5-verticillate, upper alternate	3–5-verticillate, upper opposite to alternate	Four-verticillate, upper opposite to alternate	(3–)4–6-verticillate, upper alternate
Shape	Linear to linear-elliptic	Linear to linear-elliptic	Linear	Elliptic to linear-lanceolate	Narrowly elliptical or obovate to linear
Size (mm)	3.0–15.0 × 0.4–1.9	2.0–20.0 × 0.3–1.0	4.0–12.0 × 0.5–1.2	7–26 × 2–7	2.5–25.0 × 0.6–5.0
Inflorescence					
Racemes (anthesis)	±Dense	Dense	Dense, corymbiform	Dense	Dense to ± lax
Length in flower (cm)	to 3	0.8–1.5(–2.0)	to 1.5	to 5	to 12 cm
Axis	Glandular-hairy	Glandular-hairy	Glandular-hairy	Glandular-hairy	Glabrous (sometimes with glanduliferous hairs)
Hair length (mm)	0.2–1.0	0.1–0.6	0.2–0.8	(0.1–)0.2–0.7	0.3–1.7
No. flowers	1–5(–8)	1–5(–8)	2–7(–8)	2–10	1–12
Bract size (mm)	3.0–10.0 × 0.5–1.2	(2.0–)2.5–4.0(–5.0) × 0.5–1.1	2.0–5.0 × 0.3–0.9	12.0–20.0 × 1.2–3.0	2.7–10.0 × 0.5–1.6
Flower (measures in mm)					
Pedicel length fl.	1–6	0.5–2.0	(0.1–)0.2–0.5	0–3	1.5–12.0
Pedicel length fr.	(2–)3–14	(1–)2–3(–4)	1.0–1.5	2.5–7.1	2.5–15.0
Calyx lobes	Slightly unequal, glandular-hairy	Unequal, glandular-hairy	Unequal, glandular-hairy	Unequal, glandular-hairy	Unequal, glabrous, rarely glandular-hairy
Calyx adaxial lobe fl.	4.5–5.0 × 0.4–0.9	4.5–5.5 × 0.3–0.8	3.5–4.5 × 0.6–0.9	9.0–11.0 × 1.0–1.4	3.5–6.0 × 0.5–0.9
Calyx adaxial lobe fr.	4.5–6.0 × 0.5–1.1	5.5–6.0 × 0.5–0.8	4.0–6.0 × 0.6–0.9	11.0–13.0 × 1.0–1.5(–2.0)	4.5–6.1 × 0.5–1.0
Calyx abaxial lobe fl.	3.5–4.0 × 0.5–1.2	3.0–4.0 × 0.6–1.0	2.5–3.0 × 0.6–0.8	8.0–10.0 × 0.8–1.6	3.0–5.0 × 0.6–1.4
Calyx abaxial lobe fr.	3.5–4.5 × 0.7–1.3	3.5–4.6 × 0.5–1.0	3.0–3.5 × 0.6–0.8	10.0–11.1× 1.2–2.1	3.4–5.2 × 0.6–1.7
Corolla colour (all four species have a yellow, orangish, to dark brown palate)	Greyish-rose to pinkish-purple, with conspicuous dark veins	Yellow, with conspicuous dark veins	Pinkish-violet, with conspicuous dark veins	Violet or violet-greyish, sometimes whitish or violet-whitish, with conspicuous violet veins	Blue-violet, pink or yellow
Corolla length	18–27	(11–) 13–17	12–14	19–31	12–30
Width tube	5–6	2.7–3.5	(2.0–)2.5–3.5	5–7	(1.5–)2.0–4.0(–4.5)
Spur shape	Slightly curved	±Curved	Straight or slightly curved	Straight or ± curved	Straight or somewhat curved
Spur length	7.5–10.5	5.0–8.5	4.0–5.5	7–15	(5–)8–14
Spur width	1.0–1.7	1.0–1.3	0.7–1.5	4.0–5.5	1–2
Capsule					
Size (mm)	4.5–6.5 × 4.5–6.5	4.5–5.5 × 4.0–5.0	4–6 × 4–6	(5–)7–8(–10) × 7–8(–10)	3.0–7.0 × 3.0–7.1
Indument	Glabrous or glandular-hairy at apex	Glandular-hairy at apex	Glandular-hairy at apex	Glabrous to glandular-hairy at apex	Glabrous

(Continued)

Table 1. Comparison of *Linaria sagrensis* with its closest relatives in *L.* sect.

	*Linaria pruinosa**	*Linaria nevadensis**	*Linaria sagrensis*	*Linaria glacialis**	*Linaria alpina subsp. alpina**
Seed					
Size (mm)	2.2–3.5 × 1.5–3.0	1.2–2.0 × 1.1–1.5	2.4–3.0 × 2.5–3.5	2.4–3.1 × 2.4–2.6	1.6–3.3 × 1.5–3.1
Disc colour	Black to dark grey	Dark grey	Black to dark greyish	Grey-whitish or black	Dark grey, brown or black
Disc surface	Smooth	Smooth or tuberculate (sometimes with anastomosed tubercles forming ± sinuose ridges)	Smooth, sometimes with very few and scattered small tubercles	Smooth or tuberculate (sometimes with anastomosed tubercles forming ± sinuose ridges)	Smooth or tuberculate
Wing width (mm)	(0.4–)0.5–0.9(–1.2)	0.2–0.4	(0.5–)0.6–0.8	0.6–1.0	0.3–0.7
Wing colour	Black or greyish	Grey or grey-yellow	Light grey	Whitish or dark grey	Grey or black
Distribution	Sierra de Tramuntana (Majorca, Balearic Islands)	Sierra Nevada (Almeria and Granada provinces, Spain)	SE Spain (Sierra de la Sagra, Granada province)	Sierra Nevada (Almeria and Granada provinces, Spain)	Mountains of C & S Europe (to N & C Iberian Peninsula)
Habitat	Calcareous screes	Schistous screes	Calcareous screes	Schistous screes	Calcareous or siliceous stony and rocky

tubercles (Fig. 3k); wing (0.5–)0.6–0.8 mm wide, subentire (Fig. 3l), not thickened, light grey.

Seed morphology

Figure 3 and 4 show the characteristics of the seeds of the species studied. *Linaria pruinosa* (Fig. 3a) has seeds 2.2–3.5 × 1.5–3.0 mm, with a smooth and black or dark-grey disc surface, and a noticeably broad wing (0.4–)0.5–0.9(–1.2) mm wide (Fig. 3c) that is black or greyish. Testa-cells from disc showing thick and hardly sinuate anticlinal walls, and scarcely verruculate periclinal walls (Fig. 3b). See also the SEM photos provided by Sáez et al. (2004).

Linaria nevadensis has the smallest seeds among all species studied (1.2–2.0 × 1.1–1.5 mm), with a smooth (Fig. 3d) or prominently tuberculate (Fig. 3g) and dark-grey disc surface, and wing 0.2–0.4 mm wide (Fig. 3f, i) and grey or greyish-yellow. Testa-cells from disc show sinuate anticlinal walls, and finely striate-verruculate periclinal walls (Fig. 3e, h); in tuberculate seeds, the tubercles sometimes anastomose forming ± sinuose ridges (Fig. 3i).

Linaria sagrensis (Fig. 3j) produces seeds 2.4–3.0 × 2.5–3.5 mm, with a smooth and black to dark-greyish disc surface, sometimes with very few, small, scattered tubercles (Fig. 3j, k) with wing (0.5–)0.6–0.8 mm wide (Fig. 3l) and light grey. Testa-cells from disc show sinuate anticlinal walls, and a finely verruculate periclinal walls (Fig. 3k).

Linaria glacialis has seeds 2.4–3.1 × 2.4–2.6 mm, with a smooth (Fig. 4a) or prominently tuberculate (Fig. 4d) and grey-whitish or black disc surface, and a wing 0.6–1.0 mm wide (Fig. 4c, f) that is whitish or dark grey. Testa-cells from disc show sinuate anticlinal walls, and reticulate-verruculate periclinal walls (Fig. 4b, e); in tuberculate seeds, the tubercles sometimes anastomose forming ± sinuose ridges (Fig. 4d-f).

Finally, *Linaria alpina* subsp. *alpina* produces seeds that are 1.6–3.3 × 1.5–3.1 mm, with a smooth (Fig. 4g) or tuberculate (Fig. 4j) and dark-grey, brown or black disc surface, and a 0.3–0.7 mm wide wing (Fig. 4i, l) that is grey or black. Testa-cells from disc show sinuate anticlinal walls, and reticulate periclinal walls (Fig. 4h, k).

Phenology

The flowering period of *L. sagrensis* spans June–July, although depending on the yearly climatic conditions it can start in mid-May. The fruiting time also spans June–July.

Habitat and distribution

Linaria sagrensis should be considered an endemic species of Sierra de la Sagra (Huéscar, N Granada province), which forms part of the Betic Massif in the south-eastern Iberian Peninsula (Fig. 5). The species grows in periglacial calcareous screes (Jurassic age), above 2200 m a.s.l., under a Mediterranean pluviseasonal continental bioclimate with a Oromediterranean thermotype and Subhumid to Humid ombrotype (Rivas Martínez et al. 2002), on very steep slopes that can cause slight displacement of the stones (Fig. 5a). There it coexists, for example, with *C. granatensis* (Willk.) Blanca and Cueto and *Platycapnos saxicola* Willk. i.e. species with

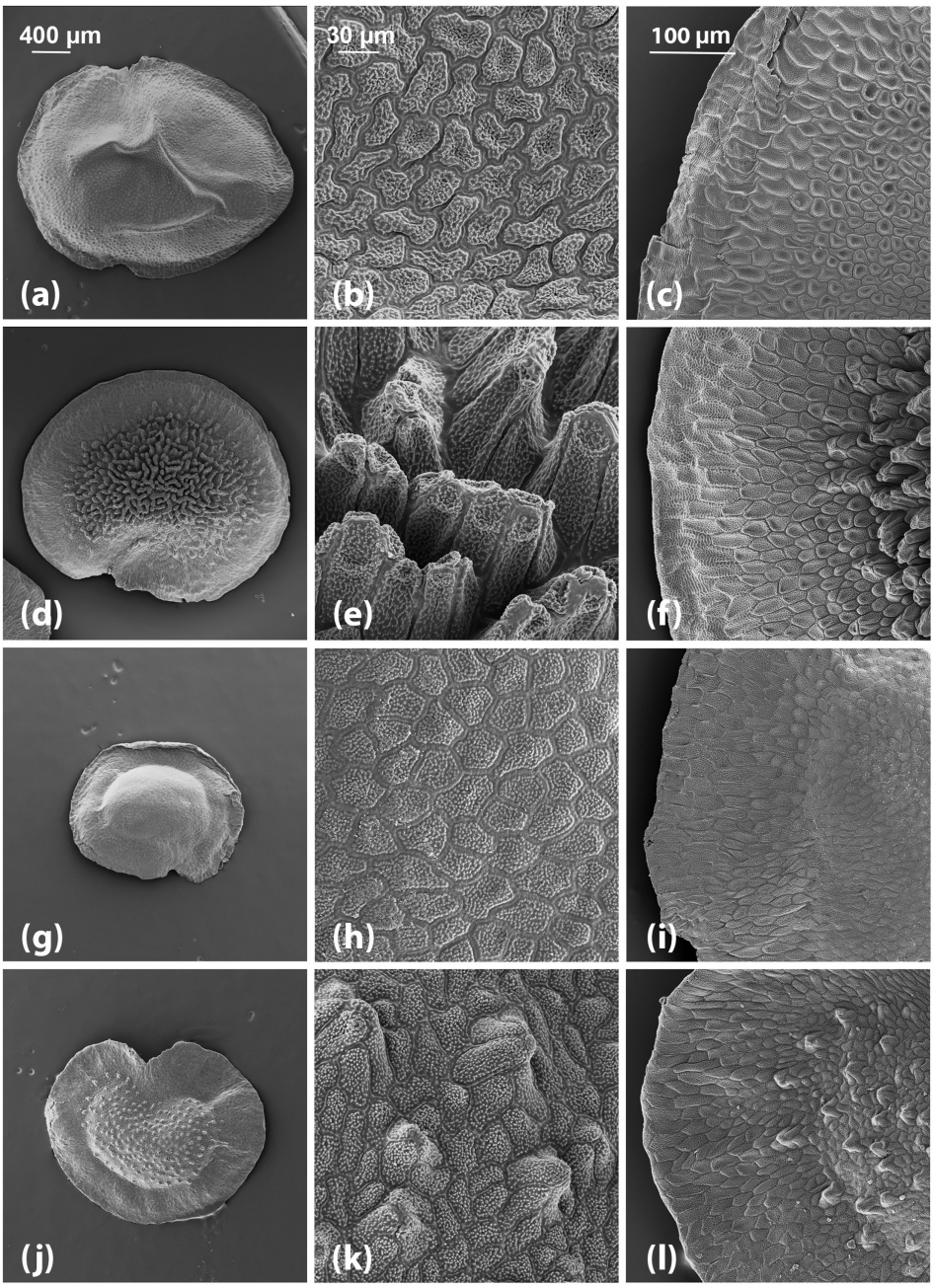

Figure 4. Seeds SEM micrographs of: (a–c) *Linaria glacialis*, smooth seed (GDA 39409), (d–f) *Linaria glacialis*, tuberculated seed (GDA 9188), (g–i) *Linaria alpina* subsp. *alpina*, smooth seed (GDA 23346), (j–l) *Linaria alpina* subsp. *alpina*, tuberculated seed (GDA-Fanero 69005). [Scale bars: (a, d, g, j) overview of the seeds 200 µm; (b, e, h, k) disc detail 30 µm; (c, f, i, l) wing detail 100 µm].

which it shares the same adaptations: they all are hemicryptophytes (according to the terminology of Raunkiaer 1934), which present buds that remain at ground level, but in this case in the more consolidated substrate below the layer of stones that forms the scree. As the stone cover is subject to displacements, *L. sagrensis* has developed an intricately branched root system, which remains firmly anchored in the substrate underlying the rocky debris, while the underground part of the stems are leafless, fragile and flexible, winding between the stones until they reach the surface. As the stones move, the stems break easily, but the persistent bud and root remains intact to send out a new aerial structure.

Discussion

The genus *Linaria* is one of the most diversified in the Iberian Peninsula, as indicated by the 54 species considered by Sáez and Bernal (2009) in the most recent review conducted for 'Flora iberica'. Some of these species include

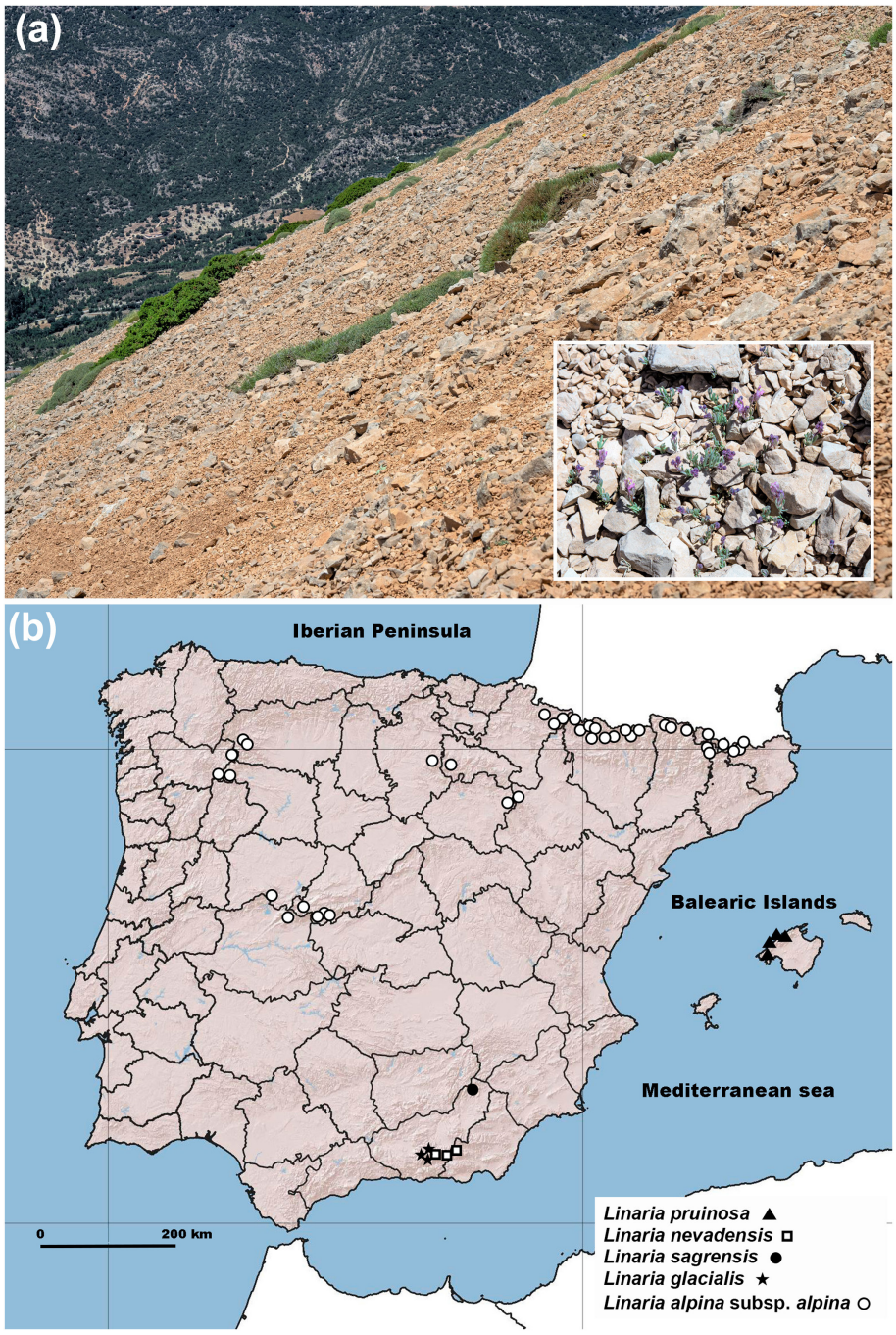

Figure 5. Habitat of *Linaria sagrensis* (a), and distribution map of the species and localities studied (b).

numerous subspecies, and furthermore several new species or subspecies have been described in more recent years (Vigalondo et al. 2015, Blanca et al. 2017, 2018, Juan et al. 2018, Casimiro-Soriguer and Cabezudo 2019, Luceño et al. 2019, Jiménez et al. 2020, Blanca et al. 2022, 2023).

Table 1 lists the main morphological differences between *L. sagrensis* and its most closely related species. *Linaria sagrensis* is characterized (Fig. 1–2) by being perennial and entirely glandular-hairy, having inflorescence dense and corymbiform, calyx lobes unequal, corolla small, pinkish-violet, with conspicuous dark veins and yellow to orangish palate, and spur shorter than the rest of the corolla, capsule globose, glandular-hairy at apex, seeds large, black to dark greyish, with apparently smooth disc, although with very few and scattered small tubercles (Fig. 3j–l), and light-grey wing. These constitute the main characters that easily differentiate *L. sagrensis* from related species, particularly its minute flowers with a pinkish-violet corolla, and the characteristics of its seeds.

Linaria aeruginea is a highly variable and complex species, which in the recent treatment of the genus for *F. iberica*, Sáez

and Bernal (2009) included four subspecies, two of which are more closely related to *L. sagrensis* and are here considered to have specific status: *L. pruinosa* and *L. nevadensis*.

Linaria pruinosa (Fig. 2e) differs from the new species mainly in being glandular-hairy only in the inflorescence, having larger bracts and pedicels, calyx lobes slightly unequal, greyish-rose to pinkish-purple corolla and larger, with longer spur, and smooth (i.e. not tuberculate) seeds (Fig. 3a–c) with a black or greyish wing.

Linaria nevadensis (Fig. 2f) differs in being glandular-hairy only in the inflorescence or sometimes in the upper half, and having a yellow corolla with a longer spur, and smaller seeds with smooth or tuberculate disc surface (Fig. 3d–i), sometimes with anastomosed tubercles forming ± sinuose ridges.

Linaria glacialis and *L. alpina* subsp. *alpina* are much more different morphologically. The former (Fig. 2g) differs in having four-verticillate leaves, elliptic to linear-lanceolate, and longer inflorescence, bracts, calyx lobes, corolla and spur, and lastly, a larger capsule, while *L. alpina* subsp. *alpina* (Fig. 2h) differs in being glabrous (only sometimes with glandular-hairy inflorescence), and having longer leaves, inflorescence, and pedicels, as well as a blue-violet, pink or yellow corolla that is larger, with longer spur, and finally a glabrous capsule, and grey or black seed wing.

To incorporate *L. sagrensis* into the recent comprehensive treatment of the Iberian taxa of *Linaria* (Sáez and Bernal 2009), thereby facilitating its identification, we present here a partial modification of the key provided in Flora iberica. The key is the same until couplet no. 16, where it should be modified as follows:

16 Annual plant; calyx lobes subequal; capsule 3.0–4.0 × 3.0–3.8 mm; seeds 1.3–2.0 × 1.3–2.0 mm, with tuberculate (short and acute tubercles) and papillose disc..... *L. diffusa*
– Perennial plant; calyx lobes unequal; capsule (3.5–) 4.0–7.0 × (3.4–)4.0–6.8 mm; seeds 1.7–3.0(–3.2) × 1.6–3.5 mm, with smooth or tuberculate (obtuse tubercles) and non-papillose disc..... 17
17 Leaves linear; inflorescence up to 1.5 cm long; bracts 2.0–5.0 × 0.3–0.9 mm; corolla 12–14 mm long…*L. sagrensis*
– Leaves linear-oblong, elliptic or ovate; inflorescence up to 18 cm long; bracts 4–10 × 1–3 mm; corolla (15–) 26–33 mm long..... *L. verticillata*

Seed morphology is quite important in the taxonomy of the genus *Linaria*, in particular the presence or absence of a marginal wing (Dumortier 1827, Valdés 1970, Chater et al.1972, Viano 1978a, 1978b, Sutton 1988). Howevwer, as we have previously commented (Blanca et al. 2022, 2023a), authorities diverge concerning the criteria related to the disc-surface ornamentation. In fact, several authors (Sáez and Bernal 2009) have pointed out the variability of the seed-disc surface ornamentation within the same species. That is, for example, Boissier (1841) described *L. glacialis* as having seeds with a tuberculated disk surface, and later Cosson (1852) described a var. *leiosperma* characterized by seeds having a smooth disc surface; long afterwards, Sutton (1988) described *L. glacialis* as having seeds with a smooth disk surface, while Sáez and Bernal (2009) indicated that the surface was smooth or tuberculated.

However, new species of *Linaria* have recently been described from the Iberian Peninsula for which seed ornamentation constitutes one of the main characteristics (Blanca et al. 2018, Juan et al. 2018, Luceño et al. 2019, Jiménez et al. 2020, Blanca et al. 2022, 2023). In all these cases, the populations of these new species have been included in the variability of other more widely distributed species (Blanca et al. 2022, 2023), so that at least in some instances it could be a matter of cryptospecies not yet detected.

In our study, we found variability in the morphology of the seeds of three species that inhabit the high mountains of the Iberian Peninsula, *L. nevadensis*, *L. glacialis* and *L. alpina*, since all of them have both smooth and tuberculate seeds (Fig. 3–4), although these are characters often used to distinguish the species. In the case of *L. alpina*, this morphologically highly variable species has a wide distribution in the C and S mountains of Europe, so the variation in seed morphology may correspond to its broad distribution.

On the other hand, *L. nevadensis* and *L. glacialis* are two species that are well characterized, have only slightly variable morphology and that have a relatively restricted geographic distribution, both being endemic to the Sierra Nevada peaks (SE Iberian Peninsula), between 2000–3400 m. a. s. l. As pointed out above, in *L. glacialis* the variability of its seed morphology was detected some time ago. In the case of *L. nevadensis*, Sáez and Bernal (2009, sub *L. aeruginea* subsp. *nevadensis*) indicated that it has seeds with a disc covered with more or less sinuose ridges, rarely smooth. However, as observed here by us, the ridges appear when the development of the tubercles is so great that they become anastomosing and laterally weld together. Indeed, both *L. nevadensis* and *L. glacialis* have smooth, tuberculate or sometimes crested seeds (Fig. 3–4), but instead the size remains quite constant, since *L. nevadensis* has small seeds while those of *L. glacialis* are almost twice as large.

Further research will be needed to determine whether the variation in seed morphology within the same species is due to genetic transfer with related species, for example by introgressive hybridization, or whether there really are species that show variability for this character.

Finally, from the standpoint of their ecological behaviour, significant differences divide the species studied, with the exception of *L. pruinosa*, which also inhabits calcareous screes, although at much lower elevations (500–1420 m); also, the species are widely distant geographically given that this latter species is endemic to the island of Majorca (Balearic Islands, Spain). Both *L. nevadensis* and *L. glacialis* inhabit schistous screes from 2300–3300 and 2700–3400 m in elevation, respectively, both endemic to Sierra Nevada (southern Spain). Finally, *L. alpina* subsp. *alpina* inhabits calcareous or siliceous stony and rocky habitats at 1500–3300 m in the mountains of the N and C of the Iberian Peninsula.

List of related accepted taxa and their synonyms (in alphabetical order)

Linaria alpina Miller (1768) subsp. *alpina*

Basionym: *Antirrhinum alpinum* Linnaeus (1753)

Ind. loc.: 'Hab. In Helvetia, Austria, Baldo'

Lectotype: Herb. Burser XII: 32 (UPS) [designated by E. Fischer (1997)]

Distribution: mountains of C and S of Europe.

Linaria glacialis Boissier (1838)

Ind. loc.: 'Hab. In summis Sierra Nevada in glareosis schistosis rara. Alt. 9000′–10.500″

Lectotype: G-BOIS [designated by B. Valdés (1970)]

Distribution: SE Iberian Peninsula (Sierra Nevada, Granada province).

Linaria nevadensis (Boiss.) Boissier and Reuter (1852)

Basionym: *Linaria supina* var. *nevadensis* Boiss. (1841)

– *Linaria aeruginea* subsp. *nevadensis* (Boiss.) D. A. Sutton (1988)

Ind. loc.: 'In cultis superioribus et glareosis sterilibus regionis alpinae, Sierra Nevada, pars superior in utroque latere locis Borreguiles dictis. Alt. 7000′–10.000″

Lectotype: G-BOIS [designated by B. Valdés (1970)]

Distribution: SE Iberian Peninsula (Sierra Nevada, Granada and Almería provinces).

Linaria pruinosa (Sennen and Pau) L.Sáez, F.B.Navarro, L.Gutiérrez, J.Fuentes, Cueto and Blanca, comb. nova

Basionym: *Linaria aeruginea* var. *pruinosa* Sennen and Pau in Pau, Butll. Inst. Catalana Hist. Nat. 11: 18 (Pau 1911) ['ceruginea']

– *Linaria aeruginea* subsp. *pruinosa* (Sennen and Pau) Chater and Valdés (1972)

Ind. loc.: '… recogidas en las cercanías de Sóller, ó en su jurisdicción, por el hermano Bianor'.

Neotype: BC 44400 [designated by B. Valdés (1970) –cf. Sáez et al. (2004)–].

Remarks. Although in recent taxonomic treatments this taxon has been recognized as a subspecies of *L. aeruginea* (Chater and Valdés 1972, Sutton 1988, Sáez et al. 2004, Sáez and Bernal 2009), it is easily recognizable by a set of uncommon (usually non-overlapping) morphological characters: long fruiting pedicels (2)3–14 mm long, relatively long bracts (up to 10 mm long), relatively long spur (compared with the rest of the corolla) and smooth seeds with scarcely verruculate periclinal walls. A re-evaluation of the morphologic distinctions between *L. pruinosa* and *L. aeruginea* (in a broad sense) and the allopatric distribution of both taxa support their recognition at species level. Therefore, the necessary nomenclatural combination is proposed here.

Key to the taxa studied

1. Bracts 12–20 mm long; calyx adaxial lobe 9–11 mm long in flower and 11–13 mm long in fruit ..... *L. glacialis*
– Bracts 2–10 mm long; calyx adaxial lobe 3.5–6.0 mm long in flower and 4.0–6.1 mm long in fruit 2
2. Inflorescence up to 1.5(–2.0) cm long at flowering; corolla (11–)12–17 mm long 3
– Inflorescence up to 3–12 cm long at flowering; corolla 12–30 mm long 4
3. Corolla pinkish-violet, with spur 4.0–5.5 mm long; seed 2.4–3.0 × 2.5–3.5 mm, with wing (0.5–)0.6–0.8 mm wide ..... *L. sagrensis*
– Corolla yellow, with spur 5.0–8.5 mm long; seed 1.2–2.0 × 1.1–1.5 mm, with wing 0.2–0.4 mm wide ..... *L. nevadensis*
4. Inflorescence up to 3 cm long, with glandular-hairy axis and calyx lobes; corolla greyish-rose to pinkish-purple; seed disc surface smooth ..... *L. pruinosa*
– Inflorescence up to 12 cm long, with glabrous axis and calyx lobes (more rarely glandular-hairy); corolla blue-violet, pink or yellow; seed disc surface smooth or tuberculate ..... *L. alpina* subsp. *alpina*

Conservation status

The distribution area of *L. sagrensis* extends exclusively over the summit of Sierra de la Sagra. Although located very close, the area lies outside the Natural Parks of Sierra de Cazorla, Segura y las Villas (province of Jaén) and the Sierra de Castril (Granada province). Nevertheless, it is included in a 'Special Area of Conservation' (SAC) and, therefore, is part of a protected area in the Nature 2000 Network. The scree habitat is also protected by the European directive 92/43/CEE, under the name Western Mediterranean and Thermophilous Scree, code Natura 8130.

Potential threats include the limited distribution area (occupation area less than 2 km^2), low number of individuals (around 2000) and climate change. The practice of sports activities in the periglacial scree of the Sierra de la Sagra, where *L. sagrensis* occurs, is also placing this species at serious risk due to the movement of people through the scree without due control (Rosillo et al. 2016), despite the fact that this habitat is included in the Inventario andaluz de Georrecursos de la Junta de Andalucía, and also in the Inventario español de Lugares de Interés Geológico (LIG) of the Instituto Geológico y Minero de España.

Regarding the climate change, Mediterranean high-mountain endemic species are particularly vulnerable. González-Hernández et al. (2021) discovered a disparate demographic structure of Spanish fir (*Abies pinsapo* Boiss.), that is, in populations at different elevations in Cádiz and Málaga provinces, young saplings were found at higher elevations than mature trees i.e. where temperatures are lower and rainfall is higher. This is compelling evidence that the cooler, wetter regions offer the optimal conditions for promoting new tree

growth. In the same way, Mendoza-Fernández et al. (2022) have shown that for *Moehringia fontqueri* Pau [now *Arenaria suffruticosa* Fior and P.O. Karis (cf. Fior and Karis 2007)], an endemic species of Sierra Nevada (Almería province, southeast of Spain), the lowest subpopulations were identified as the most vulnerable to climate change effects while the highest ones were the nearest to future suitable habitats. Thus, due to climate change, it seems that there is a migration of the species towards higher elevations, which in the case of *L. sagrensis* would not be possible because it grows at the summit peaks of Sierra de la Sagra.

According to the IUCN categories (IUCN 2012) and recommendations provided by IUCN (2017), we propose labelling *L. sagrensis* as 'Critically Endangered' (CR), according to the following criteria: B1ab(iii,v) + 2ab(iii,v). This species may require conservation action and a management plan, and therefore it should be included in the Andalusian and Spanish Red Lists of vascular plants (Cabezudo et al. 2005, Bañares et al. 2008).

Additional specimens examined (selection)

Linaria alpina Mill. subsp. *Alpina*

Andorra, Andorra, Puerto de Envalira, en la emisora, exp. N, esquistos, 31TCH9311, 2540 m, 31 Aug. 1976, Castroviejo and Valdés-Bermejo (MA 429465). Spain, Ávila: El Barco de Ávila, entre la laguna del Barco y el pico de la Covacha, en borde de arroyo, 30TTK7956, 1950 m, 27 July 1982, R. Calvo et al. (MA 431977); Macizo Central, fuente de la Mira, pedreras, 30TUK1459, 2200 m, 28 Sept. 1985, G. López et al. (MA 783936); Sierra de Gredos, am Weg zum Circo de Gredos, ca Am höchsten Punkt des Weges bei Peña Rayo, 2090 m, 17 July 1997, R. Morales and E. Vitek (BC 877860); Sierra de Gredos, estribaciones del Morezón, sobre el Gargantón, UK06, 2000 m, 9 July 1975, A. M. Hernández and A. González (BC 617311, MGC 2738); subida a la Laguna de Gredos, 1900–2000 m, 25 Aug. 1974, E. Valdés Bermejo (GDA 23346). Burgos: Sierra de San Millán, refugio de San Millán, 5 July 1975, E. Fuertes (MA700419). Cáceres: Sierra de Majarreina, au-dessus de Gerte, près Plasencia, 22 June 1863, E. Bourgeau (MA 720839). Gerona: La Cerdanya, Guils de Cerdanya, pr. Pla dels Empedrats, prados subalpinos, terreno pedregoso granítico, 2585 m, 29 June 2011, J. Calvo (MA 840190); Núria, 7 July 1970, A. M. Hernández (MGC 1742); Pirineos catalanes, montes de Nuria, 2 y 3 Nov. 1928, Hno. Gonzalo (BC 849270); Tosses, pr. La Molina, calizas, 31TDG0988, 2400 m, 21 July 1993, C. Aedo et al. (MA 529134); Vallter, 8 June 1990, E. del Castillo (BC 808348-2). Huesca: Aísa, Collado de Blancas, roca caliza triturada, 30TXN9935, 2040 m, 16 July 1970, P. Montserrat and L. Villar (BC 636665, MA 333311); Aisa, paso de la Garganta de Aisa, 1870–2100 m, 19 July 1966, J. Puig de Fábregas and S. Silvestre (SEV 3813); Aso de Sobremonte (Valle de Tena), cascajales, 14 Aug. 1965, Montserrat (SEV 3787); Baños de Benasque, lecho del río Pizarra, 1400 m, 23 July 1969, S. Silvestre and B. Valdés (SEV 7324); Benasque, subida a Renclusa, 2000 m, 9 Aug. 1982, J. Devesa (SEV 95209); Jaca, Candanchú, El Tobazo, 10 Aug. 1991, B. Cabezudo (MGC 32519); Ordesa, Cotatuero, 5 Aug. 1973, E. Fuertes (MGC 2655); Sallent, Llano de Anayet, 2190 m, 1 Aug. 1966, S. Silvestre (SEV 98437); Sallent del Gallego, Monte Lapazuzo, suelo esquistoso, 1800 m, 4 Aug. 1978, J. A. Devesa, J. Pastor and S. Talavera (SEV 51125); Torla-Ordesa, Pirineos, Sierra de Sandaruelo, hacia Ibón de Bernatuara, pedregales calizos de alta montaña, 30TYN3733, 2200 m, 29 June 2018, J. Fuentes and A. Delgado (GDA 64858); Urdiceto, no lejos de la central, piso subalpino silíceo, 31TBH7528, 1850 m, 20 June 1996, M. Carrasco, C. Martín Blanco and M. Velayos (MA 609509); valle de Ansó, entre Ansó y Turiza, 2 Aug. 1978, J. A. Devesa, J. Pastor and S. Talavera (SEV 51126); valle de Gistaín, subida al pico Bachimala, pastos de montaña y glera, 2600 m, 15 Sept. 2013, P. Barberá, A. Quintanar and J. V. Ferrández (MA 876739); valle de Hecho, Selva de Oza, ruderal, 30TXN8744, 1200 m, 18 June 1996, C. Morales Torres et al. (GDAC 41118); valle de Tena, July 1881, A. Zubilla (MA 110024). León: Astorga, Cabrera Alta, Teleno, 2000 m, 6 Nov. 1933, W. Rothmaler (BC 80013); Ponferrada, Montes Aquilianos, Peñalba de Santiago, 29TQG0297, 1950 m, 5 July 1978, E. Temprano (MA 279028). Lérida: Aigues Tortes, Aug. 1964, J. Novo (SEV 3814); Pallars Sobirà, Vall Ferrera, barranc d´Aixeus hacia el Monteixo, praderas de *Festuca eskia* y canchales, esquistos, 2185 m, 12 Sept. 2009, C. Aedo et al. (MA 791355); Pirineo catalán, Estanys de la Pera, Les Pollineres, gleras sobre sustrato silíceo, 31TCH8500, 2152 m, 30 June 2004, C. Morales et al. (GDA 57915); Pirineo catalán, Sierra de Cadí, Parque Natural del Cadí-Moixeró, cima del Mont Fesa, fisuras de rocas calizas, 31 TCG8182, 2361 m, 29 June 2004, C. Morales et al. (GDA 57838); Pirineo leridano, Alto Arán, puerto que cruza del Lac de Montoliu a Montgarri, próximo a Taula de Parros, pastizales y cascajares alpinos, 2480 m, 8 Aug. 2021, F. B. Navarro (GDA-Fanero 69005); Puerto de la Bonaigua, 28 May 2011, J. L. Blanco Pastor (MA 882313). Logroño: Monte de San Lorenzo, pedregales, 2000 m, 19 July 1935, F. Cámara (MA 110000). Navarra: Isaba, Barranco Aztaparreta, XN 7953, 1350 m, 4 Aug. 1987, C. Aseguinolaza, P. M. Uribe-Echebarría and P. Urrutia (SEV 160666); Isaba, Puerto Belagua, roquedos calizos, 1590 m, 20 June 2017, P. Vargas (MA 938592); Isaba, Valle del Roncal, subida al portillo de Eraice, calizas y esquistos, pizarras, 30TXN7657, 1350 m, 23 May 1982, A. Barra, G. López and G. Nieto (MA 426611); Ochagabía, subida al Orhy desde Puerto Larrau, 30TXN6360, 1600 m, 13 July 1994, C. Aedo et al. (MA 545661); Valle del Roncal, Puerto de Arlas, 1300 m, 27 July 1969, E. F. Galiano, S. Silvestre and B. Valdés (SEV 7278). Orense: Casayo, carretera a Peña Trevinca, sobre pizarras, 29TPG7299, 1800 m, 28 July 1983, E. Bayón, S. Castroviejo and G. Nieto (MA 279009); Fonte da Coba, Casayo, Carballeda de Valdeorras, gleras de pizarras finas, 29TPG88, 1800 m, 27 July 1980, V. R. Gracia (MA 782681). Salamanca: Candelario, subida al Calvitero, cara noroeste, TK6864, 2300 m, 18 July 1980,

E. Valdés-Bermejo et al. (MA 430618); Sierra de Béjar, El Calvitero, 30 July 1974, Fernández Díez (SEV 22422); Sierra de Béjar, El Calvitero, pedregales cuarcíticos, 30TKK6865, 2300 m, 18 July 1980, B. Casaseca et al. (BC 640308, GDA 13176, MGC 10335, SEV 68064). Soria: Beratón, Sierra del Tablado, Barranco del Frontal, gleras y erosiones, silíceo, 30TWM9716, 1600–1700 m, 28 May 1988, M. L. Gil Zúñiga and J. A. Alejandre (MA 468040, MGC 41604); Moncayo, 1600–2000 m, 2 July 1964, E. F. Galiano and E. Paunero (SEV 98438). Zamora: San Martín de Castañeda, 17 June 1976, B. Casaseca (MA 207832). Zaragoza: ladera NE del Moncayo, matorrales de enebro y roquedos, 2250 m, 15 July 2012, C. Aedo (MA 864175); Tarazona, Sierra de Moncayo, en gleras y conos de avalancha sobre suelos móviles, substrato ácido, 30TWM9626, 2100 m, 26 Aug. 1989, J. A. Alejandre (MA 485440).

***Linaria glacialis* Boiss.**

Spain, Granada: Capileira, Crestones de Río Seco, en la cumbre, en los pedregales, VG7001, 3180 m, 10 Sept. 1977, J. Molero Mesa (GDA 9189); Capileira, Sierra Nevada, próximo a la Laguna de la Caldera, pedregales esquistosos, 30SVG60, 3000 m, 27 June 1983, Molero Mesa and Molero Briones (GDA 17917); Puerto de Capileira y Veleta, 24 July 1935, Cortés (GDA 39409); Sierra Nevada, barranco Trevélez, 30SVF7398, 15 July 1996, F. B. Navarro (GDAC 42017); Sierra Nevada, Cauchiles, 2750 m, 18 July 1969, J. Varo (GDAC 2194); Sierra Nevada, collado de las Minas, July 1969, C. Morales (GDAC 2199); Sierra Nevada, Corral del Veleta, pedregales, 3100–3200 m, 23 Aug. 1985, M. Luceño, P. Vargas and M. Guzmán (MA 427035); Sierra Nevada, Lagunillos de la Virgen, pastos pedregosos secos, 2850 m, 25 Aug. 1985, M. Luceño, P. Vargas and M. Guzmán (MA 427032); Sierra Nevada, Los Borreguiles, Laguna de las Yeguas, 30SVG6602, 2800 m, 18 July 1976, A. Barra, S. Castroviejo, S. Cirujano and E. Valdés-Bermejo (MA 426490); Sierra Nevada, Mulhacén, 24 July 1944, J. Muñoz Medina (GDA 39410); ibidem, 1 Aug. 1907, J. L. Díez Tortosa (GDA 39406); ibidem, 3000 m, 13 Aug. 1923, E. Gros (MA 378443); Sierra Nevada, pico del Cuervo, 30 July 2010, J. L. Blanco (MA 882355); Sierra Nevada, pico del Toval, 24 July 1981, A. T. Romero and C. Morales (GDA 45800); Sierra Nevada, río San Juan, 2600 m, 10 July 1970, C. Morales (GDAC 2198); Sierra Nevada, Siete Lagunas, 13 Aug. 1976, G. Blanca and J. A. Gil (GDAC 2433); Sierra Nevada, sobre esquistos en la zona cacuminal, 3 July 1974, E. Valdés and G. López (MA 836757); Sierra Nevada, Valle del Lanjarón, 2900–3200 m, in rupestribus saxosisque schistosis, 6 Aug. 1930, L. Ceballos and C. Vicioso (MA 110205); Sierra Nevada, Veleta, 20 July 1987, G. Blanca (GDAC 43817); ibidem, 21 July 1980, F. Valle (GDAC 9796); ibidem, Aug. 1913, F. Beltrán (MA 110206); Trevélez, cañada de Siete Lagunas, en derrubios, VG7301, 3100 m, 12 Sept. 1978, J. Molero Mesa (GDA 9187); Trevélez, loma del Mulhacén a Siete Lagunas, en pedregales, VG7201, 3200 m, 31 July 1978, J. Molero Mesa (GDA 9188).

***Linaria nevadensis* (Boiss.) Boiss. and Reut.**

Spain, Almería: Sierra Nevada, El Almirez, 9 July 1996, J. Lorite (GDA 52132). Granada: Bajada Pico del Cuervo, 30 July 2010, J. L. Blanco Pastor (MA 882354); Capileira, alrededores de la laguna de la Caldera, VG7001, 3050 m, 16 Sept. 1977, J. Molero Mesa (GDA 9195); Capileira, proximidades del río Veleta, en fisuras de rocas, VG6996, 2000 m, 17 Sept. 1978, J. Molero Mesa (GDA 9192); entre Peñones de San Francisco y Monte Dornajo, bordes removidos de la carretera, 2300 m, 4 June 1966, E. Getliffe and B. Valdés (MA 194811; SEV 3802); Faldas del Pico Veleta, cerca del viejo observatorio astronómico, matorrales y pastos psicroxerófilos en substrato ácido, esquistos, 2600 m, 4 July 2010, E. Glazkova and A. Quintanar (MA 836394); Fuente de San Jerónimo, 2000 m, 21 July 1978, B. Cabezudo, S. Talavera et al. (SEV 96150); Hoya de la Mora, pedregales, 2300 m, 2 June 1966, E. Getliffe and B. Valdés (MA 194815); Laroles, barranco del Hornillo, en suelo arenoso compacto, VG 9705, 1900 m, 22 June 1976, J. Molero Mesa (GDA 9196); Peñones de San Francisco, junto al Albergue Universitario, suelo esquistoso, 2500 m, 21 July 1978, B. Cabezudo, S. Talavera et al. (SEV 95544); Sierra Nevada, au Borreguil de S. Geronimo, région alpine, 5 July 1851, E. Bourgeau (MA 109920); Sierra Nevada, Barranco de San Juan, 2600 m, 5 July 1971, J. Fernández-Casas (MA 609537); Sierra Nevada, base del pico Veleta, 3000 m, 3 June 1966, F. Getliffe and B. Valdés (SEV 3803); Sierra Nevada, base del Veleta, 2 Aug. 1968, S. Silvestre (SEV 3812); Sierra Nevada, Borreguiles, 15 July 2010, J. L. Blanco Pastor (MA 882363); Sierra Nevada, Borreguiles, 2700 m, 27 June 1980, J. A. Devesa, T. Luque, C. Romero and S. Talavera (SEV 98408); Sierra Nevada, Cáñar, in rupestribus, 27 July 1930, C. Vicioso (MA 109840); Sierra Nevada, carretera del Veleta, 2700 m, 9 July 1972, Fernández Casas (MGC-Cormof 84227); Sierra Nevada, carretera de Pradollano, 4 June 1968, C. Morales (GDAC 2286); Sierra Nevada, Cauchiles, 2750 m, 18 July 1969, J. Varo (GDAC 2205); Sierra Nevada, Cerro de los Machos y Barranco de Bacares, Las Minillas, Aug. 1908, C. Pau (MA 109919); Sierra Nevada, Dehesa de San Jerónimo, 2000 m, 2 June 1966, F. Getliffe and B. Valdés (BC 606905, SEV 3801); Sierra Nevada, Hoya de la Mora, 2300 m, 2 June 1966, F. Getliffe and B. Valdés (BC 606904, SEV 3800); Sierra Nevada, Hoya de la Mora, 7 July 1970, C. Morales (GDAC 2285); Sierra Nevada, Jerez del Marquesado, río Alhorí, subida al Picón de Jerez desde el Puerto del Alhorí, pastizales orófilos sobre sustrato silíceo, 30SVG7908, 2350 m, 22 July 2022, J. Fuentes (GDA-Fanero 70259); Sierra Nevada, Laguna de las Yeguas, 29 June 1962, J. Arroyo, I. Fernández and J. Pastor (SEV 82661); Sierra Nevada, Laguna de las Yeguas, 2830 m, 27 June 1980, J. A. Devesa, T. Luque, C. Romero and S. Talavera (SEV 95218); Sierra Nevada, Laguna de las Yeguas, suelo esquistoso, 2550 m, 21 July 1978, S. Talavera, B. Cabezudo et al. (SEV 95988); Sierra Nevada, loma del Calvario, 2600 m, 8 July 1976, L. García del Moral (GDAC 3536); Sierra Nevada, montée à la Veleta, 2750–3050 m, 21 July 1978, B. Cabezudo and S. Talavera (BC 647307); Sierra Nevada, Mulhacén, 2800 m,

21 July 1988, A. Segura Zubizarreta (SEV 160616); Sierra Nevada, Mulhacén, 15 July 1981, J. M. Nieto (MGC 8639); Sierra Nevada, Peñón Colorado, 30 July 1930, C. Vicioso (MA 109841); Sierra Nevada, peñones de San Francisco, Aug. 1976, J. A. Gil and M. Casares (GDAC 2368); ibidem, 2400 m, 10 June 1990, L. Campos (HUAL 14963); ibidem, 2500 m, 3 June 1966, F. Getliffe and B. Valdés (MA 194814; SEV 3805); Sierra Nevada, peñones de San Francisco, base del 1º peñón, comunidades de fisuras de rocas, 2000 m, 20 May 1987, J. M. Losa Quintana (BC 834775); Sierra Nevada, pico Veleta, 20 June 1972, E. Domínguez, P. E. Gibbs and S. Talavera (SEV 15623); Sierra Nevada, pico Veleta, esquistos, 3100 m, 20 July 1987, G. Blanca (GDAC 43846); ibidem, Virgen de las Nieves, 29 June 2009, J. L. Blanco Pastor (MA 882392); Sierra Nevada, pr. Laguna de la Caldera, pedregales, esquistos, 30SVG7101, 3000 m, 18 July 1998, Aedo, Muñoz Garmendia, Navarro and Sáez (MA 614207, MGC-Cormof 84268); Sierra Nevada, Prado Llano, 2500 m, 29 Nov. 1973, S. Talavera (SEV 98406); Sierra Nevada, Prado Llano, 21 Nov. 1979, J. Fernández-Casas (MA 393851); Sierra Nevada, subida al Veleta, 2900 m, 21 July 1978, B. Cabezudo and S. Talavera (SEV 44235); Sierra Nevada, subida al Veleta, Cruce con los Borreguiles, 2700 m, 29 June 1982, J. Arroyo, I. Fernández and J. Pastor (SEV 82662); Sierra Nevada, Valle del Lanjarón, Peñón Colorado, in rupestribus, 3000 m, 6 Aug. 1930, L. Ceballos and C. Vicioso (MA 109917); Trevélez, lagunillos del Goterón, en pedregales, VG7402, 2800 m, 7 Aug. 1979, J. Molero Mesa (GDA 9194); Trevélez, loma del Mulhacén, cerca del Chorrillo, en borde de carretera, suelo arenoso, VG7397, 2800 m, 13 Aug. 1978, J. Molero Mesa (GDA 9193).

Linaria pruinosa (Sennen and Pau) L.Sáez et al.

Spain, Mallorca: Baixada de Lluc a Sóller, vora carretera, 800 m, 11 May 1974, M. A. Cardona and R. M. Masalles (BC 617270); Barranc de Bini, Puig Mayor, 30 June 1936, E. W. Kennedy (MA 109990); Lluc, Puig d´en Galileu, en matorral y roquedos calizos, 31SDE8807, 1020 m, 4 June 1998, C. Aedo et al. (MA 618185); monte de Puigpunyent a Galatzó, éboulis calcaires près du col, 750 m, 45 June 1975, A. Charpin et al. AC19344 (G 287633); Puig de Massanella, 1200 m, 12 July 1956, A. Bolòs and O. Bolòs (BC 137327); Puig des Teix, Valldemossa, 31SDE7098, 950 m, 7 Apr. 1999, L. Sáez (L. Sáez, pers. herb.); Puig Major, Rochers des Montagnes, depuis 500 m jusq'a 1500 m, 12 May 1912, F. Bianor (SEV 83132); Puig Major, 31SDE8206, 1420 m, 16 June 2002, L. Sáez (L. Sáez, pers. herb.); Puig Mayor de Torrellas, 27 Apr. 1897, C. Bicknell (MA 109757); Puig Mayor de Torrellas, ad pedrem supinum cale, 1400 m, 28 Mar. 1956, A. Bolòs and O. Bolòs (BC 136103); Serra d'Alfabia, terreno pedregoso, 1000 m, 12 May 1987, J. Orell Casasnovas (GDA 20445); Sierra Tramuntana, subida a Puig de Massanella desde Coll de Sa Línia, claros de matorral, entre pedregales y guijarrales de naturaleza caliza, 31S4884405, 1160 m, 12 May 2022, J. Fuentes (GDA-Fanero 70260); sobre Sa Coma de N'Arbona (Puig Major), sól pedregós calcari, 1000 m, 13 May 1978, A. Bonner and A. Cardona (BC 52964); Sóller, montagnes du sud, 11 May 1920, F. Bianor (BC 44414, MA 109758, 109759, SEV 84244); Sóller, Puig Mayor, rochers des montagnes, 500–1500 m, 11 May 1920, Bianor (BC 44414); subida al Puig Major, paredones calizos, 31SDE8005, 820–880 m, 17 June 1980, S. Castroviejo and R. Morales (MA 430521).

Linaria sagrensis Blanca et al. (paratypes)

Spain, Granada province: Huéscar, Sierra de la Sagra, cascajares orófilos, calizas, 2260 m, 13 July 2021, F. B. Navarro and L. Gutiérrez (GDA-Fanero 69003); Huéscar, Sierra de la Sagra, orientación Noroeste, gleras de naturaleza caliza, dispersa y escasa, cohabita con *C. granatensis*, UTM 30S WG3799, 2250 m, 23 June 2022, J. Fuentes and F. B. Navarro (GDA-Fanero 70257); Huéscar, Sierra de la Sagra, vertiente norte, sobre canchales carbonatados con orientación umbría, 2200 m, 8 June 2021, F. B. Navarro and L. Gutiérrez (GDA-Fanero 70258).

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Author contributions

Gabriel Blanca: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Miguel Cueto**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Visualization (equal); Writing – review and editing (equal). **Julián Fuentes**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Resources (equal); Writing – review and editing (equal). **Leonardo Gutiérrez**: Conceptualization, Data curation, Formal analysis, Resources, Writing – review and editing. **Llorenç Sáez**:

Conceptualization, Data curation, Investigation, Resources, Writing – review and editing. **Francisco Bruno Navarro**: Conceptualization, Data curation, Formal analysis, Resources, Writing – review and editing.

Data availability statement

There is no additional data for this paper.

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