A new spineless species of *Vella* (Brassicaceae) from the high mountains of south-eastern Spain

MANUEL B. CRESPO^{1*}, SEGUNDO RÍOS¹, JOSÉ L. VIVERO², JOSEFA PRADOS², ESTEBAN HERNÁNDEZ-BERMEJO² and M. DOLORES LLEDÓ³

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Vella castrilensis sp. nov. is described from the high mountains of Granada and Jaén provinces (south-eastern Iberian Peninsula), where it grows on calcareous soils. It is a hexaploid (2n = 68) spineless dwarf shrub, woody at the base, with oblong-lanceolate, entire to shallowly dentate leaves and fruit with an acute tongue-shaped stylar segment and strongly reticulate-nerved valves. The characteristic unique combination of vegetative, karyological and reproductive features of V. castrilensis is not present in any described taxon of the genus, and warrants recognition at the species rank. Affinities and differences with other related taxa are discussed. Phylogenetic, biogeographical, bioclimatic, ecological data and conservation proposals are also reported. © 2005 The Linnean Society of London, Botanical Journal of the Linnean Society, 2005, 149, 121–128.

ADDITIONAL KEYWORDS: Baetic mountains – conservation – Cruciferae – ecology – endemic – Iberian Peninsula – phylogeny – taxonomy.

INTRODUCTION

Vella L. (subtribe Vellinae, tribe Brassiceae) includes shrubs with sessile, entire to lobed leaves bearing vestigial stipules and two-segmented fruits with a flattened, linguliform to cochleariform, aspermous upper segment (beak) and a bilocular, mostly dehiscent, 1–2 seeded lower segment, with oblong, navicular (boat-shaped), convex, usually 3-nerved valves (description modified from Gómez-Campo, 1993). The genus is endemic to the south-western Mediterranean areas, namely to Spain, Morocco and Algeria (Greuter, Burdet & Long, 1986).

Taxonomic revisions of the genus (Gómez-Campo, 1981; Crespo, 1992; Crespo et al., 2000) recognized up to eight taxa, five of which, V. aspera Pers., V. lucentina M.B. Crespo, V. pseudocytisus L. ssp. pseudocytisus and ssp. paui Gómez-Campo and V. spinosa Boiss., are restricted to the Iberian Peninsula and three, V. anremerica (Litard. & Maire)

Gómez-Campo (including *V. charpinii* Fern. Casas), *V. mairei* Humbert and *V. pseudocytisus* ssp. *glabrata* Greuter, are found only in North Africa. Most of them are endemics with narrow distribution areas and grow in either high mountains or dry steppes. Usually, high elevation taxa are spiny dwarf plants with fewflowered inflorescences, whilst steppe plants are tall spineless plants with many-flowered racemes (Gómez-Campo, 1981).

Molecular studies (Warwick & Black, 1994; Crespo $et\ al.$, 2000) have provided evidence of the close relationships between Vella and other shrubby Spanish plants of subtribe Vellinae usually previously treated as separate genera such as Boleum Desv. and Euzomodendron Coss. Molecular data plus an analysis of unique shared features (e.g. inner stamens long connate, navicular fruit valves and the same basic chromosome number x=17) led Warwick & Al-Shehbaz (1998) to unite all three in Vella. Crespo $et\ al$. (2000), using a combined parsimony analysis of nuclear ribosomal internal transcribed spacers (ITS) and morphology, opted for a different taxonomic approach.

¹CIBIO (Instituto Universitario de la Biodiversidad), Universidad de Alicante, Apdo. 99, E-03080 Alicante, Spain

²Jardín Botánico de Córdoba, Avda. Linneo s/n, E-14004 Córdoba, Spain

³Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, UK

^{*}Corresponding author. E-mail: crespo@ua.es

They reincluded the former genus *Boleum* (= *V. aspera*) in *Vella*, as originally described by Persoon (1806), to make *Vella* monophyletic. Conversely, they retained *Euzomodendron* at the generic rank, even though it was sister to *Vella*. This conclusion was based on the fact that *Euzomodendron* shows some morphological autapomorphies (e.g. the long petiolate, pinnate leaves and the long, linear-lanceolate, flattened siliqua), and other morphological characters (e.g. leaf stipules lacking, and seed flattened and broadly winged, numerous in each locule) which are plesiomorphic in *Vella*.

Recently, populations of a spineless *Vella* were found in the high mountains of south-eastern Spain, in the border between Granada and Jaén provinces. These plants showed a peculiar combination of characters making their assignment to any of the known taxa of the genus difficult. Morphological, phylogenetic, ecological and biogeographical data are reported as evidence for the recognition of this taxon as a new species.

MATERIAL AND METHODS

Observations were based on both living plants and dried specimens from ABH, COA and MA (acronyms in Holmgren, Holmgren & Barnett, 1990; Holmgren & Holmgren, 1993).

Taxonomic treatment of the genus and nomenclature follow that of Crespo *et al.* (2000). When not explicitly stated, authorities of taxa mentioned in the text are those that appear in Halliday & Beadle (1983) and Castroviejo *et al.* (1986–2003). Author abbreviations follow Brummitt & Powell (1992). Both biocli-

matic and biogeographical data follow Rivas-Martínez *et al.* (2001). Authorities and circumscription of syntaxa follow data in Rivas-Martínez *et al.* (2002).

Chromosome number was counted from root tips obtained from seedlings. Roots were kept on ice for 3 h and then fixed with acetic acid:ethanol (1:3 v/v) for 24 h. Later, they were treated with 1 N HCl at 60 °C for 5–6 min, and finally stained with acetic acid-orcein (1%) for 1 h.

Leaf material of V. castrilensis was collected in silica gel, using the method of Chase & Hills (1991), and a voucher was deposited at ABH (num. 43663). DNA extraction and ITS sequencing was carried out following the standard techniques described in Crespo *et al*. (2000) and this ITS sequence was added to the data matrix of that study. The new ITS sequence has been deposited in the EMBL database (accession number AJ841702). Morphological characters were coded (Table 1) according to the matrix in Crespo et al. (2000). An exhaustive branch and bound search was conducted for the combined ITS and morphological matrix using PAUP v. 4*0b (Swofford, 1996), under equal weights. Clade support was examined by 100 runs of bootstrap (BP; Felsenstein, 1985), using branch and bound algorithms.

RESULTS AND DISCUSSION

VELLA CASTRILENSIS VIVERO, J. PRADOS, HERN. BERM., M. B. CRESPO, S. RÍOS & LLEDÓ SP. NOV.

Diagnosis: Frutex inermis, usque 30 cm altus, pulvinatus, ramosissimus. A Vella anremerica foliis minus

Table 1. Morphological data matrix

Euzomodendron bourgaeanum	00100	01101	01111	01110	00000	02021	0
Carrichtera annua	10200	01111	01010	01021	01010	00000	0
Psychine stylosa	10001	11110	{12}1000	01000	01110	02020	0
Succowia balearica	10200	01101	00000	01000	02011	10001	0
Vella castrilensis	00011	00011	01110	00010	01011	11111	0
Vella aspera	00011	01011	01111	01010	12011	11111	0
Vella anremerica	00011	01011	01110	00010	00011	01111	0
Vella mairei	01011	01001	01110	00010	0{01}011	01111	0
Vella lucentina	00011	00011	01110	00010	01011	11111	0
Vella spinosa	01011	00011	01110	00010	00011	11111	0
Vella pseudocytisus ssp. paui	00011	01011	01110	00021	00011	11011	0
Vella pseudocytisus ssp. glabrata	00011	01011	01110	00021	00011	11011	0
Vella pseudocytisus ssp. pseudocytisus	00011	01011	01110	00021	01011	11011	0
Schouwia purpurea	10011	11100	{12}1001	11100	00110	00001	0
Savignya parviflora ssp. parviflora	10001	01100	{12}0000	00100	00010	02020	0
Savignya parviflora ssp. longistyla	10001	01100	{12}0000	00100	00010	02020	0
Zilla spinosa ssp. macroptera	01001	01100	11001	11100	10111	11101	1
Fortuynia garcinii	00001	01100	11001	11100	10111	11101	1
Diplotaxis erucoides	10101	01100	20001	00100	00000	00000	1
Brassica balearica	00001	01100	00010	00100	00000	00001	1

profunde dentatis, fructu reticulato-nervoso stylo basi valde dilatato atque partem seminiferam aequanti vel paulo superanti, seminibus majoribus differt. A $Vella\ lucentina$ foliis latioribus obovato-lanceolatis plerumque dentatis, indumento brevi adpresso totam plantam tegenti differt. 2n=68.

In vegetationibus fruticosis humilibus pulviniformibus habitat, in solis saxosis argillaceo-calcareis a cacuminibus 'Cañada de Tañasca' et 'Cerro de la Vaca' oriundis, prope montem 'Tornajuelo' inter Castril et Cazorla, in finibus inter provincias austro-orientales hispanicas Granatae Giennaeque incolens.

Holotype: SPAIN, Granada: Castril, Cañada de Tañasca, 30SWG1486, 1850 m, 12.vii.2000, J. M. Nieto, S. Ríos, J. L. Solanas & M. B. Crespo (ABH no. 43663). Isotypes: MA, RNG, COB.

Other observed specimens: Jaén: Cazorla, Cañada de Tañasca, 30SWG1486, 1850 m, 12.vii.2000, J. M. Nieto, S. Ríos, J. L. Solanas & M. B. Crespo (ABH 43664). Jaén: Sierra de Castril, Cerro de la Vaca, cerca del Pico Tornajuelo, 30SWG1385, 1900 m, 15.ii.1997, Luque (COA 24647). Ibidem, 4.x.1996, Vivero & Hernández Bermejo (COA 24643). Ibidem, 20.iii.1997, Vivero & Hernández Bermejo (COA 24646).

Illustration: Figure 1.

Description: SHRUB, spineless, to 30 cm high, cushionshaped, many branched, setose-hispid with bicellular setae with the lower cell very short and thickened at the base, and the upper much longer, conic and minutely tuberculate. STEM thick, terete, with greyish bark; young branches green, turning whitish, slightly striate lengthwise, densely scabrous by antrorse, curvate-appressed setae varying from 0.06-0.4 mm in size. Leaves persistent, entire or rarely shallowly 2-4-dentate, densely covered with short (0.4–0.7 mm) appressed setae which are conspicuous on the margin, and with the midrib sometimes prominent in a dried state; the upper oblong-lanceolate, $9-21 \times 1.5-4$ mm (length/width ratio: 5-10), acute; the lower shorter, $3-6 \times 1.2-1.5$ mm, oblong or elliptic, subobtuse. INFLORESCENCE racemose, ebracteate, with 4–10 flowers on short peduncles up to 1 mm long; axis scabrous as in branches. Petals 11-16.5 mm long; limb suborbicular or widely obovate (3–5 mm), vellow and finally whitish, always brown- to violetnerved; claw filiform (8-11 mm long), long overtopping calyx (2–3 mm). SEPALS erect, $4-6.5 \times 1.5-2$ mm, covered with curvate-appressed setae, very narrowly scariose, with a triangular apex, and tardily caducous in fruit. STAMENS, INNER 8-10.5 mm long, outer stamen 7.5-9 mm long. SILICULES erect, mostly oneseeded (rarely 2-seeded), on a peduncle 1–2 mm long; the seed-bearing part bilocular, dehiscent, elliptic, subglobose, about $3-5\times 2-3$ mm, on a gynophore 0.5-1.0 mm long, with valves indurate, navicular, carinate and reticulate, laxly covered with both long (0.3 mm) and short (0.1 mm) setae; the stylar part (beak) equalling or a little longer than the seeded part, flattened, tongue-shaped $(5-6\times 2.5-4.5 \text{ mm})$, acute, wider in the lowest third and slightly thickened at the base, caducous, glabrous though minutely scabrous on margins at the apex. SEEDS cylindrical, about $2-2.5\times 1-1.5$ mm, smooth and reddish-brown, with a vestigial wing. Cotyledons setose, acutely and deeply notched at the apex. 2n=68.

Etymology: The name V. castrilensis refers to the type locality of the species.

Flowering time: March–June. Fruiting time: July–August.

ECOLOGY, BIOGEOGRAPHY AND PHYTOSOCIOLOGY

Vella castrilensis occurs in the eastern summits of Sierra de Castril, on the border of Granada and Jaén provinces (south-eastern Iberian Peninsula). It is known only from a small area around 'Cañada de Tañasca' and 'Cerro de la Vaca', near 'Pico Tornajuelo' and 'Pico Tejo', between Castril and Cazorla. This site is strongly influenced by winds and endures long periods under snow (four to six months per year or even more). Four subpopulations close to one another and functioning as a single metapopulation are found on stony clayish-calcareous soils, with active karstic processes (water dissolution of limestone rocks). Grazing by wild (deer, Spanish goat) and domestic (goats and sheep) herbivores is severe, and consequently plants of V. castrilensis are usually found growing in low, cushionlike bushes of various thorny plants (e.g. Erinacea anthyllis Link and Genista longipes Pau) belonging to the phytosociological alliance Xeroacantho-Erinaceion (Quézel, 1953) O. Bolòs 1967. It is also found in grasslands dominated by hemicryptophytes and dwarf chamaephytes of Seseli granatensis-Festucetum hystricis Mart. Parras et al. 1987, and sometimes also into rock crevices inaccessible to herbivores.

The region has an Oromediterranean-humid bioclimate (Rivas-Martínez et al., 2001) and is biogeographically included in the Baetic chorological province (western Mediterranean Region), Sub-Baetic sector, Cazorlense subsector (Rivas-Martínez et al., 2001). Vella castrilensis can be regarded as a narrow endemic and part of the serial calcicolous vegetation of the Baetic mountains of southern Spain. This preference for calcareous soils is shared with other taxa of the genus such as V. lucentina or the aggregate of V. pseudocytisus. The plant is notably absent from

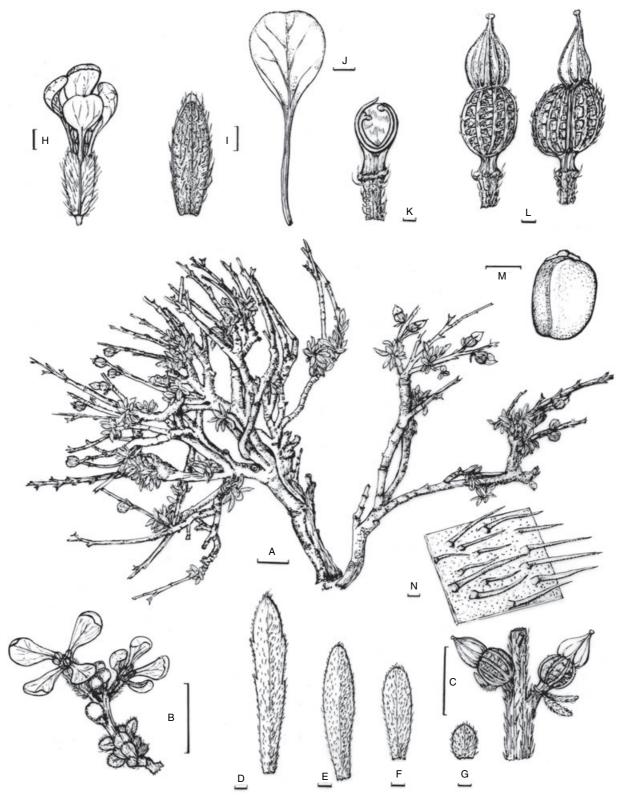


Figure 1. *Vella castrilensis* Vivero *et al.* **sp. nov.** (ABH 43663 *holotype*; COA 24646): A, habit; B, flowering branchlet; C, fruiting branchlet; D–G, leaf shapes from base to apex of branches; H, detail of flower; I, sepal; J, petal; K, fruit after valves opening; L, front and side view of mature fruit; M, seed; N, detail of leaf indument. Scale bars: A-C=1 cm; D-M=1 mm; N=0.1 mm.

neighbouring mountains such as Sierra Seca and Sierra de Segura, both with a similar climate and vegetation but with a local abundance of dolomitic soils on which *Vella castrilensis* has never been observed (recent survey by the authors).

CHROMOSOME NUMBER

Vella castrilensis is tetraploid (2n = 68). Base chromosome numbers in subtribe Vellinae vary from x = 8 and 9 in Carrichtera and Succowia, respectively, to x = 17 typical from core Vellinae, which includes both Vella and Euzomodendron. Within this core group, ploidy levels vary from diploids to tetraploids, and only one species has a hexaploid number (Fig. 2). Although V. castrilensis has the same number as V. mairei and V. pseudocytisus ssp. pseudocytisus, morphological affinities with both taxa are weak.

PHYLOGENETIC RELATIONSHIPS

For the purposes of elucidating the phylogenetic position of *V. castrilensis*, only the combined tree is shown

in Figure 2. When morphology and ITS were run separately, the position of V. castrilensis did not change. Separate molecular and morphological analyses (excluding the newly described species) can be found in Crespo $et\ al.\ (2000)$. The aligned ITS matrix consisted of 694 characters plus 31 morphological ones. A total of 269 characters (37.1%) were variable and 174 (24%) phylogenetically informative. The exhaustive branch and bound search produced two most parsimonious trees, tree length 531 steps, consistency index (CI) = 0.68 and retention index (RI) = 0.77. The two trees differed only in the relative position of the three subspecies of V. pseudocytisus (Fig. 2).

Relationships among subtribes Vellinae, Zillinae and Saviginyinae are the same as previously published and therefore are not discussed here. Within core-Vellinae (Vella + Euzomodendron; bootstrap percentage (BP) 100), clades previously reported are also similar. The three subspecies of V. pseudocytisus (BP 96) are sister to V. aspera (BP 63), and this group is sister to V. anremerica and V. mairei (BP 73). Vella castrilensis is sister to the south-eastern Spanish endemic V. lucentina, and this relationship is moderately supported (BP 72). The position of V. spinosa, unresolved

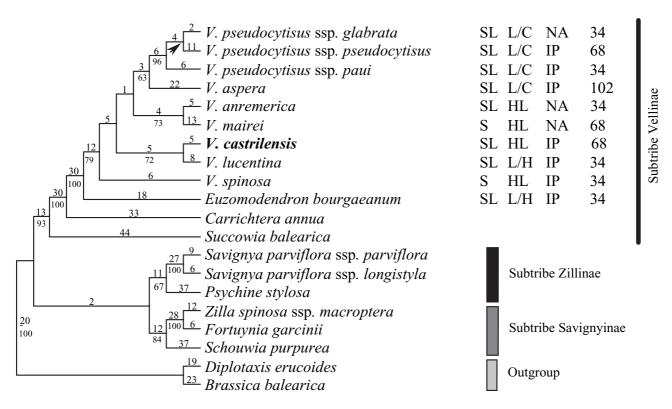


Figure 2. One of the two most parsimonious trees found with the combined ITS and morphology data. Fitch lengths (DELTRAN optimization) are shown above the branches, and bootstrap percentages (BP) are shown below. Clades not present in the strict consensus tree are marked with an arrowhead. The codes in the table on the right-hand side for core-Vellinae refer to: habit: SL, spineless; S, spiny; habitat: L/C, lowland/cool; HL, highland; L/H, lowland/hot; geographical range: NA, North Africa; IP, Iberian Peninsula; and chromosome numbers (2n).

in the 2000 analysis, is sister to the rest of *Vella*, and this relationship also has a moderate BP support (79).

Vella castrilensis and its sister taxa, V. lucentina, are both spineless. The tetraploid V. castrilensis is a high elevation taxon, whereas the diploid V. lucentina is native to the hot, dry steppes of Alicante (southeastern Spain). The fruit of both V. castrilensis and V. lucentina is similar and has an acute broader beak, which is at most a little longer than the seeded segment, and with valves strongly reticulate-nerved (Figs 1, 3). Seeds are also bigger than in the other taxa. These characters are also present in the high elevation diploid V. spinosa. The phylogenetic position of V. spinosa as sister of the rest of the genus suggests that this type of fruit is plesiomorphic in the genus.

The two northern African species, *V. anremerica* and *V. mairei*, have broad and usually lobate leaves. The fruits have long pedicels (up to 6 mm), with a fruit beak that is narrowly linguliform, acute, 3–4 times longer than the seeded part. The latter opens via valves that are three-nerved (Fig. 3A, B) and the seeds are small (Bengoechea & Gómez-Campo, 1975). These two species are endemic to the Atlas Mountains (Morocco). Whereas *V. anremerica* is diploid and spineless, *V. mairei* is a tetraploid spiny bush.

The *V. pseudocytisus* aggregate is defined by its obtuse, oblong-spathulate leaves, and its fruits with a

cochleariform, roundish beak. Diploid and tetraploid taxa are found in this group, all of them growing in dry steppes of Spain, Morocco and Algeria. The hexaploid *V. aspera* from the cold subdesert areas of northeastern Spain is placed in a long branch sister to this group (Fig. 2).

Vella castrilensis combines morphological characters of some of those groups (Figs 1, 3). The appressed short indumentum of leaves and sepals (Fig. 1N) is a distinctive character, only shared with *V. anremerica* (Gómez-Campo, 1981). Leaves are also broad and acute as in the latter, but they are mostly entire (sometimes only shallowly dentate) and not lobate (Fig. 3F, H). According to our tree, these characters have developed independently in the group at least twice. Fruit and seed features are remarkably different in the Moroccan and the Spanish species (Fig. 3B, D), which suggest different evolutionary trends, as previously discussed by Crespo *et al.* (2000).

Ploidy levels have been related to the habitat of the plant (highland vs. lowland plants), and the habit of the shrub (spiny vs. spineless). Gómez-Campo (1981) argued that high-elevation taxa with high ploidy levels and derived characters, such as spiny branches or cushion-forming habit, evolved from more primitive diploid steppe plants. This hypothesis is not fully corroborated by our phylogenetic tree, as diploid and

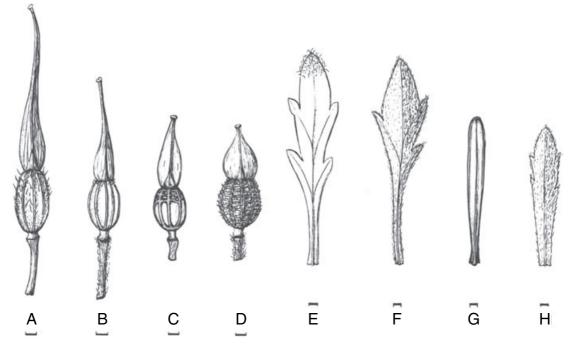


Figure 3. Comparative features of the high elevation taxa of *Vella*. Scale bars = 1 mm. A, fruit of *V. mairei* (MA 615836); B, fruit of *V. anremerica* (MA 299762, as *V. charpinii* Fern. Casas); C, fruit of *V. spinosa* (ABH 4747); D, fruit of *V. castrilensis* (ABH 43663); E, leaf of *V. mairei* (MA 615836); F, leaf of *V. anremerica* (MA 299762, as *V. charpinii* Fern. Casas); G, leaf of *V. spinosa* (ABH 4747); H, leaf of *V. castrilensis* (ABH 43663). Fruit and leaf characteristics of *V. aspera* Pers., *V. lucentina* M.B. Crespo and *V. pseudocytisus* L. s.l. are similarly illustrated in Gómez-Campo (1993).

polyploid species of *Vella* do not fit those patterns. Diploid taxa occur both in low areas (*V. pseudocytisus* ssp. *glabrata* and ssp. *paui* and *V. lucentina*) and high mountains (*V. anremerica* and *V. spinosa*), but tetraand hexaploids are also distributed in both high elevation (*V. mairei* and *V. castrilensis*) and low territories (*V. pseudocytisus* ssp. *pseudocytisus*, and *V. aspera*). In the case of *V. castrilensis* and *V. lucentina*, Gómez-Campo's hypothesis applies to ploidy levels, although not to morphological features. Therefore, different evolutionary trends seem to have contributed to the diversity of this genus and perhaps the current distribution of some taxa is the result of a reduction from a wider area of occurrence in the past (Crespo *et al.*, 2000).

CONSERVATION PROPOSALS

Vella castrilensis is known only from an area no larger than 1 km², in which about 20 000 individuals are estimated to exist in four subpopulations. This single location belongs to the Natural Park of Cazorla, Segura and Las Villas, a nature reserve in which the

Campo (1981) and Crespo (1992):

conservation of the taxon should be assured. However, over-grazing by goats and sheep is currently a serious threat. Therefore, grazing activities in the park should be urgently regulated. *Vella castrilensis* should be regarded as critically endangered, and labelled as CR B1ab(i,ii,iii,v) +2ab(i,ii,iii,v) following the IUCN criteria (IUCN, 2001). The establishment of microreserves of flora (Laguna, 1996, 2001), even delimited by fences, would be a helpful tool for effective conservation of this endemic.

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1. Spiny bush, with pauciflorous inflorescences
1. Spiny bush, with pauciflorous inflorescences 2 1. Spineless bush, usually with multiflorous inflorescences 3
2. Fruit valves reticulate-nerved on the apical half, glabrous. Fruit beak equalling the seeded part in length,
widened at the base. Leaves narrowly linear up to 2 mm width, mostly entire (rarely with 1-2 shallow
lobes)
2. Fruit valves not reticulate-nerved, hispid (rarely glabrous). Fruit beak up to four times longer than the seeded part,
narrow at the base. Leaves obovate-cuneate up to 5 mm width, mostly pinnatisect
3. Fruit beak roundish, cochleariform. Leaves with obtuse roundish apex
a. Leaves densely hispidssp. pseudocytisus
a. Leaves glabrescent or rarely glabrousb
b. Hairs only at the edge of leafssp. paui Gómez-Campo
b. Hairs on both surfacesssp. glabrata Greuter
3. Fruit beak acute, linguliform. Leaves with acute or subacute apex
4. Leaves with erect or erect-patent straight hairs. Inflorescence axis densely covered with very short (0.1 mm) hairs
and long (up to 0.8 mm) erect setae
4. Leaves with appressed hairs, curved at the base. Inflorescence axis glabrous or with short appressed setae similar in
size (0.2–0.4 mm long)
5. Fruit indehiscent, with the seeded part densely covered with very long (up to 3 mm) white hairs hiding the valves.
Leaves lanceolate, broad (up to 5 mm), usually shortly lobate
5. Fruit dehiscent, with the seeded part sparsely covered with short setae not hiding the valves. Leaves narrowly linear,

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