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Centaurea kunkelii (Asteraceae, Cardueae), a new hybridogenic endecaploid species of sect. *Acrocentron* from Spain

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Centaurea kunkelii Garcia-Jacas, a new species from Andalusia, Spain, is described, akin to the Iberian complex of *Centaurea ornata* Willd. (sect. *Acrocentron* (Cass.) DC.). The new species is an endecaploid with 2n = 110, the highest ploidy level hitherto known in the genus *Centaurea* L. On the basis of morphological evidence (especially some features of the cypselas) and polyploidy, the hybrid origin of *C. kunkelii* between species of sections *Acrocentron* and *Chamaecyanus* is hypothesized.

Key words: *Acrocentron*, *Centaurea*, hybridogenic species, karyology, speciation, taxonomy

INTRODUCTION

Sect. *Acrocentron* (Cass.) DC. is one of the best defined and most prolific sections of the genus *Centaurea* L. (Asteraceae), with about 100 species and a high percentage of endemics (Gardou 1975, Wagenitz 1975). The Ibero-North African region stands as the second most important centre of diversification after Turkey and the Balkans (Garcia-Jacas & Susanna 1992): of the 24 species in the west Mediterranean region, only two (*C. collina* L. and *C. scabiosa* L.) are not endemic.

In 1996, we collected in the Sierra de Gádor (Almería, Spain) a *Centaurea* similar to the species of the complex of *C. ornata* Willd., a taxonomically difficult group of Iberian endemics of sect. *Acrocentron*. At first sight, it was difficult to place it in any of the species of the group. After thorough examination, including chromosome counting, we concluded that it was a new species. The plant had been hidden by its resemblance to *C. ornata sensu amplo*, frequent in Andalusia. It could also be responsible for some unbelievable citations in Almería of *C. rupestris* L., a species from the eastern Mediterranean which has also blackish appendages in its bracts.

The new taxon presented some characters that suggested a hybrid origin. The same characters were already known from two species usually placed in sect. *Acrocentron*: *Centaurea crocata* Franco and *C. saxifraga* Coincy (Garcia-Jacas 1992, Garcia-Jacas & Susanna 1994). As in the case of the new species, we concluded that they were species of intersectional hybrid origin between *Acrocentron* and *Chamaecyanus* Willd. (sect. *x Chamaecentron* Fernández Casas & Su-

sanna, cf. Fernández Casas & Susanna 1982). Both sections are closely related and hybridization between them is frequent (Fernández Casas & Susanna 1986, Garcia-Jacas & Susanna 1992, Wagenitz & Hellwig 1996): besides *C. crocata* and *C. saxifraga*, six species have a confirmed hybrid origin as they were found between their parental species. In all cases, hybridization was evident in the characters of the cypselas (Fernández Casas & Susanna 1986).

The aim of this paper is to describe the new species and to suggest its hybrid origin on the basis of carpologic characters and ploidy level. We shall compare its features with morphological data from two species of probable hybrid origin, *C. crocata* and *C. saxifraga*, and other species from the two sections involved: *C. prolongi* Boiss. and *C. ornata* (sect. *Acrocentron*) and *C. haenseleri* Boiss. & Reuter (sect. *Chamaecyanus*).

MATERIAL AND METHODS

Mitotic chromosome count of *Centaurea kunkelii* was made on somatic metaphases using the squash technique. Root meristems from germinating seeds (for pop. S-1613 of *C. kunkelii*) or living plants collected in the wild were used. Samples were pretreated with 8-hydroxyquinoline at 4°C for 8 hours. The material was fixed with Carnoy for 24h at low temperatures. Before staining, the material was hydrolysed with 5N HCl for 1 h at room temperature. It was stained with 1% acetic orcein and mounted in 45% acetic acid. The observations of the meiosis of *C. saxifraga* were made on mother cells of the pollen grains using the squash technique. Floral buds of wild plants were fixed with Carnoy at room temperature, hydrolysed with 5N HCl at room temperature, stained with Feulgen and mounted with acetic carmine. The mitotic metaphase plate of *C. saxifraga* was obtained with this procedure. For *C. saxifraga*, two different collections from the only population of the species were counted. As for *C. kunkelii*, the only two populations known were counted. For all the counts, a minimum of twenty plates from different individuals were examined.

Preparations were made permanent by freezing with CO_2, dehydrating in ethanol and mounting in Canada balsam. Photographs were taken through a Zeiss Standard microscope. The preparations, the negatives and the herbarium vouchers are preserved in the Botanical Institute of Barcelona (BC).

Measurements of the cypselas were taken through a Zeiss binocular microscope with micrometric ocular. Final numbers are the mean values of 100 cypselas for each species (63 in the case of *Centaurea kunkelii*; Appendix 1).

RESULTS AND DISCUSSION

Karyology

Centaurea kunkelii, 2n = 110 (Fig. 1a, Fig. 2)

There are three ploidy levels among the five species described in the *Centaurea ornata* complex: two are diploid with 2n = 20 (*C. galianoi* Fernández Casas & Susanna, not widely accepted, and *C. gabrielis-blancae* Fernández Casas), two are tetraploid with 2n = 40 (*C. ornata* Willd. *s.str.*, a species of wide distribution, and *C. legionis-septimae* Fernández Casas & Susanna, a species restricted to the NW of the Iberian Peninsula) and one is hexaploid with 2n = 60 (*C. saxicola* Lagasca). *Centaurea kunkelii* has the highest level recorded in the whole genus *Centaurea s. lat*. This number (2n = 110) has been found only in three subspecies of *C. spruneri* Boiss. & Heldr.: subsp. *spruneri*, subsp. *guicciardi* (Boiss.) Hayek and subsp. *minoa* (Heldr.) Rech. fil. (Phitos 1970, 1971). *Centaurea spruneri* also belongs to sect. *Acrocentron*.

Our count could be alternatively interpreted as a decaploid (2n = 10×) with basic chromosome number x = 11 (also known in sect. *Acrocentron*) instead of x= 10. However, the basic chromosome number x =11 has never been reported in the *Centaurea ornata* complex and it is very infrequent among Western Mediterranean species of the section (Garcia-Jacas & Susanna 1992). In sect. *Chamaecyanus*, only one species has the basic chromosome number x = 11: *C. lagascana* Graells, a rare endemic species of northern Spain.

It is impossible to ascertain the origin of the extremely high chromosome number of *Centaurea kunkelii* with our present data. In any case, none of the crosses between species of the *C. ornata* group and sect. *Chamaecyanus* would result in this number: at least two hybridization events are needed.

Specimens examined. — See holotype and the BC paratype of *Centaurea kunkelii* cited below.

Centaurea saxifraga, 2n = 6× = 60 (Figs. 1b and c)

This chromosome count is new, according to our records. It was reported by Garcia-Jacas (1992), but it was never published in a widely distributed

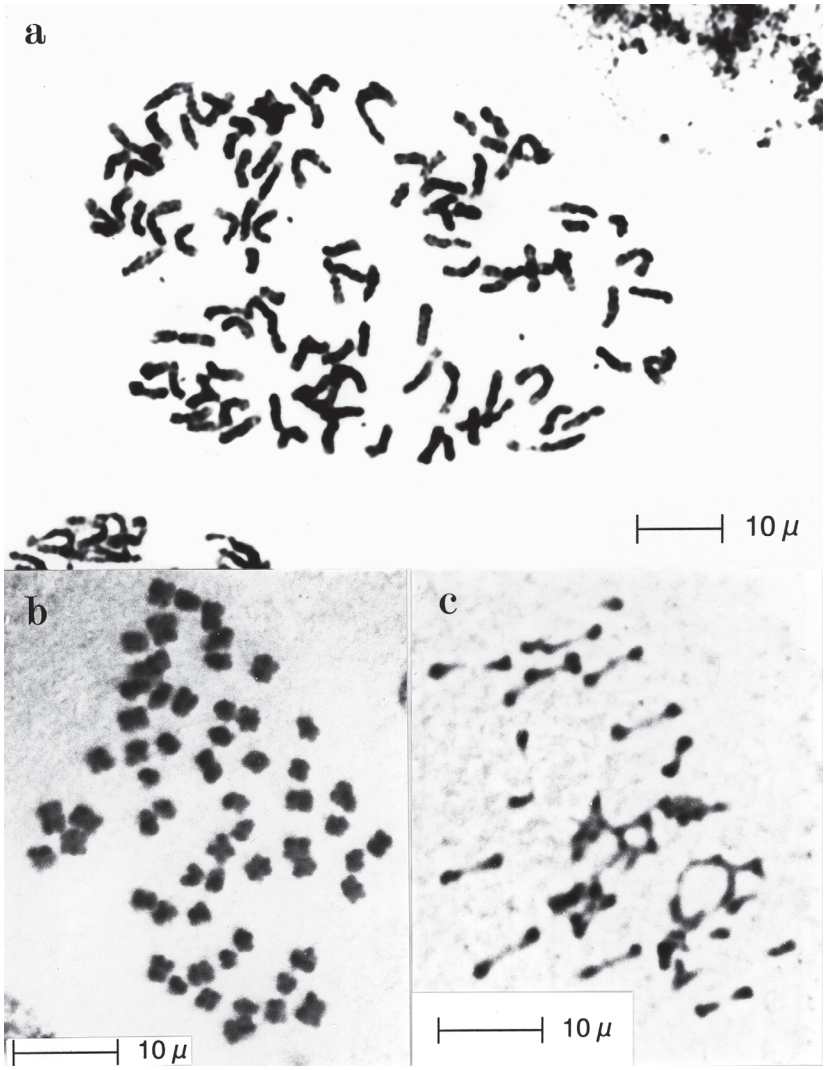


Fig. 1. — a: Somatic metaphase of *Centaurea kunkelii* Garcia-Jacas (*S-612*). — b: Somatic metaphase of *C. saxifraga* Coincy (*S-1233*). — c: Metaphase I → anaphase I of *C. saxifraga* showing two rings of multivalents.

journal. It is worth publishing here because a similar hybrid origin was postulated for *Centaurea saxifraga* (Garcia-Jacas 1992). It also has an infrequently high chromosome number, like *C. kunkelii*. The meiosis in mother of pollen cells is irregular, with the formation of two rings of multivalents (Fig. 1c). This supports the hypothesis of a hybrid origin for this taxon.

Centaurea saxifraga is a hexaploid whose origin can be traced to hybridization between a tetraploid species, probably *C. ornata s. str.* (sect. *Acrocentron*) and a diploid one, probably *C. mariana* Nym. (sect. *Chamaecyanus*). None of the purportedly parental species grows in the only locality of the hybrid, but they are frequent in the vicinity (Garcia-Jacas 1992). The hybrid origin was evident from its description by Coincy (1897), who classified it in sect. *Acrocentron* even recognizing its resemblance to the species of sect. *Chamaecyanus*. Fernández Casas & Susanna (1986) also considered *C. saxifraga* as a hybridogenic species, but intrasectional rather than intersectional, with both parental species from sect. *Acrocentron*: *C. ornata* × *C. granatensis* Boiss.

The origin of the frequent polyploidy in sect. *Acrocentron* can be explained in two ways. First, there are no barriers against hybridization between species of the section and even other related sections as sect. *Chamaecyanus* (Fernández Casas & Susanna 1986). The second reason is the pattern of growth in small, scattered, not fully connected populations (Wagenitz & Gamal-Eldin 1985) in

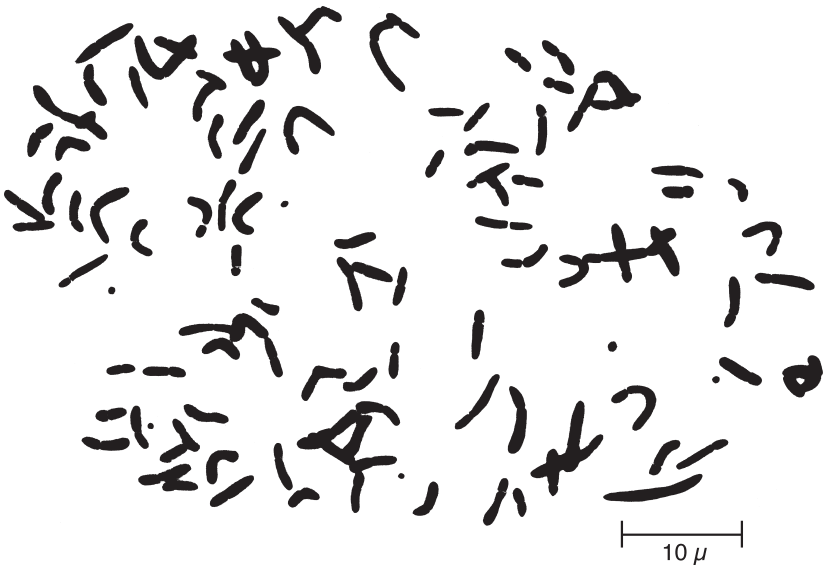


Fig. 2. Interpretation of the somatic metaphase of Fig. 1a.

which genetic drift results in interpopulational incompatibility.

Specimens examined. — Spain. Granada: near Zújar, summit of mount Jabalcón, UTM 30SWG15, 1400 m, 2.VIII.1988, *Garcia-Jacas & Susanna 1233* (BC); ibid., 6.VII.1990, *Garcia-Jacas, Susanna 1381 & Vallès* (BC).

Morphology of the cypsela

According to Fernández Casas and Susanna (1986), the most useful characters for detecting hybridization between sect. *Acrocentron* and sect. *Chamaecyanus* are found in the cypselas. Fig. 3 shows the cypselas of six species. First, there are two species of *Acrocentron*: *Centaurea prolongi* and *C. gabrielis-blancae* (Figs. 3a and b), both with a long outer pappus differing in structure and length from the inner. Second, there is a species of *Chamaecyanus*, *C. haenseleri* (Fig. 3c), with a very short outer pappus of the same length as the inner. Two putative hybrids between both sections follow, *C. saxifraga* (Fig. 3d) and *C. crocata* (Fig. 3e), with intermediate characters; and finally *C. kunkelii* (Fig. 3f). The extreme variability in shape and length of the pappus of *C. crocata* is remarkable (Fig. 3e) and, to a lesser extent, *C. haenseleri* (Fig. 3c) and *C. saxifraga* (Fig. 3d). The cypselas of *C. kunkelii* are similar in shape to those of *C. haenseleri*.

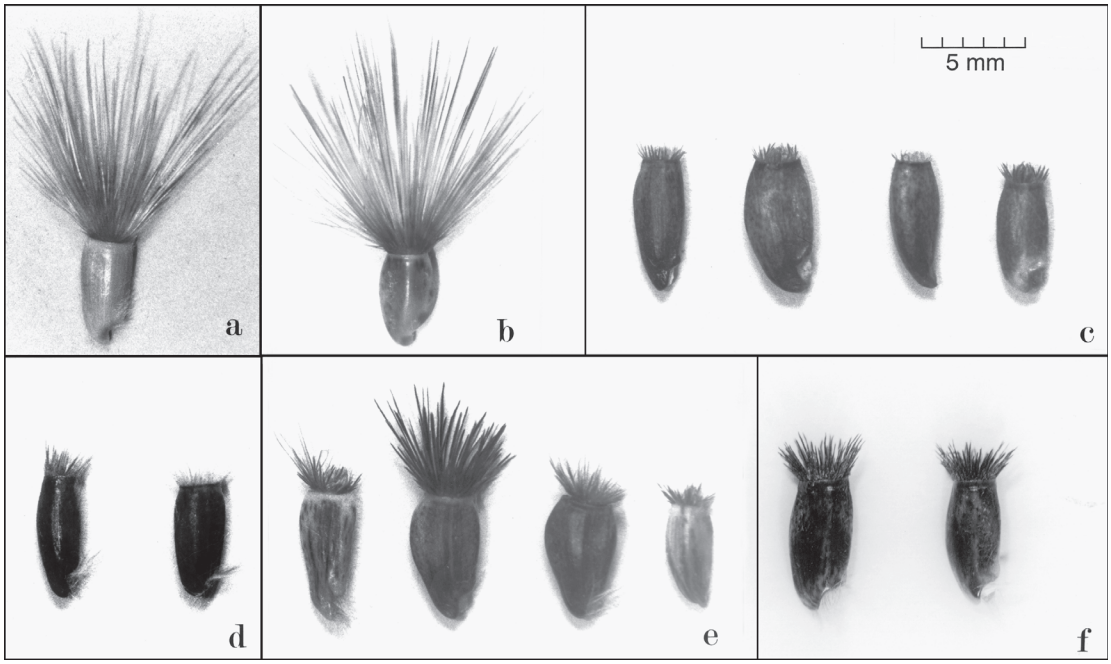
We have represented the length of the pappus of all the illustrated species in a chart (Fig. 3): the cypselas of *Centaurea kunkelii* are closer to the measures of the two purported hybrids, especially to those of *C. crocata*.

As is usual in hybridogenic species, cypselas of *Centaurea kunkelii* show characters from both parental species: the structure of the pappus, well differentiated in outer and inner pappus, points towards sect. *Acrocentron*. The shape of the cypselas and the short pappus points towards sect. *Chamaecyanus*.

Finally, the surface of the cypselas also supports the hypothesis of the hybrid origin between species of sections *Acrocentron* and *Chamaecyanus* of *Centaurea kunkelii*. The shape and the size of the cells of the pericarp are a good indicator of hybridization according to Fernández Casas & Susanna (1986). In *Acrocentron*, cells are three times longer than they are wide, and their margins are sinuate. In *Chamaecyanus*, cells are from five to ten times longer than wide, they are narrower and their margins are parallel. Hybrids usually have intermediate characters (Fernández Casas & Susanna 1986). The new species has both kinds of cells of the pericarp: some cypselas have the *Acrocentron* model and others have the *Chamaecyanus* model.

CONCLUSIONS

We believe that morphology and karyology demonstrate that *Centaurea kunkelii* is a new species



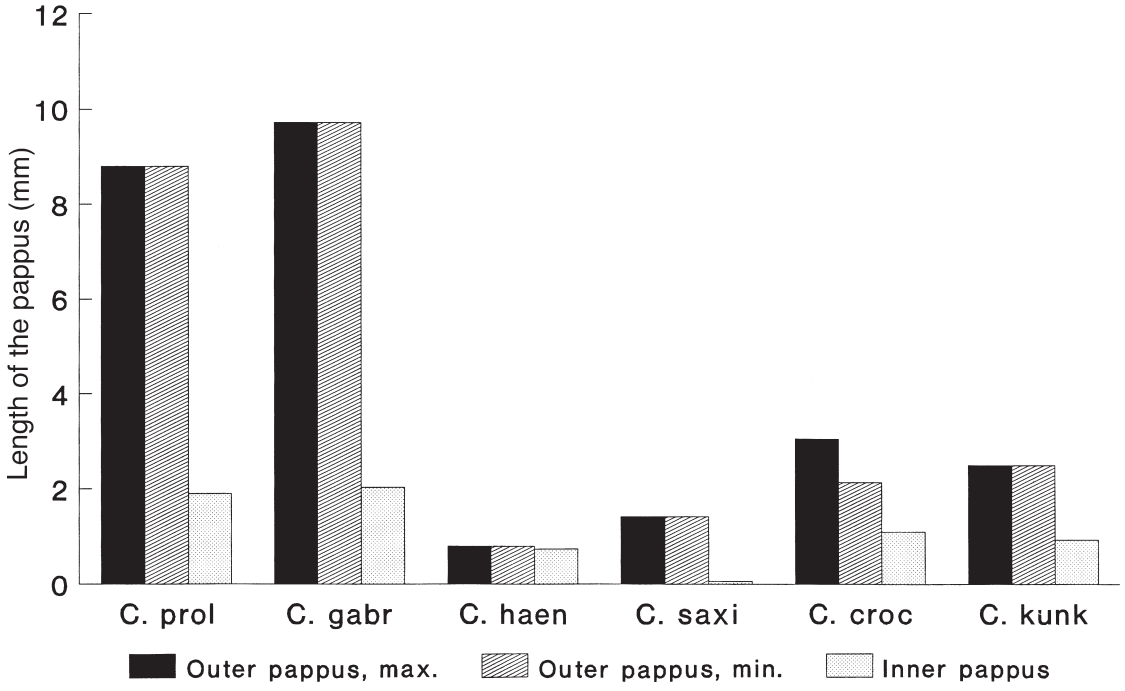


Fig. 3. Cypselas. — a: *Centaurea prolongi* Boiss. (*S-1335*). — b: *C. gabrielis-blancae* Fdez. Casas (*S-1413*). — c: *C. haenseleri* (Boiss). Boiss. & Reut. (*JMM-1853*). — d: *C. saxifraga* Coincy (*S-1233*). — e: *C. crocata* Franco (*S-1360*). — f: *C. kunkelii* Garcia-Jacas (*S-1613*). — g: Measurements of the pappus of the cypselas of the same populations. C. prol = *C. prolongi*; C. gabr = *C. gabrielis-blancae*; C. haen = *C. haenseleri*; C. saxi = *C. saxifraga*; C. croc = *C. crocata*; C. kunk = *C. kunkelii*.

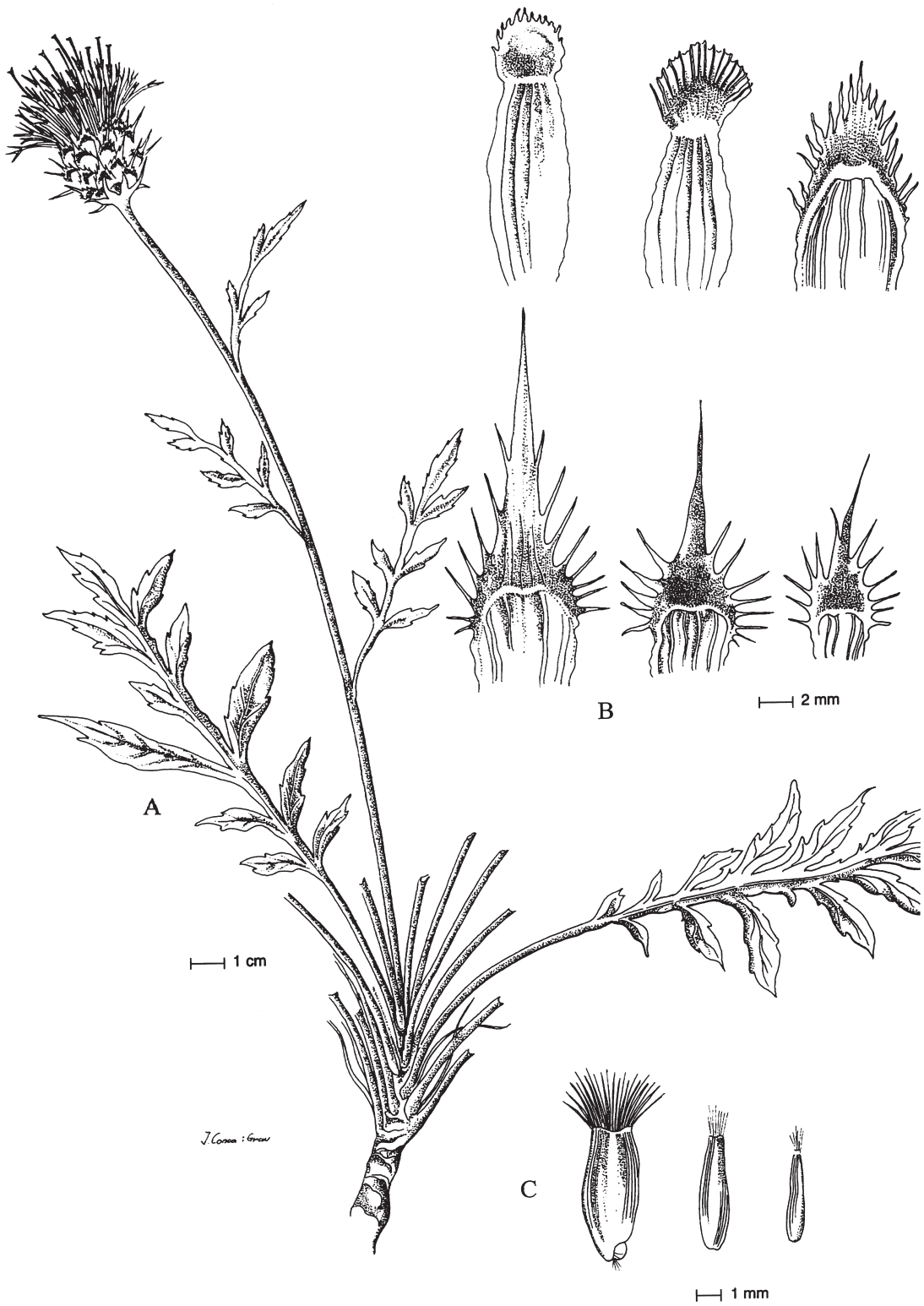


Fig. 4. *Centaurea kunkelii* Garcia-Jacas (holotype). — A: Habit. — B: Bracts of the capitulum, from the most internal (upper left) to the most external. — C: Fertile cypsela and two sterile cypseloids.

of hybrid origin between sections *Acrocentron* and *Chamaecyanus*. We cannot identify the parental species of sect. *Chamaecyanus*, but some characters of the bracts (the blackish appendages with a robust spine) point to *C. haenseleri*. This species grows in the mounts of Málaga and its present eastern limit is only 100 km from Gádor. The geographically closer *C. mariana* can be ruled out because it has a dense, snow-white indument whereas *C. kunkelii* is glabrescent. The parental species from sect. *Acrocentron* should be sought in the complex of *C. ornata*; probably, the hexaploid *C. saxicola*.

Centaurea kunkelii Garcia-Jacas, *sp. nov.* (Fig. 4)

Differt a C. gabrielis-blancae, C. ornata et C. saxicola floribus intensius luteis, bractearum appendicibus nigricantibus (nec stramineis) cypselisque multo maioribus, nigris (nec stramineis), pappo brevissimo instructis; a C. granatensi primo ictu nostra dignoscitur cum sit glabrescens atque robustior floresque intense luteos (nec aurantiacos) emittat; ab exiliore C. prolongi, denique, bractearum appendicibus in spinam multo validiorem abeuntibus atque cypselis nigris brevissimoque pappo instructis (nec stramineis atque longe papposis). Species amicissimo Günther Kunkel dicata, de Botanica scientia bene merito, scriptori fecundissimo necnon amoenissimo, indefesso peregrinatori fere universalis Florae studioso, nunc incolae felici deserti almeriensis, cuius addictus amator atque propugnator singularis evasit.

Type: Spain. Almera, Sierra de Gádor, carretera AL 411 de Roquetas a Canjáyar 200 m más allá del cruce al Marchal de Antón López, 30SWF38, 900 m, matorrales sobre calizas, 24.VI.1996, *Garcia-Jacas, Susanna 1613 & Vilatersana* (holotype BC, isotypes BC).

Subrosetted hemicryptophyte (18–25–40–45) cm high, with stolon-bearing rhizome.

Leaves light green, sparsely woolly with septate hairs, minutely glandular. Primordial leaves lanceolate, entire; adult, interruptedly runcinate-pinnatisect with pinnatifid segments, or rarely interruptedly runcinate-bipinnatisect, very long attenuate, of variable size, 9–25 × 3–11 cm, with lateral segments 1.6–5.5 × 0.8–2.5 cm; thickened margin, remotely denticulate with cartilaginous denticules. Cauline leaves as those of the rosette but smaller, pinnatifid, 3–9 × 1.2–4 cm; uppermost bracteiform, linear, sessile. Scape cylindric, striate, sparsely woolly, 16—40 cm high. Capitules terminal, solitary, subglobose, frequently umbilicate, 2–3 × 2–2.5 cm without flowers. Middle bracts of the involucre widely oval, 6–8 mm wide and 15–30 mm long (including the terminal spine), green, nerveless, densely aculeolate, sparsely woolly. Appendix widely triangular, decurrent, 7–11 mm wide (including the fimbriae) and 4–6 mm long, rusty-blackish to blackish, densely aculeolate, sparsely woolly; pectinate-fimbriate with lateral fimbriae 3–5 mm long, aculeolate, apically ending in a stout spine fimbriate in its basis, prickly, 5–23 mm. Outer bracts like the middle ones but smaller; inner bracts linear-lanceolate, green, with appendix widely elliptic or rounded, 2–7 mm wide, cochlear, pectinate-fimbriate, deep brown, aculeolate mostly on the fimbriae.

Florets deep yellow; outer sterile, with variable number (2–4) of petals, 6–5.5 × 1 mm, linear, acute; inner florets fertile, hermaphrodite, slightly zygomorphic, with five unequal petals linear, acute, 5–6.6 × 0.8 mm, thickened in the margins and the apex. Stamens 8–9 × 0.5–0.7 mm with basal appendix 1 mm long, lacerate. Filaments 3.5–4 mm long (when extended) and 0.4 mm wide, papillose. Stigma symmetrically bifid, 1.5 × 0.4 mm; basal brush 0.7 mm wide. Cypsela oblong, 5.7–6.5 × 2.5–3 mm, compressed, deep brown blotched with black or almost black, very sparsely sericeous. Hilum lateral, sericeous, with elaiosome. Pappus double, whitish; outer with pinnulate paleae 2–3 mm long; inner pappus 1.25–0.75 mm long or almost absent, with paleae of double width than outer, without lateral pinnules, lacerate in the apex.

By now, only known from the Sierra de Gádor, a limestone range in the south east extreme of Andalusia, Spain. There are two populations at a distance of 200 m.

Additional specimens examined (paratypes). — Spain. Almera, Sierra de Gádor, carretera AL 411 de Roquetas a Canjáyar junto al cruce del Marchal de Antón López, 30SWF38, 900 m, cunetas y campos secos sobre calizas, 24.VI.1996, *Garcia-Jacas, Susanna 1612 & Vilatersana* (BC); ibid., El Marchal, Enix, 36°53´N, 2°36´W, 985 m, filitas, matorral de *Ulex parviflorus*, 28. IV. 1997, *C. Aedo & al. CA4029*" (MA, as *C. ornata*).

Key to the related species of sections *Acrocentron* and *Chamaecyanus* of South Iberia

1. Adult leaves entire, glabrous, carnose; plant subscapose; appendages of the bracts blackish, muticous; plant without fertile seeds ..... *C. lainzii*
1. Adult leaves pinnatifid or pinnatisect, very rarely subentire, not glabrous; plants fertile 2
2. Plant woolly, snow-white; florets orange or orange-yellow 3
2. Plant glabrescent or araneose-pubescent; florets pale yellow, yellow or saffron yellow 5
3. Plant with stem, very rarely stemless; appendages of the bracts blackish; pappus more than 5 mm long ..... *C. granatensis*
3. Plant more or less stemless; appendages of the bracts straw-coloured; pappus no more than 2 mm long 4
4. Appendages of the bracts with spine no more than 10 mm long; pappus 1 mm long, inner row absent ..... *C. mariana*
4. Appendages of the bracts with stout spine 15–20 mm long; pappus 2 mm long ..... *C. saxifraga*
5. Appendages of the bracts blackish with slender spines no more than 8 mm long 6
5. Appendages of the bracts blackish or straw coloured with stout spines (10–) 30–40 mm 7
6. Divisions of the leaves acute; florets pale yellow; cypselas straw-coloured of uniform shape, with pappus 7–11 mm long ..... *C. prolongi*
6. Divisions of the leaves rounded; florets saffron yellow; cypselas blackish of variable shape, with pappus 1–5 mm long ..... *C. crocata*
7. Plant glabrescent 15–30 cm high; leaves interruptedly pinnatifid or pinnatisect with terminal lobe five times wider and longer than the lateral ones .... *C. saxicola*
7. Plant araneose-pubescent or hirsutiuscule, 30–80 cm high; leaves interrumptedly bipinnatifid or bipinnatisect with terminal lobe as the lateral ones or slightely wider 8
8 Bracts with straw-coloured appendages; cypselas straw-coloured with pappus 8–12 mm; florets pale yellow 9
8. Bracts with blackish appendages; cypselas blackish with pappus 1–3 mm; florets intense yellow 10
9. Heads 2–3 cm wide (without appendages) ..... *C. gabrielis-blancae*
9. Heads 4–5 cm wide (without appendages) ..... *C. ornata*
10. Plant stemless, araneose-pubescent; leaves interruptedly runcinate-pinnatisect with oval segments; pappus 1.5–2 mm ..... *C. haenseleri*
10. Plant with stem, hirsutiuscule; leaves interruptedly runcinate-pinnatisect with pinnatifid segments, or bipinnatisect; pappus 2–3 mm ..... *C. kunkelii*

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Appendix 1. Origin of the populations of *Centaurea* species included in the study of the cypselas. Vouchers in BC.

C. crocata	Portugal. Faro, near Monchique, 10 km N on the road to Odemira, 29SNB32, 500 m, 10.VI.1990, *Garcia-Jacas & Susanna S-1360*.
C. gabrielis-blancae	Spain. Granada, Sierra de la Sagra, between La Losa and La Puebla de Don Fadrique, 30SWG49, 1000 m, 19.VII.1990, *Vallès & Susanna S-1413*.
C. haenseleri	Spain. Málaga, Sierra Bermeja de Estepona, 30SUF03, 800 m, 4.VII.1988, *Garcia-Jacas, Julià, Montserrat JMM-1863, Susanna & Veny*.
C. kunkelii	Spain. Almería, Sierra de Gádor, road AL 411 from Roquetas to Canjáyar 200 m beyond the deviation to El Marchal de Antón López, 30SWF38, 900 m, 24.VI.1996, *Garcia-Jacas, Susanna 1613 & Vilatersana*.
C. prolongi	Spain. Málaga, 3 km N of Ojén on the way to Coín, 30SUF35, 400 m, 19.VI.1989, *Garcia-Jacas & Susanna S-1334*.
C. saxifraga	Spain. Granada, near Zújar, summit of mount Jabalcón, 30SWG15, 1400 m, 2.VIII.1988, *Garcia-Jacas & Susanna 1233*.