



Taxonomical and nomenclatural notes on *Centaurea*: A proposal of classification, a description of new sections and subsections, and a species list of the redefined section *Centaurea*

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Abstract

TAXONOMICAL AND NOMENCLATRURAL NOTES ON *CENTAUREA*: A PROPOSAL OF CLASSIFICATION, A DESCRIPTION OF NEW SECTIONS AND SUBSECTIONS, AND A SPECIES LIST OF A REDEFINED SECTION *CENTAUREA*.— In this paper, we summarize the results of our long-date research on the genus *Centaurea*. The first part of the paper deals with the overall classification of the genus, which we propose to divide into three subgenera: subgenus *Centaurea*, subgenus *Cyanus* and subgenus *Lopholoma*. The second part of this publication gives a recopilation of the species of the redefined section *Centaurea*, a group that includes former sections *Acrolophus* (sect. *Centaurea s. str.*), *Phalolepis* and *Willkommia*, together with taxonomical, geographical, ecological and karyological considerations. Finally, new descriptions or nomenclatural combinations are proposed to correlate nomenclature to the new classification: a new combination (sect. *Acrocentron* subsect. *Chamaecyanus*) is proposed in subgenus *Lopholoma*; three new sections (sects. *Akamantis*, *Cnicus*, and *Hierapolitanae*) are described in subgenus *Centaurea*; two subsections (subsects. *Phalolepis* and *Willkommia*) in sect. *Centaurea*; and three subsections (subsects. *Exarata*, *Jacea*, and *Subtilis*) in sect. *Phrygia*.

Key words: *Acrocentron*; *Acrolophus*; *Akamantis*; *Chamaecyanus*; *Cyanus*; *Exarata*; *Hierapolitanae*; *Jacea*; *Lopholoma*; *Phalolepis*; *Phrygia*; *Subtilis*; *Willkommia*.

Resumen

NOTAS TAXONÓMICAS Y NOMENCLATURALES EN *CENTAUREA*: PROPUESTA DE CLASIFICACIÓN, DESCRIPCIÓN DE SECCIONES Y SUBSECCIONES NUEVAS, Y LISTA DE ESPECIES DE UNA SECCIÓN *CENTAUREA* REDEFINIDA.— En este trabajo presentamos los resultados de nuestras investigaciones de larga fecha en el género *Centaurea*. La primera parte del trabajo trata de la clasificación del género, que proponemos dividir en tres subgéneros: subgénero *Centaurea*, subgénero *Cyanus* y subgénero *Lopholoma*. La segunda parte es una recopilación de las especies de la redefinida sección *Centaurea*, que incluye las antiguas secciones *Acrolophus* (sect. *Centaurea s. str.*), *Phalolepis* y *Willkommia*, junto con consideraciones geográficas, ecológicas y cariológicas. Por último, proponemos nuevas secciones, subsecciones y combinaciones para correlacionar nomenclatura y clasificación: proponemos una nueva (sect. *Acrocentron* subsect. *Chamaecyanus*) en el subgénero *Lopholoma*; se describen tres secciones nuevas (sects. *Akamantis*, *Cnicus* y *Hierapolitanae*) en el subgénero *Centaurea*; dos subsecciones (subsects. *Phalolepis* and *Willkommia*) en la sección *Centaurea*; y tres subsecciones (subsects. *Exarata*, *Jacea* y *Subtilis*) en la sección *Phrygia*.

Palabras clave: *Acrocentron*; *Acrolophus*; *Akamantis*; *Chamaecyanus*; *Cyanus*; *Exarata*; *Hierapolitanae*; *Jacea*; *Lopholoma*; *Phalolepis*; *Phrygia*; *Subtilis*; *Willkommia*.

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INTRODUCTION

Systematics of *Centaurea* L. has changed dramatically during the past two decades. Molecular methods have resolved the old problem of the delimitation of the genus (for details see Susanna *et al.*, 1995; Garcia-Jacas *et al.*, 2000, 2001, 2006; Hilpold *et al.*, 2014). To put it shortly, *Centaurea* as defined traditionally (e.g. Linnaeus, 1753; Bentham, 1873; Hoffmann, 1894; Dostál, 1976) was polyphyletic, and molecular studies showed that some clades, including the former section *Centaurea* (including the type species, *Centaurea centaurium* L.) had to be excluded in order to make the genus monophyletic. To prevent the renaming of hundreds of species, the type species was changed: the type is now *C. paniculata* L. (Greuter *et al.*, 2001). The old section *Centaurea* acquired the rank of genus on its own, namely *Rhaponticoides* Vaill. (Greuter, 2003; Greuter *et al.*, 2005). However, there are some open questions on the classification of the genus that are discussed in the work here presented.

Centaurea constitutes an important member of tribe Cardueae Cass. (Compositae). It is formed by annual, biennial or perennial herbs, less often shrubs, with usually unarmed leaves (Susanna & Garcia-Jacas, 2007). They are also characterized by a lateral hilum (Dittrich, 1968), and a specialized floral morphology with showy sterile peripheral florets without staminodes (Wagenitz & Hellwig, 1996a). The main morphological character used for systematics within *Centaurea* is the form of the scarious bract appendages. *Centaurea* is insect pollinated, mainly by bees and bumblebees (Harrod & Taylor, 1995; Bilisik *et al.*, 2008; Albrecht *et al.*, 2009; McIver *et al.*, 2009). The genus occurs mainly in the Mediterranean and Irano-Turanian regions, with some species (especially from sect. *Jacea*) extending northwards to temperate Europe. Redefined *Centaurea* is the largest genus within subtribe Centaureinae encompassing some 250 species (Susanna & Garcia-Jacas, 2007, 2009), but these figures are conservative and somewhat disputed because of wide differences in taxonomical treatments. Besides, the numbers are steadily rising with the description of new species in the Eastern Mediterranean (Aksoy *et al.*, 2008).

We published a general outline of a classification of the genus in Susanna & Garcia-Jacas (2007, 2009), but these were general works and we only

indicated that we classify *Centaurea* three subgenera, namely *Centaurea*, *Cyanus* (Mill.) Cass. ex Hayek, and *Lopholoma* (Cass.) Dobrocz. Thereafter, our aims with this paper are: (1) to present an overall classification of the genus, detailing especially our proposal for subgenus *Centaurea*; (2) to offer a list of species of the newly defined section *Centaurea*; and (3) to propose some new nomenclatural combinations within subgenera *Centaurea* and *Lopholoma*.

MATERIAL AND METHODS

For subgenera *Cyanus* and *Lopholoma*, our outline is based on the studies by Boršić *et al.* (2011) and Font *et al.* (2002, 2009), respectively. Regarding subg. *Centaurea*, our proposal follows the layout suggested by Garcia-Jacas *et al.* (2006) and Hilpold (2012), and is partly provisional for the Eastern Mediterranean (EMC) and Western Mediterranean (WMC) clades, which are in need of a more complete molecular survey.

As regards to the list of species of sect. *Centaurea*, we have followed current literature, basically floras. Taxonomy follows Euro+Med Plantbase (Euro+Med, 2006–2013) for the Eastern and Central Mediterranean region, and López & Devesa (2008a, b, c, d, 2010, 2011) and López *et al.*, (2011) for the Iberian Peninsula. More details on the construction of the Table 2 are given below.

DISCUSSION AND CONCLUSIONS

On the light of our previous results, we summarize our proposal of a classification for the genus (new sections, subsections and nomenclatural combinations are formally proposed at the end of the article):

Centaurea L.

Subgenus *Lopholoma* (Cass.) Dobrocz.

Sect. *Acrocentron* (Cass.) DC.

Subsect. *Acrocentron*

Subsect. *Chamaecyanus* (Willk.) new status and combination

Sect. *Stephanochilus* (Coss. & Durieu ex Benth. & Hook. f.) O. Hoffm.

Subgenus *Cyanus* (Mill.) Cass. ex HayekSect. *Cyanus*Subsect. *Cyanus*Subsect. *Perennes* Boiss.Subgenus *Centaurea*

Eastern Mediterranean Clade (EMC)

Sect. *Calcitrapa* DC. [incl. sects. *Seridioides* DC. and sect. *Tetramorphaea* (DC.) Boiss.]Sect. *Chartolepis* (Cass.) DC.Sect. *Cheirolepis* (Boiss.) O. Hoffm. [incl. sect. *Plumosipappus* (Czerep.) Wagenitz, sect. *Pseudoseridia* Wagenitz *p. p.* and sect. *Pteracantha* Wagenitz]Sect. *Cynaroides* Boiss. ex Walp. [incl. sect. *Paraphysis* (DC.) Wagenitz]Sect. *Grossheimia* (Sosn. & Takht.) DittrichSect. *Microlophus* (Cass.) DC.Sect. *Phaeopappus* (DC.) O. Hoffm.Sect. *Pseudophaeopappus* WagenitzSect. *Ptosimopappus* (Boiss.) O. Hoffm.Sect. *Rhizocalathium* Tzvelev (incl. sect. *Pseudoseridia* Wagenitz *p. p.*)

Western Mediterranean Clade (WMC)

Sect. *Hymenocentron* (Cass.) DC.Sect. *Melanoloma* (Cass.) DC. (incl. sect. *Gymnocyanus* Maire)Sect. *Mesocentron* (Cass.) DC.Sect. *Seridia* (Juss.) DC.

Circum-Mediterranean Clade (CMC)

Sect. *Centaurea*Subsect. *Centaurea*Subsect. *Phalolepis* (Cass.) new combinationSubsect. *Willkommia* (Blanca) new combinationSect. *Akamantis* new sectionSect. *Ammocyanus* Boiss.Sect. *Cnicus* (L.) new status and combinationSect. *Hierapolitanae* new sectionSect. *Phrygia* Pers.Subsect. *Phrygia*Subsect. *Exarata*, new subsectionSubsect. *Jacea* (L.) new status and combinationSubsect. *Subtilis*, new subsection

The genus *Centaurea* contains three well delimited subgenera: *Lopholoma* (often named *Acrocentron*), *Cyanus* and *Centaurea* (the latter corresponds to the *Jacea* group *sensu* Garcia-Jacas *et al.*, 2006). *Cyanus* has been also treated as separate genus (e.g. Greuter, 2003). We suggest treating them in the rank of subgenera. These three subgenera are well separated on the basis of molecular markers (Garcia-Jacas *et al.*, 2001; Susanna *et al.*, 2006; Barres *et al.*, 2013) and correspond to the existing pollen types.

The pollen of the genus *Centaurea* is, like that of all Compositae (Blackmore *et al.*, 2009), tricolporate and the ectexine is formed by two layers of columellae (Wagenitz, 1955). Within the genus, four clearly distinct pollen types can be found, which correspond to the three subgenera (Wagenitz, 1955; Martín & Garcia-Jacas, 2000; Susanna & Garcia-Jacas, 2009). *Centaureinae* show a dysploid chromosome series, with basic chromosome numbers ranging between $x = 16$ and $x = 7$ (Garcia-Jacas *et al.*, 1996). Low numbers can be found in more evolved groups and have been interpreted as an adaptation to dry conditions (Susanna & Garcia-Jacas, 2009). Chromosome numbers in *Centaurea* range from $x = 12$ to $x = 7$ (Table 1). Whereas subgenera *Cyanus* and *Centaurea* have a broad range of chromosome numbers, subgenus *Lopholoma* is more conservative, showing only two chromosome numbers. Chromosome numbers in the EMC and in the WMC follow largely the sectional division. The lowest chromosome number known to date in the genus was found in the annual *Centaurea patula* DC. with $x = 7$.

Centaurea is rich in secondary metabolites, which may mostly be a protection against herbivores (Olson & Kelsey, 1997; Susanna & Garcia-Jacas, 2009). Some of them show antimicrobial activity (Karioti *et al.*, 2001; Ugur *et al.*, 2009). Metabolites are predominantly sesquiterpene lactones (Tarasov *et al.*, 1975; Koukoulitsa *et al.*, 2005; Karamenderes *et al.*, 2007), but also flavonoids (Zapesoch-naya *et al.*, 1978; Nacer *et al.*, 2006), essential oils (Altintas *et al.*, 2004) and phenols (Bubenchikov *et al.*, 1992). Many phytochemical studies have been published over the last decade but only very few address explicitly systematic questions (but see Yildirim *et al.*, 2009).

Table 1. Chromosome numbers in *Centaurea*. ? = unknown number.

Genus <i>Centaurea</i>	Basic chromosome number <i>x</i>
Subgenus <i>Lopholoma</i>	
Sect. <i>Acrocentron</i>	10, 11
Sect. <i>Stephanochilus</i>	?
Subgenus <i>Cyanus</i>	
Sect. <i>Cyanus</i>	8, 9, 12
Sect. <i>Perennes</i>	10, 11
Subgenus <i>Centaurea</i>	7, 8, 9, 10, 11, 12
East Mediterranean Clade (EMC)	8, 9, 10
West Mediterranean Clade (WMC)	8, 10, 11, 12
Circum-Mediterranean Clade (CMC)	
Sect. <i>Akamantis</i>	9
Sect. <i>Ammocyanus</i>	7, 8
Sect. <i>Centaurea</i>	9
Sect. <i>Cnicus</i>	11
Sect. <i>Hierapolitanae</i>	8, 9
Sect. <i>Phrygia</i>	11

Subgenus *Lopholoma*

This subgenus comprises about 100 species (Font *et al.*, 2002) and is distributed all over the Mediterranean with one species, *Centaurea scabiosa* L., reaching the high north of Europe. The flower heads of *Lopholoma* are usually larger than in the other subgenera, and the bract appendages often ends in a long spine (Fig. 1A). The group is also morphologically well differentiated by presenting an only and characteristic pollen type, the *Centaurea scabiosa* type (Wagenitz, 1955). This subgenus was studied applying molecular tools by Font *et al.* (2002, 2009). There are two groups within the subgenus that should be treated as two different sections: The former monotypic genus *Stephanochilus* Coss. & Dur. ex Benth. is sister to all other members of the subgenus (Font *et al.*, 2002) and constitutes the first section. The second section, section *Acrocentron*, encompasses all other species of the subgenus. On molecular basis, Font *et al.* (2009) suggested that sect. *Chamaecyanus* Willk. is not clearly distinguishable from sect. *Acrocentron* despite clear morphological differences (a very short and simplified pappus combined with acaulescent habit). We propose to merge *Chamaecyanus* as subsection in section *Acrocentron*.

Subgenus *Cyanus*

The subgenus stands out by its predominantly bright blue flowers, as shown by its most prominent member, the cornflower (*Centaurea cyanus* L.; Fig. 1B). Further characters for this subgenus are two pollen types (*Cyanus* and *Montana* types of Wagenitz, 1955) and the pectinate-ciliate, unarmed, decurrent appendages of the phyllaries (Wagenitz & Hellwig, 1996a). The subgenus comprises about 40 species, also concentrated in the Mediterranean, reaching central Asia and the Caucasus. Molecular studies of the group were carried out by Boršić *et al.* (2011), Olšavská *et al.* (2011) and Löser (2013). The study of Boršić *et al.* (2011) confirmed the existence of two clearly distinct clades already marked by the pollen types and life cycles, corresponding to subsections. *Cyanus* (annuals) and *Perennes* (perennials).

Subgenus *Centaurea*

This subgenus corresponds to the *Jacea* group sensu Garcia-Jacas *et al.* (2006) and it is the most species-rich. It is represented by several hundreds of species mainly in the Mediterranean Region but also in Western Asia and Central and Eastern Europe. The most



Figure 1. Photographs of the genus *Centaurea*, with special emphasis on subgenus *Centaurea* and sect. *Centaurea*. (A), Subgen. *Lopholoma*: *C. ornata*, Soria, Spain (Photograph: A. Susanna); (B), Subgen. *Cyanus*: *Centaurea cyanus*, Soria, Spain (Photograph: A. Susanna). (C) Subgen. *Centaurea*: East-Mediterranean Clade (EMC): (C), *C. lycopifolia*, Barcelona Botanical Garden (Photograph: A. Susanna). (D–N), Circum-Mediterranean Clade (CMC). (D), *C. benedicta*, Barcelona Botanical Garden (Photograph: A. Susanna); (E), *C. akamantis*, Avakas gorge, Cyprus (Photograph: M. Galbany); (F), *C. hierapolitana*, Afon lake, Turkey (Photograph: A. Susanna); (G), *C. hyrcanica* (*Jacea-Phrygia* group), Iran (Photograph: A. Pirani); (H), *C. exarata*, Barcelona Botanical Garden (Photograph: A. Susanna); (I), *C. patula*, Barcelona Botanical Garden (Photograph: A. Susanna). (J–N), Sect. *Centaurea*. (J), *C. tenorei*, Minori, Italy (Photograph: A. Hilpold); (K), *C. alba*, Sierra de Aracena, Spain (Photograph: L. Barres); (L), *C. pulvinata*, Sierra de Abrucena, Spain (Photograph: G. Blanca); (M), *C. horrida*, Sardinia (Photograph: S. Pisanu); (N), *C. princeps*, Barcelona Botanical Garden (Photograph: A. Susanna); (O), *C. panormitana*, Sferracavallo, Sicily (Photograph: A. Hilpold).

characteristic trait of the subgenus is the pollen type, the so-called *Jacea* pollen type (Wagenitz, 1955; Garcia-Jacas *et al.*, 2000). New systematic insights of the subgenus on molecular grounds were provided by Garcia-Jacas *et al.* (2006). One of the main results of this study, based on ITS sequence analyses, was the separation of subgen. *Centaurea* into three clades, which were named after their main geographic distribution: the Eastern Mediterranean Clade (EMC) comprises species often with spiny bract appendages from the Eastern Mediterranean (Fig. 1C shows *C. lycopiifolia* Boiss. & Kotschy ex Boiss.), including the widely distributed weed *Centaurea calcitrapa* L.; the Western Mediterranean Clade (WMC), the members of which also show pronounced spiny bract appendages, well visible in the common weeds *Centaurea solstitialis* L. or *C. sulphurea* Willd.; and the Circum-Mediterranean Clade (CMC), the members of which are predominantly not or only slightly spiny in their bract appendages. Despite their wide distribution, their importance as weeds, and the high species diversity, our knowledge about systematics within the EMC and the WMC is poor and would need a more comprehensive study with molecular methods. The CMC, however, was already the centre of attention of profound molecular work (see below).

The most distinctive characters of the CMC are also the bract appendages (Fig. 1D–N). There are three extreme forms: membranaceous, long ciliate-fimbriate, and reduced or missing appendages. According to Garcia-Jacas *et al.* (2006) most species within the CMC belong to two main clades: the *Jacea-Phrygia* group (hereafter referred to as section *Phrygia*) and the *Centaurea* group (formerly *Acrolophus* subgroup; hereafter referred to as section *Centaurea*; Wagenitz & Hellwig, 1996a). Following Hilpold (2012), besides these two groups, four more sections belong to the CMC: the new monotypic section *Akamantis* consisting of *Centaurea akamantis* T. Georgiadis & Hadjik. from Cyprus, section *Ammocyanus* composed of *C. ammocyanus* Boiss. and *C. patula*, the new monotypic section *Cnicus* consisting of *Centaurea benedicta* (L.) L. (formerly *Cnicus benedictus* L.) and the new section *Hierapolitanae*, including *C. hierapolitana* Boiss. and *C. tossiensis* Freyn & Sint. ex Freyn from Turkey.

Section Phrygia — Members of section *Phrygia* can be distinguished from those of section *Centaurea* by (1) the basic chromosome numbers, $x = 11$ vs. $x = 9$ respectively, (2) the leaf shape, since *Phrygia* leaves are entire, while in section *Centaurea* at least the basalmost leaves are deeply divided. Section *Phrygia* also has a different ecology and distribution: species of sect. *Centaurea* are much more dry adapted and bound to Mediterranean climate, whereas the vast majority of species of sect. *Phrygia* are typical elements of montane and subalpine meadows, influenced by frequent mowing, grazing or avalanches. They are dependent on a good and constant water supply and are quite resistant to cold periods. These adaptations permitted the group also to disperse into the high north of Europe, with species like *Centaurea nigra* L. or *C. jacea* L. Taxonomy within sect. *Phrygia* is highly complex, and the latest attempts to elucidate it using molecular markers (Koutecký *et al.*, 2011; López-Alvarado, 2012) are only partially satisfying because of the very low levels of variation found. The apparent lack of any intrinsic breeding barriers led to the description of many hybrids on one hand (Vanderhoeven *et al.*, 2002; Koutecký, 2007; Vonica & Cantor, 2011). On the other hand, a split of the breeding communities into diploid and tetraploid lineages, connected by frequent polyploidization events, was observed (Hardy *et al.*, 2000; Koutecký, 2007; Koutecký *et al.*, 2011). Traditional systematics based on morphology within this group uses merely the shape of the bract appendages for the subdivision into two groups: *Phrygia* (formerly *Leptanthus*) with long, fimbriate bract appendages and *Jacea* with either short ciliate or membranaceous bract appendages. Intermediate forms between these extremes are commonly attributed to hybridization events (Vanderhoeven *et al.*, 2002; Koutecký, 2007; Vonica & Cantor, 2011). We suggest keeping these two groups the rank of subsections.

Section Centaurea — The type section has its centre of distribution around the Mediterranean and the Black Sea (Fig. 2). Highest species numbers can be found in the Balkan Peninsula, Italy, Turkey and the Iberian Peninsula (in order of abundance). Almost all African species are concentrated in the NW of the continent, in the Atlas mountain ranges. A few widespread species reach central Europe and the Baltic Sea (*C. stoebe* L.) and Middle Asia, Afghanistan and Pakistan (*C. virgata* Lam.).

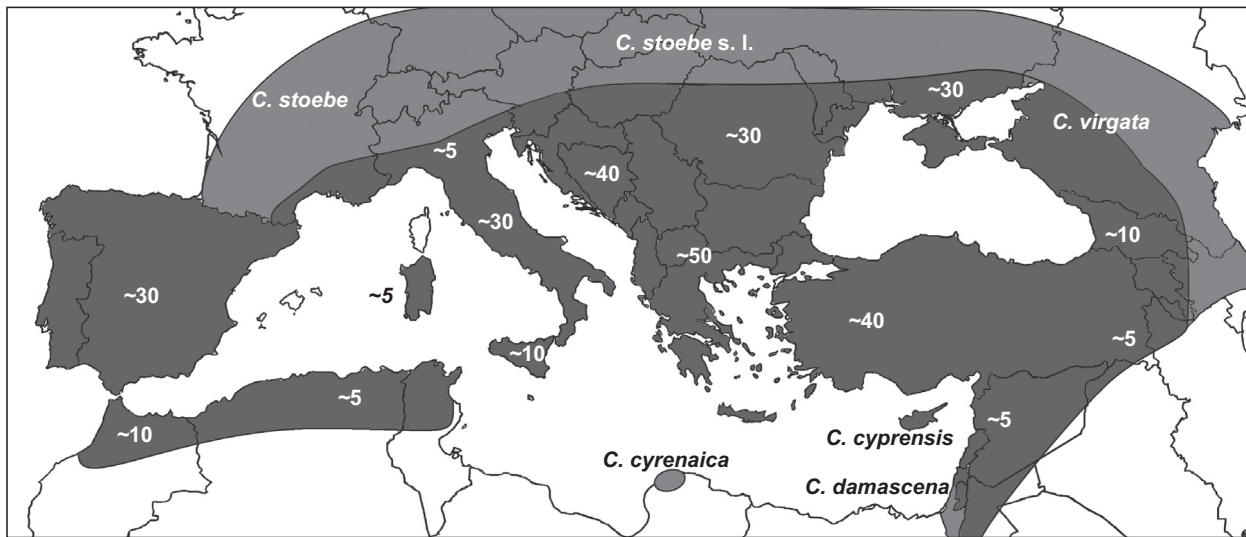


Figure 2. Distribution of sect. *Centaurea* (without introduced populations). Dark grey: areas with more than one species occurring. Light grey: only one species occurring, species name is given. Numbers show the approximate species number in the area. Note that the species numbers reflect, besides real differences in diversity, also the species concepts used in the different areas.

All members of sect. *Centaurea* grow in dry, open vegetation. Many species can be found in frequently pastured garrigues, on the coast or in the interior. Furthermore, open rocks are inhabited. Only exceptionally, high mountain areas were colonized. Some species are specialized in sandy beaches (e.g. *C. spinosa* L.). Both substrates, calcareous and siliiceous soils are inhabited with predominance on the first ones. Members of sect. *Centaurea* are rarely selfing or even obligate outcrossers (Harrod & Taylor, 1995; Hardy *et al.*, 2004). Reproduction is usually sexual (Noyes, 2007), although facultative apospory has been reported (Cela Renzoni & Viegi, 1982).

Species of sect. *Centaurea* have a basic chromosome number of $x = 9$. Most counted populations are diploid ($2n = 18$; Fig. 3). Tetraploids ($2n = 36$) are frequent, and they have been subject of recent scientific work (Španiel *et al.*, 2008; Mráz *et al.*, 2012). Three species are hexaploid ($2n = 6x = 54$): *C. carystea* Trigas & Constantin., *C. cithaeronea* Phitos & Constantin. and *C. tuzgoluensis* Aytaç & H. Duman; *cf.* Phitos & Constantinidis, 1993; Martin *et al.*, 2009; Trigas *et al.*, 2008, respectively. Two species with divergent chromosome numbers ($x = 11$), *Centaurea exarata* Boiss. ex Coss. and *C. subtilis* Bertol., traditionally assigned to sect. *Centaurea*, were found to be closely related to the *Centaurea jacea* complex (sect. *Phrygia*) and thereafter were

removed from sect. *Centaurea* (Garcia-Jacas *et al.*, 2006; Hilpold *et al.*, 2009). Counts of chromosome numbers differing from the basic number $x = 9$ are extremely rare: $2n = 44$ (one single count by Baden (1983) in *C. affinis* Friv., usually with $x = 9$), $2n = 16$ (in *C. deustiformis* Adamović; Strid, 1983; only in one out of many counts in *C. diffusa* Lam.; Bancheva & Greilhuber, 2006), and $2n = 32$ (in *C. arenaria* Willd.; Bancheva & Greilhuber, 2006). Figure 3 shows the percentages of counted species and the distribution of the known chromosome numbers.

A few members of sect. *Centaurea* are used as ornamentals, like *Centaurea cineraria* L. (“Velvet *Centaurea*”, *cf.* Ellis, 1999). Some species are used as medicinals, especially in folk medicine, because of its secondary compounds (Nacer *et al.*, 2006; Akkol *et al.*, 2009). The sesquiterpene lactone cnicin, found in *Centaurea benedicta* (the name of the compound derives from its former name *Cnicus benedictus* L.) and other species of sect. *Centaurea* (Olson *et al.*, 1997; Erel *et al.*, 2011) is sometimes used for bitter tonics (Tešević *et al.*, 2007).

Most important, however, are not the benefits that members of sect. *Centaurea* provide, but their negative impacts on agriculture and landscape. *Centaurea stoebe* (= *C. maculosa* Lam.) and to a lesser extent *C. diffusa* and *C. virgata* subsp. *squarrosa* (Boiss.) Gugler, are tremendous invasive weeds in pastures of the US and Canada. *Centaurea stoebe*,

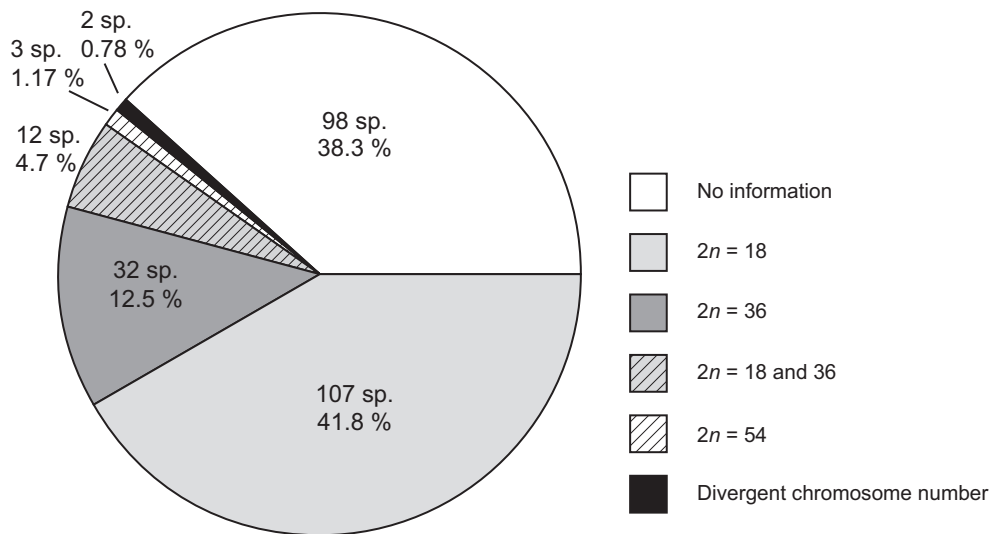


Figure 3. Pie diagram indicating the percentages of known - unknown chromosome numbers a, ploidy levels, and discording results in *Centaurea* sect. *Centaurea*.

“one of North America’s most devastating invasive plants” (Blair & Hufbauer, 2010), diminishes the fodder value of pastures infesting about 3 million ha (Di Tomaso, 2000) producing in this way economic damage of hundreds of million dollars every year. The estimated damage for the agriculture of Montana amounts to 42 million dollars (Duncan *et al.*, 2001). The fight against these weeds is also the motor of most of the research conducted in *Centaurea* (e.g. Hufbauer & Sforza, 2008; Collins *et al.*, 2011; Pollock *et al.*, 2011; Reinhart & Rinella, 2011).

Traditional, morphology-based treatments and their limitations

Section *Centaurea* is traditionally divided into two main groups based on the morphology of their bract appendages: section *Phalolepis* (Cass.) DC. (Fig. 1J) with lacerate membranaceous appendages, and sect. *Centaurea* (formerly sect. *Acrolophus* (Cass.) DC.; Fig. 1I) with ciliate to fimbriate ones. These two groups are treated as subgenera in Dostál (1976) in his treatment for *Flora Europaea* and more often as sections. The appendage morphology is the only character used for their delimitation (Dostál, 1976), but within these two groups, however, a broad range of morphological characters can be found to perform further delimitations (Fig. 1L–N): leaf shape (divided), indumentum (tomentose, glabrous), flower colors (rarely yellow, mostly purple), plant size (a

few centimetres in annual and biennial species up to 1.50 m in both biennial and perennial species, but mostly between 20 and 50 cm). A third section was upgraded to sectional rank 30 years ago: under the name of sect. *Willkommia* Blanca (Blanca, 1981a; Fig. 1K) a group of species was defined which shows perennial life form (frequently dwarf shrubs) and usually black, fimbriate bract appendages ending in a small spine. This group, contrarily to the other two sections, was defined also geographically as including only individuals from NW Africa and the Iberian Peninsula, but leaving behind morphologically similar forms from the Eastern Mediterranean. The delimitation between these three sections is more than problematic. The distinction between sections *Phalolepis* and *Centaurea* is based on one single morphological character and is thereafter highly questionable if this single character shows intermediate forms or is not present at all (as in some species from the central Mediterranean, where the bract appendages are totally or almost totally reduced). The presence of intermediate forms was demonstrated by Wagenitz (1989) and appears in many species descriptions (e.g. Breitwieser & Podlech, 1986; López & Devesa, 2008c). Intermediate forms have been commonly attributed to hybridization between the two sections, without doubting their monophyly (Garcia-Jacas *et al.*, 2006; Suárez-Santiago *et al.*, 2007b).

Delimitation and monophyly of section *Willkommia* is not clear. In the Eastern Mediterranean, *C.*

attica Nyman from Greece shows similar bract appendages, and similar species are also found in NE Libya (*C. cyrenaica* Bég. & A. Vacc.) and on the easternmost shore of the Mediterranean, for example *C. damascena* Boiss. and *C. dumulosa* Boiss. All these species are currently assigned to sect. *Centaurea*. Intermediates between sections *Willkommia* and *Centaurea* are frequent on the Iberian Peninsula, where most members of section *Centaurea* show somewhat fimbriate and at least slightly spiny bract appendages. Placement of species like *C. cordubensis* and *C. monticola* in any of these two sections is unclear, which can also be seen in incongruencies between taxonomic treatments (Blanca, 1981a vs. López & Devesa, 2008c). Delimitation between *Willkommia* and *Phalolepis* following sole morphological observations is not precise either. Partly or entirely membranaceous bract appendages within *Willkommia* are found in NW Africa (*C. debdouensis* Breitw. & Podlech, *C. pomeliana* Batt.) and in the Iberian Peninsula (*C. avilae* Pau). *Centaurea tougourensis* Boiss. & Reut., one of the only two *Phalolepis* species from NW Africa, has a perennial, subshrubby life form and a small spine on their otherwise membranaceous bract appendages—very similar to members of section *Willkommia*, of which it is surrounded by.

Besides the separation of these three subgenera, Dostál (1975, 1976) distinguished two subgroups within his subgenus *Phalolepis* and 11 within *Acrolophus*, stressing for their delimitation upon morphology of leaves, indumentum and bract appendages. Further groupings within the three sections are used in local treatments, for example in Pignatti (1982).

Hybridisation

The morphologically described species of sect. *Centaurea* are not separated through intrinsic breeding barriers. Reports about hybrids are abundant (e.g. Halácsy, 1902; Georgiadis, 1981a; Blanca, 1984). These hybrids are frequently fertile and homoploid (Blanca, 1981a; Ochsmann, 1998; Pisano *et al.*, 2011), sometimes also polyploid (Blair & Hufbauer, 2010; Mráz *et al.*, 2012). Hybrids with not closely related species—for example from the WMC—have been reported (Pau, 1914; Prodan, 1930; A. Susanna, pers. obs.), these however, produce usually no fertile offspring and therefore they do not lead to reticulation.

Systematic treatments of sect. *Centaurea* in light of molecular approaches

From the late 1990s onwards, a series of molecular investigations in sect. *Centaurea* has been conducted, using mainly DNA sequence data (Ochsmann, 2000; Garcia-Jacas *et al.*, 2006; Wagenitz *et al.*, 2006; Suárez-Santiago *et al.*, 2007b; Beltrame, 2007; Mráz *et al.*, 2012). Additionally, some work has been done, considering small species groups and using microsatellites techniques (Marrs *et al.*, 2006; Suárez-Santiago *et al.*, 2007a), isozymes (Bancheva *et al.*, 2006, 2011), RAPD (Tornadore *et al.*, 2000; Sozen & Ozaydin, 2010) and SDS-PAGE (Uysal *et al.*, 2010). Interestingly, the traditional sectional division based on morphological traits was not confirmed in any of these molecular works.

Species delimitation within sect. *Centaurea*

As taxonomic treatments within sect. *Centaurea* are highly incongruent, a really crucial question arises: what has to be considered as a species and what not? From the answer of this question depend many other investigations, like the diagnosis of the conservation status and conservation strategies (e.g. Townsend-Peterson & Navarro-Sigüenza, 1999). Modern species concepts agree in the point that species are separately evolving metapopulation lineages (De Queiroz, 2007), but members of the genus *Centaurea*, like most other plant species as well, were and are still described following a purely phenetic species concept (Michener, 1970), i.e. only by assessing morphological characters in the hope that all populations bearing these characters would correspond to a single lineage. This approach itself may be prone to produce inaccurate results, but even more difficult is the question how much morphological divergence is enough to separate two morphologically distinct plant groups as separate species. Additionally, the same or similar characters may arise separately and may therefore not be synapomorphies but rather homoplastic traits. Differences in species numbers produced by different *modi operandi* are huge. Examples can be easily seen if we compare different taxonomic treatments in *Centaurea*.

Species List

The following list includes all species of the newly defined section *Centaurea* (including former sections

Acrolophus, *Phalolepis* and *Willkommia*). Only recent literature is incorporated. Taxonomy follows Euro+Med Plantbase (Euro+Med, 2006–2013), which is the most complete listing of the genus *Centaurea*. For areas not included in Euro+Med, local floras were used. Cases where our treatment diverges from that of Euro+Med are specifically mentioned. Synonyms are only given if the name in Euro+Med diverges from the name used in this list. The second column of the Table 2 shows the currently accepted assignation to any of the three subsections *Centaurea* (C, formerly sect. *Acrolophus*), *Phalolepis* (P) and *Willkommia* (W). The third column shows the approximate distribution of the taxon. The fourth column gives information about the chromosome number. We usually give two citations per chromosome number, because further information can be easily retrieved from the indices to plant chromosome numbers (Goldblatt & Johnson, 1979–; Watanabe, 2002). The fifth column shows if there exists evidence from the ITS that the taxon belongs to the section *Centaurea*. The information derives, if not otherwise mentioned, from the studies of Ochsmann (2000), Garcia-Jacas *et al.* (2006), Suárez-Santiago *et al.* (2007a, b) and Hilpold *et al.* (2014). Column six lists revisions of the species when available. The last column gives information about the existence of subspecies (only those accepted in Euro+Med).

Iberian Peninsula — Systematic treatment follow the preparatory works for *Flora iberica* by López & Devesa (2008a, b, c, 2010, 2011) and López *et al.* (2011) for the *C. paniculata* and the *C. alba* groups, and Blanca & Suárez-Santiago (2011) for sect. *Willkommia*. Identification keys can be found in López & Devesa (2010; *C. paniculata* complex & *C. diffusa*), López & Devesa (2011; *C. alba* complex) and Blanca (1981a) for members of sect. *Willkommia*. Whether *C. paniculata* and *C. leucophaea* Jord. from the Iberian Peninsula are really closely related or even homonymous to populations from SE France and NE Italy is an open question. The same is true for *Centaurea boissieri* DC., *C. monticola* Boiss. ex DC. and *C. resupinata* Coss., all listed for the Iberian Peninsula and NW Africa.

North Africa — Most members of sect. *Centaurea* occur in the NW of the continent, namely in various ranges of the Atlas Mountains. Only *C. cyrenaica* Bég. & A. Vacc. occurs in the NE of the continent (Lybia). No recent complete treatments of the group are available, only the revision of section *Willkommia* from NW Africa by Breitwieser & Podlech (1986).

Italy, France and central Europe — All Italian *Centaurea* species are listed in Conti *et al.* (2005) and in Network Nazionale della Biodiversità (2012–) but are not treated in detail. Complete treatments for Italy are given in Fiori (1927) and in Pignatti (1982). Treatments for single groups: Arrigoni (2003; *C. paniculata* complex), Cela Renzoni & Viegi (1982; *C. cineraria* complex); Guarino & Rampone (2006; *C. dissectae* group). Many new descriptions have been published over the last 30 years. In the meantime, *C. subtilis* has been removed from the section (Hilpold *et al.*, 2009). Here we follow the very tight treatment of Euro+Med.

Balkans (including Romania, Aegean Sea and Crete) — The most complete taxonomic treatments concentrating on the Balkan area are those of Boissier (1875) and Hayek (1931). Newer treatments of the entire area other than *Flora Europaea* (Dostál, 1976) do not exist. In the NW Balkans, besides some widely distributed species, there are two main species groups: the *C. spinosociliata* group and the *C. cuspidata* group. The latter one, though only distributed in a relatively small area, was split into several microspecies of doubtful rank. These two species groups are treated in Lovrić (1968). A treatment for Romania is given in Ciocârlan (2000), for Greece in Halácsy, (1902), for the Greek Mountains in Gamal-Eldin & Wagenitz (1991), for the Aegean Sea in Rechinger (1943), for N Greece in Rechinger (1939). Listings of sect. *Phalolepis* from Greece are given in Wagenitz (1971) and Georgiadis *et al.* (1996), of the Bulgarian members of genus *Centaurea* in Assyov *et al.* (2002) of the Croatian members in Flora Croatica Database (Nikolić, 2010).

Region N of Black Sea (Russia p. p., Ukraine, Moldavia) — Most species in this area belong to five species groups: the *C. stoebe* complex, the *C. margaritacea* aggr., the *C. sterilis* aggr., the *C. ovina* aggr. and the *C. arenaria* aggr. Monophyly of these groups is not clear. The most complete treatment for Russia, Ukraine and Moldavia is given in Klokov *et al.* (1963).

Anatolia and Cyprus — *Flora of Turkey* (Wagenitz, 1975) lists nine species for section *Phalolepis* and 21 species for section *Centaurea* (= *Acrolophus*). In recent years, several new species have been described. Two species of *Phalolepis* (*C. hierapolitana* and *C. tossiensis*) do not belong to sect. *Centaurea*. The same is true for *C. akamantis* from Cyprus—where only one species remains, *C. cyprensis* (Holub) T. Georgiadis (Meikle, 1985).

Caucasus Region — The Caucasus region, including parts of Russia, Georgia, Armenia and Azerbaijan, is relatively poor in endemic taxa of sect. *Centaurea*. The most complete treatment for the area is given in Klokov *et al.* (1963).

Near-East, Middle-East — No complete listings or treatments are available postdating Boissier (1875), since Euro+Med considers only the western part of this area. Contributions for this area in the list derive mainly from regional floras; i.e. Post & Dinsmore (1932), Feinbrun-Dothan (1978) and Wagenitz (1980).

Nomenclatural proposals

Centaurea subgenus *Lopholoma* (Cass.) Dobroc. Sect. *Acrocentron* (Cass.) DC. subsect. *Chamaecyanus* (Willk.) Garcia-Jacas, Hilpold, Susanna & Vilatersana, **new combination** \equiv *Centaurea* sect. *Chamaecyanus* Willk. in Willkomm & Lange, Prodr. Fl. Hisp. 2: 150. 1870 [Basionym].

Centaurea subgenus *Centaurea*

Sect. *Centaurea*

Centaurea sect. *Centaurea* subsect. *Phalolepis* (Cass.) Garcia-Jacas, Hilpold, Susanna & Vilatersana, **new combination** \equiv *Phalolepis* Cass., Dict. Sci. Nat., ed. 2., 50: 248. 1827 [Basionym] \equiv *Centaurea* sect. *Phalolepis* (Cass.) DC., Prodr. 6: 568. 1838. \equiv *Centaurea* subgenus *Phalolepis* (Cass.) Dobroc., Bot. Zurn. 6: 63. 1949. Fig. 1K.

Centaurea sect. *Centaurea* subsect. *Willkommia* (Blanca) Garcia-Jacas, Hilpold, Susanna & Vilatersana, **new combination** \equiv *Centaurea* sect. *Willkommia* Blanca, Lagasalia 10: 138. 1981 (publ. 1982) [Basionym]. Fig. 1L.

Centaurea sect. *Akamantis* Garcia-Jacas, Hilpold, Susanna & Vilatersana, **new section**

Perennial species with heterogamous heads. Cauline leaves linear-spatulate, sparsely lanuginose. Capitula very small, exactly ovate. Bracts lanuginose; appendages much reduced, triangular, scariose, terminated in a short recurved mucro. All the florets deep purple, the central ones with darker anther-tube, the outer ones sterile, only slightly radiant.

Type and only species: *Centaurea akamantis* T. Georgiadis & Hadjik., Willdenowia 23: 157. 1993. Fig. 1E.

Centaurea sect. *Cnicus* (L.) Garcia-Jacas, Hilpold, Susanna & Vilatersana, **new status and combination** \equiv *Cnicus* L., Sp. Pl. 2: 826. 1753 (nom. cons.) [Basionym]. Type and only species: *Centaurea benedicta* L., Sp. Pl. 2: 826. 1753. Fig. 1D.

Centaurea sect. *Hierapolitanae* Garcia-Jacas, Hilpold, Susanna & Vilatersana, **new section** Annual or perennial species with heterogamous heads. Capitula minute, cylindrical, with only 10-20 florets, the outer ones sterile and radiant. Involucral bracts with orbicular, scariose, lacerate appendages, similar to those of sect. *Phalolepis*, but long decurrent. Type: *Centaurea hierapolitana* Boiss., Diagn. Pl. Orient. ser. 1, 4: 15. 1844. Other species: *Centaurea tossiensis* Freyn & Sint., Oest. Bot. Zeitschr. 44: 258. 1894. Fig. 1F.

Centaurea sect. *Phrygia*

Centaurea sect. *Phrygia* subsect. *Exarata*, **new subsection**

Stands apart from subsect. *Phrygia* and subsect. *Jacea* by the reduced appendages of the bracts, which are very small, applicate, not plumose and recurved as in subsect. *Phrygia* or very wide and covering partly or totally the bracts as in subsect. *Jacea*. Differs from subsect. *Subtilis* by having entire leaves, not pinnatisect as in *C. subtilis*. Type and only species: *Centaurea exarata* Boiss. ex Coss., Notes pl. crit.: 116. 1851. Fig. 1H.

Centaurea sect. *Phrygia* subsect. *Jacea* (L.) Garcia-Jacas, Hilpold, Susanna & Vilatersana, **new combination** \equiv *Centaurea* [infrageneric unranked] *jacea* L., Sp. Pl. 2: 909. 1753 [Basionym] \equiv *Centaurea* sect. *Jacea* (L.) DC., Prodr. 6: 570. 1837 [publ. 1838].

Centaurea sect. *Phrygia* subsect. *Subtilis*, **new subsection**

Can be easily set apart from subsect. *Phrygia*, subsect. *Exarata* and subsect. *Jacea* by the pinnatisect basal and mid-cauline leaves, which are entire in all the other subsections. Differs from sects. *Jacea* and *Phrygia* by the small and triangular bract appendages not covering the bracts. Type and only species: *Centaurea subtilis* Bertol., Flora Italica 9: 451. 1854.

Table 2. List of species of the redefined sect. *Centaurea* (including former sections *Acrolophus* = *Centaurea*, sect. *Phalolepis* and sect. *Willkommia*, all of them considered subsections). C: *Centaurea*; P: *Phalolepis*; W: *Willkommia*. For each species we indicate sectional adscription, geographical distribution, chromosome number, ITS sequences yes/no (from Garcia-Jacas *et al.*, 2000, 2001, 2006; Hilpold *et al.*, 2011; and Suárez-Santiago *et al.*, 2007a), further taxonomic literature, and number of subspecies.

Species	Subject.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. acarnanica</i> (Matthäus) Greuter	P	Greece	36 (Matthäus, 1976 as <i>C. subciliaris</i> Boiss. & Heldr. subsp. <i>acarnanica</i> Matthäus)	+		
<i>C. aenulans</i> Klokov (<i>C. diffusa</i> s. l.)	C	N Black Sea	–	–		
<i>C. aeolica</i> Lojac.	C	Italy	18 (Viegi <i>et al.</i> , 1972; Cela Renzoni & Viegi, 1982)	+	Anzalone, 1995; Hilpold <i>et al.</i> , 2011	2
<i>C. aetaliae</i> (Sommier) Bég.	C	Italy	18 (Viegi & Cela Renzoni, 1976)	+		
<i>C. affinis</i> Friv.	C	Balkans	18, 36 (Georgiadis, 1983)	+		6
<i>C. aggregata</i> DC.	C	Anatolia, Caucasus	18 (Bakshi Khaniki, 1996)	+		2
<i>C. alba</i> L.	P	Iberian Peninsula	18 (López & Devesa, 2008d, 2011)	+	López & Devesa, 2011	3
<i>C. albanica</i> Halácsy	P	Balkans	–	–	Phitos & Damboldt, 1971	
<i>C. amaena</i> Boiss. & Balansa	P	Anatolia	18 (Uysal <i>et al.</i> , 2009)	+	Atasagun <i>et al.</i> , 2013	
<i>C. ambigua</i> Guss.	C	Italy	–	+	Guarino & Rampone, 2006; Hilpold <i>et al.</i> , 2011	
<i>C. antalyensis</i> H. Duman & A. Duran	P	Anatolia	18 (Köse, 2006)	+	Duran & Duman, 2002	
<i>C. anthemifolia</i> Hub.-Mor.	C	Anatolia	–	+		
<i>C. aphrodisea</i> Boiss.	P	Anatolia	36 (Uysal <i>et al.</i> , 2009)	+		
<i>C. aplolepa</i> Moretti	C	Italy	18 (Viegi & Cela Renzoni, 1976; Arrigoni <i>et al.</i> , 1980)	+	Arrigoni, 2003; Hilpold <i>et al.</i> , 2011	10
<i>C. appendicata</i> Klokov (<i>C. margaritacea</i> aggr.)	P	N Black Sea	–	–		
<i>C. arenaria</i> Willd.	C	NE Balkans, N and E Black Sea	32, 36 (Bancheva & Greilhuber, 2006; Kuzmanov <i>et al.</i> , 1979)	+		
<i>C. argentea</i> L.	C	Greece	18 (Georgiadis, 1983; Montmollin, 1986)	+	Runemark, 1967; Turland & Chilton, 2000	
<i>C. aristata</i> Hoffmanns. & Link	C	Iberian Peninsula	36 (López & Devesa, 2008d)	+	López & Devesa, 2008a	
<i>C. arrigonii</i> Greuter	C	Italy	18 (Signorini <i>et al.</i> , 2001 as <i>C. dissecta</i> Ten. var. <i>intermedia</i> Fiori)	+		
<i>C. aspromontana</i> Brullo <i>et al.</i> (<i>C. deusta</i> s. l.)	P	Italy	–	+	Brullo <i>et al.</i> , 2001	
<i>C. attica</i> Nyman	C	Greece, W Balkans	18 (Georgiadis & Phitos, 1976; Georgiadis, 1983); 36 (Georgiadis & Phitos, 1976)	–		3
<i>C. austroanatolica</i> Hub.-Mor.	C	Anatolia	–	+		
<i>C. avilae</i> Pau	W	Iberian Peninsula	18 (Blanca, 1980a)	+		
<i>C. aziziana</i> Rech. f. (<i>C. ovina</i> aggr.)	P	Anatolia, Caucasus, Iran	18 (García-Jacas <i>et al.</i> , 1998)	+	Armağan. & Ünal, 2009	

Table 2. (Cont.)

Species	Subsect.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. baseri</i> Köse & Alan	P	Anatolia	–	–	Köse & Alan, 2013	
<i>C. besseriana</i> DC. (<i>C. ovina</i> aggr.)	C	NE Balkans, N Black Sea	18 (Bancheva & Greilhuber, 2006, as <i>C. ovina</i> Pall. ex Willd. subsp. <i>besseriana</i> (DC.) Dostál	–		
<i>C. bethurica</i> E. López & Devesa	C	Iberian Peninsula	18 (López & Devesa, 2008d)	+	López & Devesa, 2008c	
<i>C. biokovensys</i> Teyber (<i>C. cuspidata</i> aggr.)	C	W Balkans	36 (Lovrić, 1982a)	–		
<i>C. boissieri</i> DC.	W	Iberian Peninsula, NW-Africa	18 (Blanca, 1980a, 1981b)	+	Blanca & Suárez-Santiago, 2011	7 lb, 1 NA
<i>C. bombycina</i> DC.	W	Iberian Peninsula	18 + 2B (Blanca, 1981b)	+		2
<i>C. borysthematica</i> Gruner (<i>C. arenaria</i> aggr.)	C	N Balkans, N Black Sea	–	–		
<i>C. bovina</i> Velen.	C	Greece, NE Balkans	18 (Georgiadis, 1983)	–		
<i>C. breviceps</i> Iljin (<i>C. margaritacea</i> aggr.)	P	N Black Sea	–	+		
<i>C. brulla</i> Greuter (<i>C. deusta</i> s. l.)	P	Italy	–	+	Brullo, 1988	
<i>C. brunnea</i> (Halácsy) Halácsy	P	Greece, W Balkans	18 (Georgiadis & Phitos, 1977)	+		
<i>C. busambarensis</i> Guss.	C	Italy	18 (Viegi <i>et al.</i> , 1972; Cela-Renzoni & Viegi, 1982)	+	Hiipold <i>et al.</i> , 2011	
<i>C. cadmea</i> Boiss.	P	Anatolia	18 (Uysal <i>et al.</i> , 2009)	+		2
<i>C. calabra</i> G. Caruso, S.A. Giardina, Raimondo & Spadaro	P	Italy	–	–	Caruso <i>et al.</i> , 2013	
<i>C. calliactae</i> Prodan	P	NE Balkans	18 (Ciocârlan, 2000, secondary citation!)	–		
<i>C. calolepis</i> Boiss.	C	Anatolia	18 (Romaschenko <i>et al.</i> , 2004)	+	Wagenitz, 1972	
<i>C. caprina</i> Steven (<i>C. ovina</i> aggr.)	C	N Black Sea	–	–		
<i>C. cariensiformis</i> Hub.-Mor.	C	Anatolia	–	+	Davis <i>et al.</i> , 1988	
<i>C. cariensis</i> Boiss.	C	Anatolia	18 (Martin <i>et al.</i> , 2009); 36 (Georgiadis & Christodoulakis, 1984; Martin <i>et al.</i> , 2009)	+	Wagenitz, 1972	5
<i>C. carratracensis</i> Lange	W	Iberian Peninsula	18+ 0–1B (Blanca, 1980a)	+		
<i>C. carystea</i> Trigas & Constantin.	C	Greece	54 (Trigas <i>et al.</i> , 2008)	–		
<i>C. caspia</i> Grossh.	C	Caucasus	–	–		
<i>C. castellanoides</i> Talavera	C	Iberian Peninsula	18 (López & Devesa, 2008d)	+	López & Devesa, 2008a	3
<i>C. chalcidicaea</i> Hayek	C	Greece	18 (Damboldt & Melzheimer, 1974; Georgiadis, 1983)	–		
<i>C. chrysocephala</i> Phitos & T. Georgiadis	P	Greece	18 (Georgiadis & Phitos, 1977)	+		
<i>C. cineraria</i> L.	C	Italy	18, 36 (Cela-Renzoni & Viegi, 1982; Damboldt & Matthäs, 1975)	+	Hiipold <i>et al.</i> , 2011	2
<i>C. cithaeronea</i> Phitos & Constantin.	P	Greece	54 (Phitos & Constantinidis, 1993)	+	Phitos & Constantinidis, 1993	

Table 2. (Cont.)

Species	Subject.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. citricolor</i> Font Quer	W	Iberian Peninsula	36 + 1B (Blanca, 1980a)	+		
<i>C. codruensis</i> Prodan (<i>C. kanitziana</i> s. l.)	C	NE Balkans	–	–		
<i>C. consanguinea</i> DC.	C	Anatolia	–	+		
<i>C. cordubensis</i> Font Quer	C	Iberian Peninsula	36 (López & Devesa, 2008d)	+	López & Devesa, 2008c	
<i>C. corensis</i> Vals. & Filigh.	P	Italy	36 (Hilpold <i>et al.</i> , in press)	+	Valsecchi & Filigheddu, 1991	
<i>C. corymbosa</i> Pourr.	C	France	–	+		
<i>C. costae</i> Willk. (<i>C. alba</i> p. p.)	P	Iberian Peninsula	18 (López & Devesa, 2008d)	+	López & Devesa, 2011	
<i>C. coziensis</i> Nyár. (<i>C. stoebe</i> s. l.)	C	NE Balkans	–	–		
<i>C. cristata</i> Bartl. (<i>C. spinosociliata</i> aggr.)	C	Italy, W Balkans	36 (Lausi, 1966; Ochsmann, 1999; A. Hilpold unpubl. res.)	+		
<i>C. crithmifolia</i> Vis.	C	W Balkans	36 (Sijjak–Yakovlev, 1980)	+		
<i>C. cuneifolia</i> Sm.	C	Balkans, Anatolia	18 (Kuzmanov <i>et al.</i> , 1979), 36 (Georgiadis & Phitos, 1976; Georgiadis, 1983)	+		2
<i>C. cuspidata</i> Vis. (<i>C. cuspidata</i> aggr.)	C	W Balkans	18 (Lovrić, 1982a)	–		
<i>C. cylindrocephala</i> Bormm. (<i>C. stoebe</i> s. l.)	C	Greece, W Balkans	36 (Georgiadis, 1983 as <i>C. biebersteinii</i> DC. subsp. <i>cylindrocephala</i> (Borrm.) Dostál)	–		
<i>C. cyprensis</i> (Holub) T. Georgiadis	C	Cyprus	–	+	Meikle, 1985 as <i>C. veneris</i> (Sommier) Bég.	
<i>C. cyrenaica</i> Bég. & A. Vacc.	P	Libya	18 (Brullo & Pavone, 1977)	–	Alavi, 1983	
<i>C. damascena</i> Boiss.	C	Near-East	–	–		
<i>C. debdauensis</i> Breitw. & Podlech	W	NW Africa	–	+		
<i>C. delicatula</i> Breitw. & Podlech	W	NW Africa	–	+	Hilpold <i>et al.</i> , 2011	
<i>C. delucae</i> C. Guarino & Rampone	C	Italy	18 (Baltisberger, 1990 as <i>C. ambigua</i> Guss. subsp. <i>nigra</i> (Fiori) Pignatti & Lausi)	+	Guarino & Rampone, 2006	
<i>C. demetrii</i> Dumbadze (<i>C. ovina</i> aggr.)	C	N Black Sea	–	–		
<i>C. derventana</i> Vis. & Pančić (<i>C. cuspidata</i> aggr.)	C	W Balkans	18 (Strid & Franzen, 1981 as <i>C. incompta</i> Vis. subsp. <i>derventana</i> (Vis. & Pančić) Dostál)	–		
<i>C. deusta</i> Ten.	P	Italy	18 + 0–1B (Matthás, 1976; Brullo <i>et al.</i> , 1991)	+	Hilpold <i>et al.</i> , 2011	
<i>C. deustiformis</i> Adamović	P	Greece, W Balkans	16 (Strid, 1983)	+	Phitos & Damboldt, 1971	
<i>C. dichroa</i> Boiss. & Heldr.	C	Anatolia	–	+		
<i>C. diffusa</i> Lam.	C	NE Mediterranean and Black Sea, introduced to C and W Europe, N and S America, Australia	18 (Georgiadis & Phitos, 1976; Taylor & Taylor, 1977); 16 (Bancheva & Greilhuber, 2006)	+	López & Devesa, 2010	

Table 2. (Cont.)

Species	Subsect.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. diomedea</i> Gasp.	P	Italy	18 (D'Amato & Pavese, 1990; A. Hilpold unpubl. res.)	+	Hilpold <i>et al.</i> , 2011	
<i>C. djebel-amouri</i> Greuter	P	NW Africa	–	–	Quézel & Santa, 1963 as <i>C. alba</i> L. var. <i>mauritanica</i> Batt.	
<i>C. donetzica</i> Klokov (<i>C. margaritacea</i> aggr.)	P	N Black Sea	36, 18 (Romaschenko <i>et al.</i> , 2004; Mráz <i>et al.</i> , 2012)	+		
<i>C. dubjanskii</i> Iljin (<i>C. margaritacea</i> aggr.)	P	N Black Sea	–	–		
<i>C. dumulosa</i> Boiss.	C	E Mediterranean (Middle East)	–	–		
<i>C. dursunbeyensis</i> Uysal & Köse	P	Anatolia	36 (Uysal & Köse, 2009)	–		
<i>C. edith-mariae</i> Radić (<i>C. cuspidata</i> aggr.)	C	W Balkans	36 (Papes & Radić, 1982)	–		
<i>C. epapposa</i> Velen.	P	N Balkans	–	–		
<i>C. ertugruliana</i> Uysal	C	Anatolia	18 (Uysal, 2008)	+		
<i>C. erycina</i> Raimondo & Banchева	C	Italy	18 (Raimondo & Banchева, 2004)	+	Hilpold <i>et al.</i> , 2011	
<i>C. euxina</i> Velen.	P	NE Balkans	–	–		
<i>C. filiformis</i> Viv.	C	Italy	18 (both subsp.; Arrigoni & Mori, 1971)	+	Arrigoni, 1972	2
<i>C. formanekii</i> Halácsy	P	W Balkans	–	–		
<i>C. foveolata</i> Blakelock	P	Iraq	–	–	Wagenitz, 1980	
<i>C. friderici</i> Vis.	C	W Balkans	36 (Sijjak-Yakovlev, 1980)	+		2
<i>C. fusiformis</i> Blakelock	C	Iraq	–	–	Wagenitz, 1980	
<i>C. gadorensis</i> Blanca	W	Iberian Peninsula	18 (Blanca, 1981b as <i>C. sagredo</i> Blanca subsp. <i>tenuiloba</i> (Boiss.) Blanca	+		
<i>C. galicicae</i> Micevski	C	W Balkans	–	–	Micevski, 1985	
<i>C. gerberi</i> Steven (<i>C. margaritacea</i> aggr.)	P	N Black Sea	–	–		
<i>C. giardiniae</i> Raimondo & Spadaro	C	Italy	18 (Raimondo & Spadaro, 2006)	+	Bancheva <i>et al.</i> , 2011	
<i>C. glaberrima</i> Tausch	C	W Balkans	36 (Sijjak-Yakovlev, 1980; Sijjak-Yakovlev <i>et al.</i> , 2005)	+		2
<i>C. gloriosa</i> Radić (<i>C. cuspidata</i> aggr.)	C	W Balkans	18 (Papes & Radić, 1982; Sijjak-Yakovlev <i>et al.</i> , 2005)	–		
<i>C. gracilentia</i> Velen.	C	NE Balkans	–	–		
<i>C. greuteri</i> E. Gamal-Eldin & Wagenitz	P	Greece	–	–	Gamal-Eldin & Wagenitz, 1983	
<i>C. grisebachii</i> (Nyman) Heldr.	C	Greece, W Balkans	36 (Strid & Franzen, 1981; Georgiadis, 1983)	+		4
<i>C. gullissashvili</i> Dumbadze (<i>C. ovina</i> aggr.)	C	Anatolia, Caucasus	18 (Tonian, 1980)	–		

Table 2. (Cont.)

Species	Subsect.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. gymnocarpa</i> Moris & De Not.	C	Italy	18 (Viegi <i>et al.</i> , 1972)	+	Cela-Renzoni & Viegi, 1982; Hilpold <i>et al.</i> , 2011; Catoni & Gratani, 2013	
<i>C. hanrrii</i> Jord.	C	NW-Mediterranean (Spain, France)	18 (López & Devesa, 2008d)	+	López & Devesa, 2010	
<i>C. heldreichii</i> Halácsy	P	Greece	18 (Phitos & Damboldt, 1971)	+	Kalpoutzakis & Constantimidis, 2004	
<i>C. hohenackeri</i> Steven (<i>C. ovina</i> aggr.)	C	Caucasus	–	–		
<i>C. horrida</i> Badarò	C	Italy	18 (Desole, 1954)	+		
<i>C. huljakii</i> J. Wagner	P	Greece	18, 36 (Damboldt & Melzheimer, 1974; Matthäs, 1976)	–		
<i>C. ilvensis</i> (Sommier) Arrigoni (<i>C. aetaliae</i> s. l.)	C	Italy	18 (Viegi & Cela Renzoni, 1976)	+		
<i>C. incompleta</i> Halácsy	C	Greece	18 (Strid & Franzen, 1981)	+		
<i>C. incompta</i> Vis. (<i>C. cuspidata</i> aggr.)	C	W Balkans	36 (Lovrić, 1982b)	–		
<i>C. inermis</i> Velen.	C	Anatolia, NE Balkans	–	+		
<i>C. intricata</i> Boiss.	C	Iran, Iraq	18 (Bakhshi Khaniki, 1996)	–	Wagenitz, 1980	2
<i>C. ionica</i> Brullo (<i>C. deusta</i> s. l.)	P	Italy	–	+	Brullo <i>et al.</i> , 2001	
<i>C. ipeccensis</i> Rech. f.	P	W Balkans	–	–		
<i>C. jaennensis</i> Degen & Debeaux	W	Iberian Peninsula	18 (Blanca, 1980a)	+		
<i>C. jankana</i> Simonk. (<i>C. arenaria</i> aggr.)	C	N Balkans	–	–		
<i>C. japygica</i> (Lacaíta) Brullo	P	Italy	18 (Tomadore <i>et al.</i> , 2000)	+	Francini, 1951; Tornadore <i>et al.</i> , 2000	
<i>C. johnseniana</i> Strid & Kit Tan	C	Greece	–	–	Strid & Tan, 2003	
<i>C. jurineifolia</i> Boiss.	C	NE Balkans	–	–		
<i>C. kalambakensis</i> Freyn & Sint.	C	Greece	18 (Georgiadis & Phitos, 1976)	–		
<i>C. kanitziana</i> D. Brândză	C	NE Balkans	–	–		
<i>C. kartischiana</i> Scop.	C	Italy, W Balkan	18 (Lausi, 1966; Sijjak-Yakovlev, 1982)	–	Lovrić, 1971; Marcucci <i>et al.</i> , 1999	6
<i>C. kilaea</i> Boiss.	C	Anatolia, NE Balkans	36 (Meriç <i>et al.</i> , 2010)	+	Aidin <i>et al.</i> , 2013	
<i>C. konkae</i> Klokov (<i>C. margaritacea</i> aggr.)	P	N Black Sea	–	–		
<i>C. kabanica</i> Klokov (<i>C. stoebe</i> s. l.)	C	N Black Sea	–	–		
<i>C. kasanii</i> Radić (<i>C. cuspidata</i> aggr.)	C	W Balkans	36 + 1–5B (Papes & Radić, 1982; Sijjak-Yakovlev <i>et al.</i> , 2005)	–		

Table 2. (Cont.)

Species	Subject.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. lacerrata</i> (Hausskn.) Halácsy	C	Greece	36 (Georgiadis, 1983)	-		
<i>C. lactiflora</i> Halácsy	C	Greece	18 (Georgiadis & Phitos, 1976)	-		
<i>C. langei</i> Nyman	C	Iberian Peninsula	18 (López & Devesa, 2008d; López <i>et al.</i> , 2011)	+		6
<i>C. laureotica</i> Halácsy	C	Greece	36 (Georgiadis & Phitos, 1976; Georgiadis, 1981a)	-		
<i>C. lavrenkoana</i> Klokov (<i>C. ovina</i> aggr.)	C	N Black Sea	-	-		
<i>C. leonidia</i> Kalpoutz. & Constantin.	P	Greece	18 (Kalpoutzakis & Constantinidis, 2004)	+		
<i>C. leucadea</i> Lacaita	C	Italy	18 (Tornadore <i>et al.</i> , 2000)	+	Francini, 1951; Tornadore <i>et al.</i> , 2000; Hilpold <i>et al.</i> , 2011	
<i>C. leucomalla</i> Borrm.	P	W Balkans	-	-		
<i>C. leucomelaena</i> Hayek	C	W Balkans	-	-		
<i>C. leucophaea</i> Jord.	C	NW Mediterranean (Spain, France, Italy)	18 (Ochsmann, 1999; López & Devesa, 2008d)	+	Arrigoni, 2003; López & Devesa, 2010; Hilpold <i>et al.</i> , 2011	6
<i>C. limbata</i> Hoffmanns. & Link	C	Iberian Peninsula	18 (López & Devesa, 2008d)	+	López & Devesa, 2008b	2
<i>C. litigiosa</i> (Fiori) Arrigoni (<i>C. aetaliae</i> s. l.)	C	Italy	-	+		
<i>C. litchorea</i> T. Georgiadis & Phitos	P	Greece	16 (Strid & Franzen, 1981)	+	Georgiadis & Phitos, 1978	
<i>C. luschaniana</i> Heimertl ex Stapf	P	Anatolia	18 (Uysal <i>et al.</i> , 2009)	+		
<i>C. lycanica</i> Boiss. & Heldr.	P	Anatolia	18 (Uysal <i>et al.</i> , 2009; Martun <i>et al.</i> , 2009)	+	Uysal <i>et al.</i> , 2010	
<i>C. lycia</i> Boiss.	P	Anatolia	18 (Uysal <i>et al.</i> , 2009)	+		
<i>C. magistrorum</i> Arrigoni & Camarda	C	Italy	-	+	Arrigoni & Camarda, 2003	
<i>C. majorovii</i> Dumbadze (<i>C. arenaria</i> aggr.)	C	N Black Sea	-	-		
<i>C. margaritacea</i> Ten. (<i>C. margaritacea</i> aggr.)	P	N Black Sea	-	+		
<i>C. margaritalba</i> Klokov (<i>C. margaritacea</i> aggr.)	P	N Black Sea	-	+		
<i>C. marmorea</i> Borrm. & Soška	P	W Balkans	-	-		
<i>C. mayeri</i> Radić (<i>C. cuspidata</i> aggr.)	C	W Balkans	36 (Papes & Radić, 1982; Siljak-Yakovlev <i>et al.</i> , 2005)	-		
<i>C. messenicolastana</i> T. Georgiadis <i>et al.</i>	P	Greece	18 (Georgiadis <i>et al.</i> , 1996)	+	Georgiadis <i>et al.</i> , 1996	
<i>C. monticola</i> DC.	W	Iberian Peninsula, NW Africa	18, 18+1B, 19, 20 (Blanca, 1980a, 1983)	+		
<i>C. micurensis</i> Teyber (<i>C. cuspidata</i> aggr.)	C	W Balkans	36 (Lovrić, 1982a as <i>C. biokovensis</i> Teyber subsp. <i>micurensis</i> (Teyber) Hayek)	-		

Table 2. (Cont.)

Species	Subsect.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. musakii</i> T. Georgiadis	C	Greece	18 (Georgiadis, 1979)	+	Georgiadis, 1979	
<i>C. musarum</i> Boiss. & Orph.	P	Greece	18 (Constantinidis & Vassiliades, 1996)	+	Constantinidis & Vassiliades, 1996	
<i>C. niederi</i> Heldr.	C	Greece	18 (Georgiadis & Phitos, 1976)	+	Kalpoutzakis & Constantinidis, 2004	
<i>C. nobilis</i> (H. Groves) Brullo	P	Italy	18 (Brullo <i>et al.</i> , 1991; Tornadore <i>et al.</i> , 2000)	+	Tornadore <i>et al.</i> , 2000	
<i>C. nydeggeri</i> Hub.-Mor.	C	Anatolia	-	-	Davis <i>et al.</i> , 1988	
<i>C. odessana</i> Prodan (<i>C. arenaria</i> aggr.)	C	N Black Sea	-	-		
<i>C. olivieri</i> Pomel (<i>C. resupinata</i> s. l.)	W	NW Africa	-	-		
<i>C. obympica</i> (DC.) K. Koch (<i>C. cuneifolia</i> s. l.)	C	Anatolia	-	+	Wagenitz, 1972	
<i>C. orphanidea</i> Boiss.	C	Greece	18 (Georgiadis & Phitos, 1976)	-		
<i>C. ossaea</i> Halácsy	C	Greece	18 (Georgiadis, 1983)	-		
<i>C. ovina</i> Willd. (<i>C. ovina</i> aggr.)	C	Caucasus	18 (Bakhshi Khaniki, 1996; Tonian, 1980)	-		
<i>C. paczoskii</i> Klokov (<i>C. margaritacea</i> aggr.)	P	N Black Sea	-	+		
<i>C. paniculata</i> L.	C	NW Mediterranean (Spain, France, Italy)	18 (López & Devesa, 2008d)	+	Arrigoni, 2003; López & Devesa, 2010	5
<i>C. panormitana</i> Lojac.	C	Italy	18 (Viegi <i>et al.</i> , 1972; Cela Renzoni & Viegi, 1982)	+	Hilpold <i>et al.</i> , 2011	
<i>C. papposa</i> (Coss.) Greuter	C	NW Africa	-	+	Quézel & Santa, 1963; Pottier-Alapétite, 1981 as <i>C. cineraria</i> L.; Hilpold <i>et al.</i> , 2011	
<i>C. parlatoris</i> Heldr.	C	Italy	18 (Colombo & Trapani, 1990)	+	Guarino & Rampone, 2006; Bancheva <i>et al.</i> , 2011; Hilpold <i>et al.</i> , 2011	
<i>C. pau</i> Willk.	W	Iberian Peninsula	18 (Blanca, 1980a)	+		
<i>C. pauneroi</i> Talavera & J. M. Muñoz	W	Iberian Peninsula	-	+	Talavera & Muñoz, 1984	
<i>C. pawlowskii</i> Phitos & Damboldt	P	Greece, W Balkans	18 + 1B, 36 + 1B (Damboldt & Matthás, 1975; Ochsmann, 2000)	+	Damboldt & Matthás, 1979; Phitos & Damboldt, 1976	
<i>C. paxorum</i> Phitos & T. Georgiadis	P	Greece	18 (Georgiadis & Phitos, 1977)	-	Georgiadis & Phitos, 1977	
<i>C. pelia</i> DC.	C	Greece	18 (Georgiadis & Phitos, 1976; Georgiadis, 1983)	+		
<i>C. pentadactyli</i> Brullo <i>et al.</i> (<i>C. deusta</i> s. l.)	P	Italy	-	+	Brullo <i>et al.</i> , 2001	

Table 2. (Cont.)

Species	Subject.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. pestalotii</i> Ces.	P	Italy, W Balkans	18, 36 (Ochsmann, 1999; Lovrić, 1982a as <i>C. brachitii</i> Rechb. f.)	+		
<i>C. peucedanifolia</i> Boiss. & Orph.	C	Greece	18 (Georgiadis & Phitos, 1976)	-		
<i>C. pineticola</i> Iljin (<i>C. margaritacea</i> aggr.)	P	N Black Sea	-	-		
<i>C. pinetorum</i> Hub.-Mor.	C	Anatolia	-	+	Uysal <i>et al.</i> , 2010	
<i>C. pinnata</i> Vicioso	W	Iberian Peninsula	18 (Blanca, 1980a)	+		
<i>C. puculatoris</i> Greuter	C	Greece	18 (Montmollin, 1986; Routsis & Georgiadis, 1988)	+	Greuter, 1967	
<i>C. poeltiana</i> Puntillo (<i>C. deusta</i> s. l.)	P	Italy	-	+	Puntillo, 1996	
<i>C. polyclada</i> DC	C	Aegean Sea	18 (García-Jacas <i>et al.</i> , 1997; Martin <i>et al.</i> , 2009)	+	Uysal <i>et al.</i> , 2010	
<i>C. pomeliana</i> Batt.	W	NW Africa	-	+		2
<i>C. prespana</i> Rech. f.	C	Greece	-	-	Rechinger, 1974; Tan <i>et al.</i> , 2007	
<i>C. princeps</i> Boiss. & Heldr.	P	Greece	18 (Georgiadis & Phitos, 1977)	+		
<i>C. protogerberi</i> Klokov (<i>C. margaritacea</i> aggr.)	P	N Black Sea	18 (Romaschenko <i>et al.</i> , 2004)	+		
<i>C. protomargaritacea</i> Klokov (<i>C. margaritacea</i> aggr.)	P	N Black Sea	-	+		
<i>C. pseudobovina</i> Hayek (<i>C. jurineifolia</i> s. l.)	C	NE Balkans	-	-		
<i>C. pseudocadmea</i> Wagenitz	P	Greece	-	+	Wagenitz, 1971	
<i>C. pseudoleucolepis</i> Kleopow (<i>C. margaritacea</i> aggr.)	P	N Black Sea	18 (Romaschenko <i>et al.</i> , 2004)	+		
<i>C. pseudomaculosa</i> Dobrocz. (<i>C. stoebe</i> s. l.)	C	N Black Sea	18 (Probatova <i>et al.</i> , 1996)	+		
<i>C. ptarmicoides</i> Halácsy	P	Greece	-	-	Phitos & Damboldt, 1976	
<i>C. pulvinata</i> (Blanca) Blanca	W	Iberian Peninsula	18 (Blanca, 1980a)	+	Blanca, 1980b	
<i>C. radichii</i> Plazibat (<i>C. cuspidata</i> aggr.)	C	W Balkans	27+1B, 36 (Papes & Radić, 1982; Siljak-Yakovlev <i>et al.</i> , 2005 as <i>C. elegantissima</i> Bornm.)	-		
<i>C. reducta</i> Wagenitz	C	Syria	-	-	Wagenitz, 1981	
<i>C. reichenbachii</i> DC.	C	N Balkans	18 (Jasievicz & Mizienty, 1975, as <i>C. calvescens</i> DC.)	-		
<i>C. resupinata</i> Coss.	W	Iberian Peninsula, NW-Africa	18 (Blanca, 1981b as <i>C. dufourii</i> (Dostál) Blanca)	+	Blanca & Suárez-Santiago, 2011	2
<i>C. rouyi</i> Coincy	W	Iberian Peninsula	18 (Blanca, 1981b)	+	Blanca, 1981a; Figuerola <i>et al.</i> , 1991	
<i>C. rufidula</i> Bornm.	C	W Balkans	-	-		

Table 2. (Cont.)

Species	Subject.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. rutifolia</i> Sm.	C	S and NE Balkans	18+0-1B (Damboldt & Melzheimer, 1974; Georgiadis, 1983; Kuzmanov <i>et al.</i> , 1983)	-		
<i>C. saccensis</i> Raimondo <i>et al.</i>	C	Italy	18 (Bancheva <i>et al.</i> , 2006, secondary citation!)	+	Raimondo <i>et al.</i> , 2004	
<i>C. sagredo</i> Blanca	W	Iberian Peninsula	18 (Blanca, 1980a)	+	Blanca, 1980b	
<i>C. sakarensis</i> Bancheva & Raimondo	C	E Balkans	-	-	Bancheva & Raimondo, 2013	
<i>C. sarandinakiae</i> N. B. Illar. (<i>C. sterilis</i> aggr.)	P	N Black Sea	36 (Romaschenko <i>et al.</i> , 2004)	+		
<i>C. sarfattiana</i> Brullo <i>et al.</i> (<i>C. deusta</i> s. l.)	P	Italy	-	-	Brullo <i>et al.</i> , 2004	
<i>C. savranica</i> Klokov (<i>C. stoebe</i> s. l.)	C	N Black Sea	-	-		
<i>C. scannensis</i> Anzal. <i>et al.</i>	C	Italy	18 (Anzalone, 1961)	+	Hilpold <i>et al.</i> , 2011	
<i>C. schousboei</i> Lange	C/P	Iberian Peninsula	36 (López & Devesa, 2008d)	+	López & Devesa, 2008c	
<i>C. scillae</i> Brullo (<i>C. deusta</i> s. l.)	P	Italy	-	+	Brullo <i>et al.</i> , 2001; Hilpold <i>et al.</i> , 2011	
<i>C. segariensis</i> Figuerola <i>et al.</i>	W	Iberian Peninsula	18 (Boscaiu <i>et al.</i> , 1997)	+ ¹		
<i>C. semijusta</i> Juz. (<i>C. sterilis</i> aggr.)	P	N Black Sea	36 (Romaschenko <i>et al.</i> , 2004)	+		
<i>C. serpentinica</i> A. Duran & B. Doğan	C	Anatolia	-	-	Doğan & Duran, 2009	
<i>C. sicana</i> Raimondo & Spadaro	C	Italy	18 (Raimondo & Spadaro, 2008)	-	Raimondo & Spadaro, 2008; Bancheva <i>et al.</i> , 2011	
<i>C. sipylea</i> Wagenitz	C	Anatolia	-	+		
<i>C. sivasica</i> Wagenitz	C	Anatolia	18 (Bal <i>et al.</i> , 1999)	+	Wagenitz, 1974	
<i>C. sophiae</i> Klokov (<i>C. arenaria</i> aggr.)	C	N Black Sea	-	-		
<i>C. soskae</i> Košanin	C	W Balkans	-	-		
<i>C. spinosa</i> L.	C	Aegean Sea	36 (Runemark, 1967; Georgiadis & Phitos, 1976)	+	Runemark, 1967	
<i>C. spinosociliata</i> Seenus	C	W Balkans	36 (Lovrić, 1982a)	+		
<i>C. sterilis</i> Steven (<i>C. sterilis</i> aggr.)	P	N Black Sea	18 (Romaschenko <i>et al.</i> , 2004)	+		
<i>C. steveniana</i> Klokov (<i>C. ovina</i> aggr.)	C	N Black Sea	-	-		
<i>C. stoebe</i> L.	C	Europe, except Ib. Pen., introduced to N and S America	18, 36 (Lovrić, 1982b as <i>C. rhenana</i> Bor.; Španiel <i>et al.</i> , 2008)	+	Manifold, partly published as <i>C. maculosa</i>	2
<i>C. subciliaris</i> Boiss. & Heldr.	P	Greece, NE Balkans	18+2B, 36+4B (Phitos & Damboldt, 1971; Matthäs, 1976)	+		
<i>C. subsericans</i> Halácsy	C	Greece	18 (Constantinidis <i>et al.</i> , 1997)	-		

Table 2. (Cont.)

Species	Subject.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. tauscheri</i> A. Kern. (<i>C. arenaria</i> aggr.)	C	N Balkans	18 [Sz.-Borsos, 1971 as <i>C. arenaria</i> M. Bieb. ex Willd. subsp. <i>pseudorhenana</i> (Gugler) Soó]	-		
<i>C. tenacissima</i> (H. Groves) Brullo	P	Italy	18 (Brullo <i>et al.</i> , 1991)	+		
<i>C. tenoreana</i> Willk.	P	Italy	-	+		
<i>C. tenorei</i> Lacaita	C	Italy	18, 36 (Peruzzi & Cesca, 2002)	+	Guarino & Rampone, 2006	
<i>C. thasia</i> Hayek	C	Greece	18 (Georgiadis, 1981b as <i>C. ipsaria</i> Stoj. & Kitan.)	-		
<i>C. thessala</i> Hausskn.	C	Greece	36 (Georgiadis & Phitos, 1976; Georgiadis, 1983)	-		2
<i>C. tommasinii</i> A. Kern. (<i>C. spinosociliata</i> aggr.)	C	Italy, NW Balkans	36 (Lovrić, 1982; Marcucci <i>et al.</i> , 1999)	+		
<i>C. tomosii</i> Micevski	C	W Balkans	-	-	Micevski, 1985	
<i>C. tougourensis</i> Boiss. & Reut.	P	NW Africa	18 (Benamara <i>et al.</i> , 2010)	+		
<i>C. transcaucasica</i> Grossh.	P	Caucasus	-	-		3
<i>C. triniifolia</i> Heuff.	C	Balkans	-	+		
<i>C. tu-goluensis</i> Aytacı & H. Duman	C	Anatolia	54 (Martin <i>et al.</i> , 2009)	+	Vural <i>et al.</i> , 2006	
<i>C. tymphaea</i> Hausskn.	C	Balkans	18 (Georgiadis, 1983)	+		2
<i>C. ulrichiorum</i> Wagenitz <i>et al.</i>	C [?]	Anatolia	-	+	Wagenitz <i>et al.</i> , 2006	
<i>C. valesiaca</i> (DC.) Jord.	C	Switzerland, Italy	18 (Ochsmann, 1999)	+	Ochsmann, 2000	
<i>C. vandasii</i> Velen.	P	NE Balkans	-	-		
<i>C. vankovii</i> Klokov (<i>C. sterilis</i> aggr.)	P	N Black Sea	36, 18 (Romaschenko <i>et al.</i> , 2004; Mráz <i>et al.</i> , 2012)	+		
<i>C. varnensis</i> Velen.	C	N Balkans, introduced elsewhere	18 (Ochsmann, 1999 as <i>Centaurea</i> × <i>psammogena</i> Gäyer)	-		
<i>C. vatevii</i> Degen <i>et al.</i> (<i>C. stoebe</i> s. l.)	C	NE Balkans	-	-		
<i>C. veneris</i> (Sommier) Bég.	C	Italy	18 (Viegi <i>et al.</i> , 1972; Cela Renzoni & Viegi, 1982)	+	Cela-Renzoni, 1970; Hilpold <i>et al.</i> , 2011	
<i>C. vermia</i> Rech. f.	C	Greece	-	-		
<i>C. vesceritensis</i> Boiss. (<i>C. resupinata</i> s. l.)	W	NW Africa	-	.		
<i>C. virgata</i> Lam.	C	E Europe and W Asia, alien in WC Europe and N America	36 (Ghaffari & Chariat-Panahi, 1985; Martin <i>et al.</i> , 2009)	+	Wagenitz, 1972	2
<i>C. visianii</i> Radić (<i>C. cuspidata</i> aggr.)	C	W Balkans	18, 36 + 6B (Šiljak-Yakovlev <i>et al.</i> , 2005; Papes & Radić, 1982)	-		
<i>C. wagenitzii</i> Hub.-Mor.	P	Anatolia	18 (Uysal <i>et al.</i> , 2009)	+		
<i>C. wernerii</i> Wagenitz <i>et al.</i>	C	Anatolia	-	+ ³	Wagenitz <i>et al.</i> , 2006	
<i>C. wetsteinii</i> Degen & Dörfli.	C	Greece	-	-		

Table 2. (Cont.)

Species	Subsect.	Distribution	Chromosome number (2n)	ITS	Other Literature	Subsp.
<i>C. wiedemanniana</i> Fisch. & C. A. Mey.	C	Anatolia	18 (Özaydyn, 2007)	+	Sozen & Ozaydin, 2010	
<i>C. wolgensis</i> DC. (<i>C. arenaria</i> aggt.)	C	N Black Sea	–	–		
<i>C. yozgatensis</i> Wagenitz	C	Anatolia	–	+	Wagenitz & Hellwig, 1996b; Uysal <i>et al.</i> , 2010	
<i>C. zeybekii</i> Wagenitz	C	Anatolia	–	+	Wagenitz, 1974	
<i>C. zuccariniana</i> DC.	C	Greece, W Balkans	18 (Georgiadis & Phitos, 1976; Georgiadis, 1983)	+		

¹ In Suárez-Santiago *et al.* (2007a) as *C. rouyi* Coincy var. *suffrutescens* Blanca.

² Unassigned to any section (Wagenitz *et al.*, 2006).

³ Published in Wagenitz *et al.* (2006).

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