

SYSTEMATICS, PHYLOGENY AND BIOGEOGRAPHY
OF *COUSINIA* (ASTERACEAE)

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SUMMARY

The systematics, phylogeny and biogeography of *Cousinia* (Asteraceae, Cardueae), the largest genus of tribe Cardueae with more than 600 species was studied. This dissertation includes three main parts.

In the first part the phylogeny and evolution of the *Arctium-Cousinia* complex, including *Arctium*, *Cousinia* as one of the largest genera of Asteraceae, *Hypacanthium* and *Schmalhausenia*, is investigated. This group of genera has its highest diversity in the Irano-Turanian region and the mountains of Central Asia. ITS and *rpS4-trnT-trnL* sequences for altogether 138 species, including 129 (of ca. 600) species of *Cousinia* were generated. As found in previous analyses, *Cousinia* is not monophyletic. Instead, *Cousinia* subgenera *Cynaroides* and *Hypacanthodes* with together ca. 30 species are more closely related to *Arctium*, *Hypacanthium* and *Schmalhausenia* (Arctioid clade) than to subg. *Cousinia* (Cousinioid clade). The Arctioid and Cousinioid clades are also supported by pollen morphology and chromosome number as reported earlier. In the Arctioid clade, the distribution of morphological characters important for generic delimitation, mainly leaf shape and armature and morphology of involucre bracts, are highly incongruent with phylogenetic relationships as implied by the molecular data. No taxonomic solution for this conflict can be offered, and the characters named are interpreted as homoplasious. Although phylogenetic resolution in the Cousinioid clade is poor, the ITS and *rpS4-trnT-trnL* sequences contain some phylogenetic information. For example, the six annual species of the Cousinioid clade fall into two groups. Poor phylogenetic resolution probably results from lack of characters and the high number of taxa in this species-rich and comparatively young (c. 8.7 mya) lineage. It is hypothesized that speciation in the Cousinioid clade was mainly allopatric.

The second part of the dissertation investigates the role of hybridization in the evolution of *Cousinia* s.s. In order to examine the frequency of interspecific hybridization and try to assess the possible role of hybridization for the evolution and high diversity of *Cousinia* subg. *Cousinia* (*Cousinia* s.s.), a Bayesian analysis based on the nuclear-ribosomal ITS of 216 species of *Cousinia* and related genera was performed. Hypothetical hybrid combinations published in the past were critically examined, and both morphological and molecular evidence for hybridization is presented. Among 28 published putative hybrids and 11 intermediate forms, two intermediate specimens found were identified as hybrids by their morphological intermediacy and additivity of ITS sequences. Neither hybrids between the Cousinioid clade and other main clades of the *Arctium-Cousinia* complex nor between annual and perennial species of *Cousinia* s.s. have been observed. My results clearly showed that hybridization in *Cousinia* is possible and an estimation of 10.7 % of species (out of ca. 600 spp. belong to the *Cousinia* s.s.) appear to be involved in interspecific hybridization. Although hybridization does take place in *Cousinia* s.s. and may contribute to the difficulties encountered in the reconstruction of its phylogenetic history, its role for the evolution and diversity of the group appears to have been minor.

In the third part, a taxonomic revision of *C.* sect. *Cynaroideae* is presented. *Cousinia*. sect. *Cynaroideae*, the largest section of *Cousinia* with 110 published species, is characterized by a chromosome number of $2n = 24$ and by having \pm decurent to spiny-winged leaves and appendaged phyllaries. It is distributed in Iran, Iraq, the Caucasus, Turkey, Turkmenistan, Afghanistan, Pakistan, Lebanon and Anti-Lebanon, with centres of specific diversity mainly in W & NW Iran, N Iraq and SE Turkey. A comprehensive treatment of *C.* sect. *Cynaroideae*, mainly based on the study of ca. 2250 herbarium specimens, resulted in a reduction of species number to 31 species plus eight subspecies. All species are typified. Diagnostic keys, descriptions, illustrations and distribution maps for each species are given.

ZUSAMMENFASSUNG

Die Systematik, Phylogenie und Biogeographie der Gattung *Cousinia* (Asteraceae, Cardueae) als größter Gattung der Tribus Cardueae mit mehr als 600 Arten wurde untersucht. Diese Dissertation umfasst drei Hauptteile:

Im ersten Teil wurde die Phylogenie und Evolution des *Arctium-Cousinia*-Komplexes untersucht. Dieser Gattungskomplex enthält *Arctium*, *Cousinia*, *Hypacanthium* und *Schmalhausenia* und zeigt die höchste Diversität in der Irano-Turanischen Region und in den Gebirgen Zentralasiens. Es wurden ITS und *rpS4-trnT-trnL*-Sequenzen für insgesamt 138 Arten generiert, darunter von 129 (von ca. 600) Arten von *Cousinia*. Wie in früheren Analysen bereits gefunden, ist *Cousinia* nicht monophyletisch. Stattdessen sind *Cousinia* subg. *Cynaroides* und subg. *Hypacanthodes* mit insgesamt ca. 30 Arten enger mit *Arctium*, *Hypacanthium* und *Schmalhausenia* (Arctioid Clade) als mit subg. *Cousinia* (Cousinioid Clade) verwandt. Die Arctioid und Cousinioid clades werden auch durch Pollenmorphologie und Chromosomenzahl unterstützt, wie bereits früher bekannt war. In dem Arctioid Clade entsprechen morphologische Gattungsgrenzen, basierend auf Blattform, Blattbedornung und Morphologie der Involukralblätter, nicht den in der molekularen Analyse gefundenen clades. Es kann keine taxonomische Lösung für diesen Konflikt gefunden werden, und die genannten Merkmale wurden als homoplastisch betrachtet. Obwohl die phylogenetische Auflösung in dem Cousinioid Clade schlecht ist, enthalten die ITS und *rpS4-trnT-trnL*-Sequenzen phylogenetische Information. So gruppierten z.B. die sechs annualen Arten in zwei Gruppen. Schlechte phylogenetische Auflösung resultiert wahrscheinlich aus dem Mangel an Merkmalen und der großen Artenzahl in dieser artenreichen und vergleichsweise jungen (ca. 8,7 mya) Linie. Artbildung in dem Cousinioid Clade scheint hauptsächlich allopatrisch zu sein.

Der zweite Teil der Dissertation untersucht die Rolle der Hybridisierung in der Evolution von *Cousinia* s.s. Die in der Vergangenheit publizierten 28 Hybrid-Kombinationen und 11 Zwischenformen wurden kritisch geprüft, und zwei Hybridindividuen wurden morphologisch und molekular untersucht. Die vermutlichen oder nachgewiesenen Eltern der Hybriden und Zwischenformen wurden auf die aus einer Bayesischen Analyse der ITS-Sequenzen von 216 Arten von *Cousinia* und verwandten Gattungen resultierenden Phylogenie aufgetragen. Weder Hybriden zwischen dem Cousinioid Clade und anderen Haupt-Claden des *Arctium-Cousinia*-Komplexes noch zwischen annualen und perennirenden Arten von *Cousinia* s.s. wurden beobachtet. Die Ergebnisse zeigen eindeutig, dass Hybridisierung in *Cousinia* möglich ist, und dass ca. 10,7% der Arten an interspezifischer Hybridisierung beteiligt sind. Obwohl Hybridisierung in *Cousinia* s.s. stattfindet und zu den Schwierigkeiten bei der Rekonstruktion ihrer phylogenetischen Geschichte beitragen könnte, war ihre Rolle für die Entwicklung und Diversität der Gruppe offenbar gering.

Im dritten Teil wird eine taxonomische Revision der *C.* sect. *Cynaroideae* präsentiert. *Cousinia* sect. *Cynaroideae*, die größte Sektion der Gattung mit 110 veröffentlichten Arten, zeichnet sich durch eine Chromosomenzahl von $2n = 24$ und durch \pm herablaufende Blätter und Hüllblätter mit Anhängseln aus. Sie kommt im Iran, Irak, dem Kaukasus, der Türkei, Turkmenistan, Afghanistan, Pakistan, dem Libanon und Anti-Libanon vor und hat ihre Hauptzentren der Artdiversität im westlichen und nordwestlichen Iran, im Irak und in der südöstlichen Türkei. Die Revision dieser Gruppe, hauptsächlich basierend auf der Untersuchung von ca. 2250 Herbarbögen, führte zu einer Verringerung der Artenzahl auf 31 Arten mit acht Unterarten. Alle Arten werden typifiziert und ausgeschlüsselt, und Beschreibungen, Abbildungen und Verbreitungskarten werden für jede Art angegeben.

CHAPTER 1

GENERAL INTRODUCTION

Cousinia (Asteraceae, Cardueae) is the third largest genus (after *Senecio* and *Vernonia*) in the Asteraceae, the largest in tribe Cardueae (Rechinger 1986, Bremer 1994 and Petit 1997, Susanna & Garcia-Jacas 2007) and among the 50 largest of flowering plants (Frodin, 2004). It contains more than 600 currently accepted species in Southwest and Central Asia and is exceptional in containing so many species in a comparatively small area. According to Rechinger (1986), *Cousinia* probably is unique in the degree of diversification of all its parts, and definitely unique in the restricted distribution area of a high number of species.

1.1 COUSINIA WITHIN ASTERACEAE

Cousinia belongs to the monophyletic tribe Cardueae which usually has been divided into four taxonomic entities, but the rank and delimitation of these units is highly problematic (Garcia-Jacas et al. 2002, Susanna & Garcia-Jacas 2007). Susanna & Garcia-Jacas (2007) divided the Cardueae into five subtribes. Different classifications of the tribe are summarized in table 1.

Table 1. Different subtribal classifications of the Cardueae (partly after Garcia-Jacas et al. 2002).

<i>Cassini</i> (1819), <i>Dittrich</i> (1977)	<i>Bentham</i> (1873), <i>Hoffmann</i> (1894), <i>Bremer</i> (1994)	<i>Wagenitz</i> (1976), <i>Petit</i> (1988, 1997)	<i>Susanna & Garcia-Jacas</i> (2007)
Tribe Echinopeae	Tribe Cardueae	Tribe Echinopeae	Tribe Cardueae
Tribe Carlineae	Subtribe Echinopsidinae	Tribe Cardueae	Subtribe Carlininae
Tribe Cardueae	Subtribe Carlininae	Subtribe Carlininae	Subtribe Cardopatiinae
Subtribe Carduinae	Subtribe Carduinae	Subtribe Carduinae–	Subtribe Echinopsinae
Subtribe Centaureinae	Subtribe Centaureinae	Centaureinae	Subtribe Carduinae
			Subtribe Centaureinae

Tribe Cardueae includes usually perennial, biennial or more rarely annual herbs or shrubs with alternate leaves, multiseriate involucre bracts, variously chaffy or more often setose receptacles and usually tubular and actinomorphic florets with basally caudate anthers. It has tricolporate, oblate, sphaerical or more or less prolate, spiny, verrucate, scabrate or almost smooth pollen grains (Susanna & Garcia-Jacas 2007).

Within subtribe Carduinae, the genus *Cousinia* together with *Arctium*, *Hypacanthium* and *Schmalhausenia* forms a monophyletic group, the “*Arctium-Cousinia*” complex or the

Arctium group (Susanna et al. 2003a, Susanna & Garcia-Jacas 2007). Three characters never found in combination elsewhere in the tribe characterize the complex. First, the receptacle has strongly twisted scales. Second, the achenes are always tigrine with a pattern of wavy fringes, are very often winged and without a nectary. Third, the pappus is formed by free deciduous bristles (Susanna et al. 2003a).

Within the “*Arctium-Cousinia*” complex, the exact limits between genera, and particularly the limits between *Arctium* and *Cousinia* are difficult to distinguish. Species of *Arctium* and *Cousinia* have been moved between genera very often. For example, Boissier (1875) combined *Lappa* (= *Arctium*) *amplissima* Boiss. as *Cousinia amplissima* (Boiss.) Boiss., and Kuntze (1891) proposed the classification of all *Cousinia* spp. in the genus *Arctium*.

According to Susanna et al. (2003a), a precise correlation between molecular phylogeny, karyology and palynology was observed. A molecular phylogeny of the “*Arctium-Cousinia*” complex showed a clear subdivision into two clades (Susanna et al. 2003a). The first clade, the “Arctioid” clade, including *Cousinia* subgenera *Hypacanthodes* and *Cynaroides*, *Arctium*, *Hypacanthium* and *Schmalhausenia* has $2n = 2x = 36$ chromosomes and the “Arctiastrum pollen type”, while the second clade, the “Cousinioid” clade, including only *Cousinia* subg. *Cousinia*, has $2n = 2x = 22, 24$ and 26 chromosomes and the “*Cousinia* pollen type”. According to Schtepa (1966, 1976) and Kuprianova & Tscherneva (1982), the “Arctiastrum pollen type” of *Arctium* and *Cousinia* subgenera *Cynaroides* and *Hypacanthodes* is orbicular and spiny, whereas the “*Cousinia* pollen type” of *Cousinia* subg. *Cousinia* is oblong and smooth. *Schmalhausenia* (Susanna & al., 2003a) as well as *Hypacanthium* (S. López-Vinyallonga, unpubl. data) have the *Arctiastrum* pollen type. According to Ghaffari et al. (2006), chromosome numbers in *Cousinia* s.s. can be interpreted as a complex dysploid series ranging from $x = 13$ to $x = 9$. The base chromosome numbers in *Cousinia* s.s. mostly range from $x = 13$ to $x = 11$, and the two other base numbers, $x = 10$ and $x = 9$, are infrequent (Susanna et al. 2003b, Ghaffari et al. 2006).

There is also a correlation between the phylogeny of the “*Arctium-Cousinia*” complex and floral morphology. The stigma of *C.* subg. *Cousinia* (*Cousinia* s.s.) is very different from that of *Arctium* and the “Arctioid” species of *Cousinia*. *Arctium* and the “Arctioid” species of *Cousinia* have the typical “Cynaroideae” style which is glabrous and cylindrical with a ring of sweeping hairs at the thickened articulation. In contrast, in *C.* subg. *Cousinia* the apical part of the style and the stylar branches are covered with long hairs, and a ring of sweeping hairs at the articulation of the base of the stylar apex is absent (Duistermaat 1996). According to Häffner (2000), a ring of sweeping hairs is also absent in *Schmalhausenia*.

Thus, most recent work has shown that *Arctium* s.l. and *Cousinia* s.s. can be distinguished by molecular, chromosome and pollen characters. This, however, does not accord with morphology, and *Schmalhausenia*, *Hypacanthium* and parts of *Cousinia* subgenera *Cynaroides* and *Hypacanthodes*, part of the Arctioid clade on the basis of the above characters, are morphologically much more similar to *Cousinia* s.s. (Susanna & Garcia-Jacas 2007). In addition, it is entirely unclear whether the subdivision of *Cousinia* s.s. as proposed by Rechinger (1953, 1972) and Tscherneva (1962, 1988) and as discussed in more detail below, reflects the phylogeny of this group or not. In a molecular analysis of the complex by Susanna et al. (2003a), annual species of *Cousinia* had not been included. Accordingly, the relationships of these annual species requires further analysis.

1.2 TAXONOMY OF COUSINIA

The taxonomic history of *Cousinia* goes back to the early 1900th century. *Cousinia* collections made before 1800 are rare, and only few unnamed herbarium specimens today included in *Cousinia* are known (Bunge 1865). This material belongs to: *C. hablizlii* (collected 1774 by Hablizl), *C. libanotica* (collected 1790 by Billardiere), *C. arachmoidea* (collected 1793 by Sievers), *C. olivieri* (collected between 1792-1796 by Olivier) and *C. cynaroides* and *C. wolgensis* (collected between 1796-1800 by Bieberstein). The genus *Cousinia* was first described by Cassini (1827) based on *Carduus orientalis* Adams. The number of known species was smaller than 10 by 1830. After this, many new collections were made and the number of species increased dramatically. De Candolle's Prodrômus (1838) included 34 *Cousinia* spp. divided into three groups based on capitulum morphology. In a first attempt to classify the genus comprehensively, Bunge (1865) classified 126 *Cousinia* spp. into 23 sections, mainly based on habit and capitular morphology including the texture of receptacular bristles, the form of receptacular bracts, corolla colour, colour of the anther tube and presence or absence of hairs on the anther tube. Bunge's (1865) classification of *Cousinia* was the basis for a more natural taxonomy of the genus as proposed by Rechinger (1953, 1972) and Tscherneva (1962, 1988; see below). Based on Bunge's treatment, Boissier's (1875) *Flora Orientalis* (and its supplement, 1888) covered 141 *Cousinia* spp. classified in 14 sections. The second major attempt to classify the genus was published by Winkler (1892). Similar to Bunge (1865), Winkler used capitulum morphology as the most important character for the taxonomy of *Cousinia*. As an extreme, Kuntze (1891) merged *Cousinia* into the related genus *Arctium*. Winkler (1892, 1897) grouped altogether 267 *Cousinia* spp. in three subgenera. These were the two monotypic subgg. *Oligochaete* C. Winkl. (with only *C. massalskyi* C. Winkl.) and *Dichacantha* Lipsky (with only *C. annua* C. Winkl.), and subg. *Eucoousinia* with the remaining 265 spp. grouped in 19 sections. In a series of publications by Bornmüller between 1896 – 1941 (listed by Rechinger 1953), ca. 30 new *Cousinia* spp. were introduced. Later, two taxonomic treatments of *Cousinia*, mainly based on morphological and geographical evidence, were published by Tscherneva (1962) and Rechinger (1953, 1972). In her treatment of *Cousinia* for the Flora of the USSR, covering the states of the former Soviet Union in Central Asia and the Caucasus, Tscherneva (1962) grouped ca. 260 species in ca. 50 sections. Rechinger's *Flora Iranica* (1972), which covers the Iranian Plateau, Turkmenistan, Afghanistan and the mountaineous regions of Pakistan, included more than 350 species grouped in 58 sections.

Tscherneva's (1988) classification of *Cousinia* was based on morphological, anatomical, karyological and palynological evidence. She divided *Cousinia* into three subgenera: 1) subg. *Cousinia*, 2) subg. *Hypacanthodes* and 3) subg. *Cynaroides*.

As first proposed by Duistermaat (1996, 1997), Susanna & Garcia-Jacas (2007) included the species of *Cousinia* subg. *Cynaroides* in an expanded *Arctium* s.l. with 27 species.

1.3 CENTRES OF BIODIVERSITY

Cousinia is unevenly distributed in SW and C Asia. Most of the sections of *Cousinia* recognized today have several correlated morphological characters, similar ecological requirements and well-delimited and compact distribution areas (Rechinger 1986). Some sections are widely distributed, while others are endemic to relatively small regions. *Cousinia* sect. *Cynaroideae* with 110 published species is mainly western (centred in SE Turkey, N Iraq and NW and W Iran) in its distribution and most of its species are narrow endemics. Section *Alpinae* with more than 40 species is mainly eastern in distribution and most of its species are limited to the "thorn-cushion belt" where precipitation is chiefly in the form of snow (Rechinger 1986). The monotypic sect. *Winklerianae* is endemic to western Afghanistan (Rechinger 1972). According to Rechinger (1986) and Knapp (1987), eight major centres of species diversity were defined. These are:

- 1) SE Anatolian and N Zagros Mts. in SE Turkey and NW Iran, with ca. 40 spp. mainly concentrated in Iranian Azerbaijan.
- 2) Zagros mountains in Iran (mainly provinces Hamadan, Markazi and Luristan) with more than 40 spp.
- 3) Elburz mountains in Iran with ca. 70 spp.
- 4) Kopet Dag mountain range, with ca. 60 spp. in the Iranian and more than 30 spp. in the Turkmenian part.
- 5) West Hindu Kush (C & W Afghanistan), including provinces Ghorat, Ghazni and Gardez with more than 40 species.
- 6) East Hindu Kush (NE Afghanistan), an area which more or less includes Bamian, Kabul, Parvan and Kataghan (eastern part) provinces with altogether ca. 80 species.
- 7) Pamir-Alay in C Asia as the most important centre of diversity. According to Tscherneva (1974), altogether 169 species, of which 130 are endemic, belonging to 36 sections, are known from here. In the Uzbekian part, 74 species from the Surchandarin area and 43 species from the Samarkand area are listed, and 38 species are known from the Kirgizian part of Alay (Knapp 1987).
- 8) Tien-Shan in C Asia with altogether more than 60 species, of which 41 are endemic (Tscherneva 1962).

The above listed diversity centres are part of two larger biogeographical regions. The first of these with more than 250 *Cousinia* spp. expands from lowland Iraq and east Turkey to the Kopet Dag Mts. and Iranian Baluchestan and includes centres 1 – 4. The second with more than 340 *Cousinia* spp. ranges from the Hindu Kush through the Pamir-Alay to north Tien Shan and the deserts of north Kazakhstan and includes centres 5 – 8. According to Tscherneva (1974), the south-north directed valley of the Hari-Rud river and the meridian of Sistan (61 ° E) form a distinct boundary within the distribution area of *Cousinia*, and only 16 species cross the border between the two regions. Sectional and specific richness in the two regions is quickly diminishing towards their margins.

1.4 HYBRIDIZATION

Hybridization is an important factor in plant evolution and many plant species apparently have a hybrid ancestry (Gross & Rieseberg 2005, Hegarty & Hiscock 2005, Stebbins 1950, 1959, Abbott 1992, Ramsey & Schemske 1998). Despite the fact that hybrid speciation seems most likely to be important in taxa with high rates of contemporary hybridization, even rare hybridization events can be evolutionarily important, as a single, partially fertile, hybrid individual can suffice as the progenitor of a new evolutionary lineage (Ellstrand et al. 1996). There are two kinds of hybrid speciation: homoploid and polyploid. The formation of new homoploid species via hybridization is theoretically difficult because it requires reproductive isolation in sympatry (Rieseberg 1997). According to Rieseberg & Willis (2007), homoploid hybrid speciation is rarer than polyploid hybrid speciation for two reasons. First, homoploid hybrid species have strongly reduced fitness in early generation hybrids until selection has eliminated interspecific incompatibilities. Second, genome duplication protects the genetic integrity of newly derived polyploids, but no such barrier prevents homoploid hybrids from back-crossing with their parental species. Homoploid hybrid species are difficult to detect because they often lack diagnostic features such as a change in chromosome number (Rieseberg & Willis 2007).

Twenty-eight hybrids and 11 intermediate forms in *Cousinia* s.s. have been reported (Tscherneva 1962; Rechinger 1972, 1979; Kamelin 1973). According to Mehregan and Kadereit (2006), hybridization in *Cousinia* is possible, both within and between sections as recognized in the traditional classification of the genus, and within and between clades following their phylogeny, but neither hybrids between *Cousinia* s.s. and other main clades of the "Arctium-Cousinia complex", nor between annual and perennial species of *Cousinia* s.s. have been observed. In *Cousinia* the chromosome numbers of 148 species have been determined (<http://www-asteraceae.cla.kobe-u.ac.jp/search.html>), and not a single polyploid chromosome number has been reported to date. If hybrid speciation should have taken place in *Cousinia*, the chromosome numbers observed imply that hybrid speciation in *Cousinia* was exclusively homoploid.

Detection of hybrids in *Cousinia* has been mainly based on morphological evidence, especially morphological intermediacy. However, it is well known that morphological intermediacy can arise from forces other than hybridization (Rieseberg 1997). In many studies, morphological information has been augmented with evidence from secondary chemistry, ecological and geographic data, and/or the production of synthetic hybrids that resemble the natural hybrids. Sang et al. (1995) provided an example of the successful use of ITS sequence data to reconstruct reticulate evolution in plants and demonstrated that sequence data can be highly informative and accurate for detecting hybridization.

Duistermaat (1996) investigated hybridization in the Arctioid species of *Cousinia*. In order to assess the possible role of hybridization for the evolution and high diversity of *Cousinia* subg. *Cousinia* (*Cousinia* s.s.), a study of interspecific hybridization in this group was performed.

1.5 SPECIES NUMBERS IN *COUSINIA*

The number of *Cousinia* species is not entirely clear. Rechinger (1986) and Knapp (1987) reported a total number of 662 species. According to Attar and Gahreman (2006), *Cousinia* contains 705 species. Susanna & Garcia-Jacas (2007) estimated the genus to include 600 – 700 species. Because of an overlap in the regions and the *Cousinia* spp. studied by Rechinger (1953, 1972, 1979) and Tscherneva (1962, 1988), the overall number of *Cousinia* sections and species is difficult to estimate. However, a careful comparison of the systems of Rechinger and Tscherneva leads to an approximate number of 630 species in 70 sections .

It seems possible that the number of species of *Cousinia* described overestimates the number of existing species. *Cousinia* sect. *Cynaroideae* Bunge is the largest section of the genus with 110 published species (Attar and Gahreman 2006, Post 1933, Rechinger 1972 & 1979, Tamanian 1999). In order to determine the exact number of species of *C.* sect. *Cynaroideae* and to obtain a better estimate of species number in *Cousinia*, a revision of the section was necessary.

1.6 AIMS OF THIS WORK

In this dissertation, I have concentrated on the following points. 1) Phylogenetic relationships within the *Arctium-Cousinia* complex and the age and evolution of this complex have been investigated by using DNA sequences and a molecular clock approach. 2) The possible role of hybridization in the evolution of *Cousinia* s.s. was analyzed by screening the literature for reports of hybrids and by characterizing hybrids collected by myself with morphological and molecular methods. 3) *Cousinia* sect. *Cynaroideae*, the largest section of the genus with 110 published species, and apparently a monophyletic group, was revised based on a large number of herbarium specimens.

1.7 ACKNOWLEDGEMENTS

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CHAPTER 2

PHYLOGENY AND EVOLUTION OF THE *ARCTIUM-COUSINIA* COMPLEX
(COMPOSITAE, CARDUEAE-CARDUINAE)

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2.1 ABSTRACT

The phylogeny and evolution of the *Arctium-Cousinia* complex, including *Arctium*, *Cousinia* as one of the largest genera of Asteraceae, *Hypacanthium* and *Schmalhausenia*, is investigated. This group of genera has its highest diversity in the Irano-Turanian region and the mountains of Central Asia. We generated ITS and *rpS4-trnT-trnL* sequences for altogether 138 species, including 129 (of ca. 600) species of *Cousinia*. As found in previous analyses, *Cousinia* is not monophyletic. Instead, *Cousinia* subgenera *Cynaroides* and *Hypacanthodes* with together ca. 30 species are more closely related to *Arctium*, *Hypacanthium* and *Schmalhausenia* (Arctioid clade) than to subg. *Cousinia* (Cousinioid clade). The Arctioid and Cousinioid clades are also supported by pollen morphology and chromosome number as reported earlier.

In the Arctioid clade, the distribution of morphological characters important for generic delimitation, mainly leaf shape and armature and morphology of involucre bracts, are highly incongruent with phylogenetic relationships as implied by the molecular data. No taxonomic solution for this conflict can be offered, and the characters named are interpreted as homoplasious.

Although phylogenetic resolution in the Cousinioid clade is poor, our ITS and *rpS4-trnT-trnL* sequences contain some phylogenetic information. For example, the six annual species of the Cousinioid clade fall into two groups. Poor phylogenetic resolution probably results from lack of characters and the high number of taxa in this species-rich and comparatively young (c. 8.7 mya) lineage. We hypothesize that speciation in the Cousinioid clade was mainly allopatric.

KEYWORDS: ITS, *rpS4-trnT-trnL*, *Arctium*, *Cousinia*, Irano-Turanian region, Pamir-Alay, Tien Shan, molecular clock, speciation

* These authors contributed equally to this publication

2.2 INTRODUCTION

The *Arctium-Cousinia* complex (Compositae, Cardueae-Carduinae) in its most recent circumscription (Susanna & Garcia-Jacas, 2007) is a natural group composed of four genera. The largest genus of the group, one of the largest of the Compositae and among the 50 largest of flowering plants (Frodin, 2004), is *Cousinia* Cass. with more than 600 species (Mabberley, 1990). *Cousinia* traditionally has been subdivided into three subgenera, i.e., subg. *Cousinia*, subg. *Cynaroides* Tscherneva and subg. *Hypacanthodes* Tscherneva (Tscherneva, 1988a, 1988b). The other genera of the complex are *Arctium* L. s.str. with six species (for discussion of a differently circumscribed *Arctium* s.l. see below), *Hypacanthium* Juz. with two species (Tscherneva, 1983) and the monotypic *Schmalhausenia* C. Winkl. Regarding *Lipskyella* Juz. and *Tiarocarpus* Rech. f., recognized as separate genera by Häffner (2000), they were included in *Cousinia* by Susanna & Garcia-Jacas (2007).

Three characters never found in combination elsewhere in the tribe characterize this complex according to Susanna & al. (2003a). The receptacle has strongly twisted scales, the achenes are always streaky (with wavy fringes), very often winged and without a nectary, and the pappus is formed by free deciduous bristles. We regard this combination of characters as solid morphological evidence for the monophyly of the complex (Petit, 1997; Häffner, 2000; Susanna & Garcia-Jacas, 2007). Although molecular support for this monophyly is not unambiguous (Susanna & al., 2003a, 2006), no taxon possibly falling into the *Arctium-Cousinia* complex and making it paraphyletic when defined as done here has been identified in molecular analyses based on larger taxon samples (Häffner and Hellwig, 1999; Garcia-Jacas et al., 2002; Susanna et al., 2006).

According to Rechinger (1986) and Knapp (1987), the vast majority of species of the *Arctium-Cousinia* complex is distributed in the Turkestan mountain region (Tien Shan and Pamir-Alay) and the Irano-Turanian region (Fig. 1; the "Oriental-Turanian Floristic Region" of Meusel & al., 1965). Within this range, following Knapp (1987), most species of *Cousinia* subg. *Cynaroides* and subg. *Hypacanthodes* grow only in the mountainous terrain of the Pamir-Alay range and in the western Tien Shan in Central Asia. The two species of *Hypacanthium* are endemic to the western Tien Shan, and the monotypic *Schmalhausenia* is endemic to the subalpine and alpine zone in the northern Tien Shan. *Arctium* is mainly Eurosiberian in distribution.

Both morphological (Boissier, 1875; Kuntze, 1891; Dittrich, 1977; Tscherneva, 1988a, b, c; Duistermaat, 1996, 1997; Petit & al., 1996; Petit, 1997; Häffner, 2000) and molecular (Häffner & Hellwig, 1999; Garcia-Jacas & al., 2002; Susanna & al., 2003a; 2006) analyses of the *Arctium-Cousinia* complex concluded that the limits between the biennial *Arctium* and the perennial, biennial and only rarely annual *Cousinia* are unclear. This resulted in many reclassifications with many species changing generic affiliation. As one extreme, Kuntze (1891) proposed the classification of all species of *Cousinia* in *Arctium*.

The difficulties in generic delimitation arise from the incongruent distribution of several morphological, pollen, karyological and molecular characters.

Arctium has leaves which are always unarmed, often large (to 80 cm), and usually cordate. In contrast, *Cousinia* subg. *Cousinia*, nine species of subg. *Hypacanthodes*, all species of *Hypacanthium* and the monotypic *Schmalhausenia* have smaller leaves which usually are lanceolate and often very spiny. In *Arctium* and part of *Cousinia* subg. *Cynaroides* involucre bracts always end in a recurved hook whereas in most other species of *Cousinia* involucre

bracts end in an unhooked spine. Whereas in species with hooked involucre bracts usually the entire capitulum is dispersed as a burr adhering to passing animals, most species of *Cousinia* release their achenes and/or disperse as tumble weeds. As regards floral morphology, Duistermaat (1996) observed that the stigma of *Cousinia* subg. *Cousinia* is very different from that of *Arctium* and the “Arctioid” species of *Cousinia*. Whereas in the former the apical part of the style and the stylar branches are covered with long hairs, and a ring of sweeping hairs at the articulation of the base of the stylar apex is absent, the style is glabrous and cylindrical in the latter, and a ring of sweeping hairs is present at the thickened articulation. Häffner (2000) noted that a ring of sweeping hairs is also absent in *Schmalhausenia*. Outer florets in *Arctium* often have long and brightly coloured anther-tubes. Many species of *Cousinia* have brightly coloured appendages in the innermost involucre bracts, recalling those of *Carlina* L. This distribution of characters (leaf, involucre bract, style morphology) led to the proposal by Duistermaat (1996, 1997) to include the species of *Cousinia* subg. *Cynaroides* in an expanded *Arctium* s.l. with 27 species, which was followed by Susanna & Garcia-Jacas (2007). This proposal, however, does not solve the problematic placement of *Hypacanthium*, *Schmalhausenia* and *Cousinia* subg. *Hypacanthodes*.

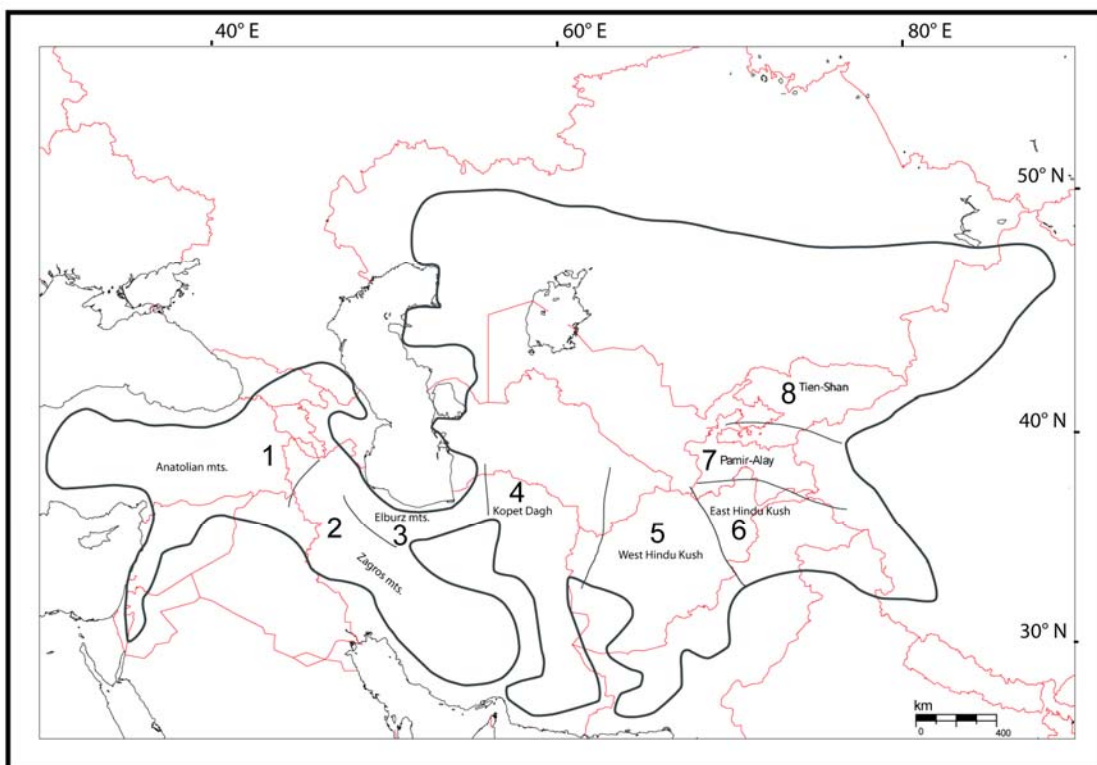


Fig. 1. Geographical distribution of the *Arctium-Cousinia* complex (excl. *Arctium* s.s.). The eight main centres of diversity recognized are based on Rechinger (1986) and Knapp (1987).

Schtepa (1966, 1976) and Kuprianova & Tscherneva (1982) found that *Cousinia* subgenera *Cynaroides* and *Hypacanthodes* have orbicular and spiny pollen grains similar to those of *Arctium*, which they called the *Arctiastrum* pollen type, whereas *Cousinia* subg. *Cousinia* has oblong and smooth pollen grains which they called the *Cousinia* pollen type.

Schmalhausenia (Susanna & al., 2003a) as well as *Hypacanthium* (S. López-Vinyallonga, unpubl. data) have the *Arctiastrum* pollen type.

According to Duistermaat (1996), *Arctium* always has $x = 18$ and $2n = 36$ chromosomes. This number is also found in all species studied of *Cousinia* subgenera *Cynaroides* and *Hypacanthodes* (Tscherneva, 1985) and in *Schmalhausenia* according to Susanna & al. (2003b), and is perfectly correlated with the *Arctiastrum* pollen type. In contrast, *Cousinia* subg. *Cousinia*, with the *Cousinia* pollen type, has $2n = 18, 20, 22, 24$ and 26 chromosomes according to Ghaffari & al. (2006) and earlier authors. Finally, a DNA sequence analysis by Susanna & al. (2003a) grouped all species with $2n = 36$ chromosomes and the *Arctiastrum* pollen type in a monophyletic clade, the Arctioid clade, and species with $2n = 22, 24$ and 26 and the *Cousinia* pollen type in a second monophyletic clade, the Cousinioid clade.

In summary, pollen morphology, chromosome number and DNA data imply a subdivision of the *Arctium-Cousinia* complex into two major lineages which are not congruent with overall morphology particularly because parts of *Cousinia* subgenera *Cynaroides* and *Hypacanthodes* (Arctioid clade) are more similar to subg. *Cousinia* (Cousinioid clade), and other parts (the Arctioid species) are more similar to *Arctium*.

Of the genera and lineages introduced above, *Cousinia* subg. *Cousinia* is most remarkable by containing a high number of species in a comparatively small geographical area. After establishment of *Cousinia* by Cassini (1827), De Candolle (1838) recognized 34 species, Bunge (1865) 126 species, Boissier (1875, 1888) 141 species (in the Flora Orientalis area), Winkler (1892, 1897) 267 species, and an additional 30 species were added in several publications by Bornmüller (1896 – 1941; listed by Rechinger, 1953). In her treatment of *Cousinia* for the 'Flora of the USSR', Tscherneva (1962) recognized about 262 species in about 50 sections, and in his treatment of the genus for 'Flora Iranica', Rechinger (1972) placed more than 350 species in 58 sections. A careful comparison of the systems of Rechinger (1953, 1972, 1979) and Tscherneva (1962, 1988a, b) reveals an approximate number of 630 species in 70 sections and three subgenera. Of these 630 species, ca. 600 belong into subg. *Cousinia*.

The molecular analysis of the *Arctium-Cousinia* complex by Susanna & al. (2003a) included 21 species of *Cousinia* subg. *Cousinia*, one species of subg. *Hypacanthodes* and five species of subg. *Cynaroides*. By increasing the sample of *Cousinia* subg. *Cousinia* to 108 species (of ca. 600), of subg. *Hypacanthodes* to six species (of 10) and of subg. *Cynaroides* to 14 species (of 20), where the sample included represents the large majority of subgeneric units recognized by Tscherneva (1962, 1988c) and Rechinger (1953, 1972, 1979), we pursue several aims. First, we want to investigate whether the subdivision of the *Arctium-Cousinia* complex into two lineages, the Arctioid clade with *Arctium* s.str., *Cousinia* subgenera *Hypacanthodes* and *Cynaroides*, *Hypacanthium* and *Schmalhausenia*, and the Cousinioid clade with *Cousinia* subg. *Cousinia* as found by Susanna & al. (2003a) and as supported by pollen morphology, chromosome number and DNA sequence data can be verified with a significantly enlarged species sample. Second, we aim at obtaining a better understanding of phylogenetic relationships within the Arctioid clade in order to resolve the character incongruencies discussed above and to arrive at a new generic classification of this clade. Third, we want to investigate phylogenetic relationships within the large subgenus *Cousinia*. The last aims both at examining the validity of the sectional (and subsectional) classification of this group

as proposed by Tscherneva (1962, 1988a, b) and Rechinger (1953, 1972, 1979), and at providing a basis for discussing possible evolutionary mechanisms underlying the species-richness of subg. *Cousinia*.

2.3 MATERIAL AND METHODS

2.3.1 Plant material

Samples for analysis were obtained either from silica-gel dried leaves of specimens collected in the wild, from fresh plants cultivated at the Botanic Institute of Barcelona, or from herbarium specimens deposited mainly in MJG, BC, KAS, LE, B, M and JE (Appendix 1). The data described and discussed here are based on a sample of 138 species for which both ITS and *rpS4-trnT-trnL* could be obtained. These 138 species represent 60 sections of *Cousinia* (out of 70 described by Rechinger (1972, 1979) and Tscherneva (1988a, b, c)), three species of *Arctium* and one each of *Hypacanthium* and *Schmalhausenia*. Four outgroup taxa were selected on the basis of previous analyses of the group (Garcia-Jacas & al. 2002; Susanna & al. 2006). These were *Saussurea elegans* Ledeb., *S. maximowiczii* Herder, *Jurinea albicaulis* Bunge and *J. humilis* (Desf.) DC. Seventy-eight additional species were sequenced for ITS and 19 for *rpS4-trnT-trnL*. Results obtained for this additional sample are not presented and discussed only briefly. Voucher data and sources of material of the above 138 species are given in Appendix 1. Some of the ITS sequences were taken from previous studies but all *rpS4-trnT-trnL* sequences were newly generated.

2.3.2 DNA extraction, amplification and sequencing

Total genomic DNA was extracted either following the protocol of the CTAB method of Doyle & Doyle (1987) and Culling (1992), or following the manufacturer's protocols of the NucleoSpin® Plant Kit (Macherey-Nagel GmbH & Co. KG, Düren, Germany) or QIAprep® Miniprep (Qiagen Inc., Valencia, CA, USA).

nrDNA ITS. — Double-stranded DNA of the internal transcribed spacer region (ITS1, 5.8S, ITS2) was amplified using 18S as forward primer and 28S as reverse primer (Muir & Schlötterer 1999). Reactions were performed in 25.0 µl volumes with 10% 10x Biotherm buffer, 5% 50 mM MgCl₂ (GeneCraft, Münster, Germany), 2% of 20 mM dNTPs mix, 2% of each primer at 25 pmol/µl conc., 1.0 unit (0.2 µl) BioTherm™ polymerase (GeneCraft) and 1.0 µl of template DNA (30-60 ng/µl). This was filled up to 25.0 µl with distilled and sterilized water. In some cases 1.0 µl DMSO (dimethyl sulfoxide) per reaction tube was added to improve PCR amplifications (Frackman & al. 1998). The profile used for amplifications consisted of a preheat for 60 s at 94 °C, followed by 35 cycles of 94 °C for 18 s, 52 °C for 30 s, and 72 °C for 60 s and a post-treatment of 78 s at 52 °C plus 8 min at 72 °C. PCR products were purified using the NucleoSpin® Extract Kit (Macherey-Nagel, Düren, Germany) following the manufacturer's protocol.

Cycle sequencing reactions were conducted using 0.5-2.5 µl of the purified PCR product and ABI-PRISM® BigDye™ Terminators v3.0 Cycle Sequencing Reagents (BD 3.0 in 10 ml reactions) for 30 cycles for 10 s at 96 °C and 4 min at 55 °C. Sequences were detected on automated sequencers (ABI 373 or 377).

For sequence analysis, ITS fragments were edited and assembled with the aid of Sequencher 4.1.2 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Edited sequences were aligned with MacClade 4.1 (Maddison & Maddison 2000).

cpDNA *rpS4-trnT-trnL*. — The double-stranded DNA intergenic spacer *rpS4-trnT-trnL* was amplified by PCR with *rpS4R2* (Shaw & al., 2005), *trnL-b* (Taberlet & al., 1991), *trnA2* (Cronn & al., 2002) and *trnA2R* (5'-AGG TTA GAG CAT CGC ATT TG-3' designed for this study) as PCR primers. When the *rpS4R2* (forward)/*trnL-b* (reverse) primer combination failed to generate double-stranded products, two separate PCR reactions were performed with the following primer combinations: *rpS4R2/trnA2R* (reverse) and *trnA2(forward)/trnL-b*. Reactions were performed in 25.0 μ l volumes with 10% 10x AmpliTaq buffer, 10% 50 mM MgCl₂, 10% of 20 mM dNTPs mix, 2% of each primer at 25 pmol/ μ l conc., 1.0 unit (0.2 μ l) AmpliTaq DNA polymerase (Applied Biosystems, Foster City, CA, USA), and 5.0 μ l of template DNA (30-60 ng/ μ l). The volume was filled up to 25.0 μ l with distilled sterilized water. The profile used for amplification consisted of a preheat for 1 min 35 s at 95 °C, followed by 35 cycles of 95 °C for 1 min 30 s, 52 °C for 1 min 30 s and 72 °C for 2 min and a post-treatment of 10 min at 72 °C.

Double-stranded PCR products were purified with either the QIAquick® Purification Kit (Qiagen Inc., Valencia, CA, USA) or DNA Clean & Concentrator-5 (Zymo Research, Orange, CA, USA) following the manufacturer's protocols. Direct sequencing of the amplified DNA segments was performed using 0.5-1.0 μ l of the purified PCR product with a "Big Dye® Terminator v3.1 kit" (Applied Biosystems, Foster City, CA, USA). The profile used consisted of a hot start at 96 °C for 1 min followed by 25 cycles of 10 s at 96 °C, 5 s at 50 °C and 4 min at 60 °C. Nucleotide sequencing was performed at the Serveis Científico-Tècnics of the University of Barcelona on an ABI PRISM 3700 DNA analyzer (Applied Biosystems, Foster City, CA, USA). Nucleotide sequences were edited with Chromas 2.0 (Technelysium Pty. Ltd., Tewantin, Australia) and aligned visually by sequential pairwise comparison (Swofford & Olsen, 1990).

Data matrices are available on request from the corresponding author.

2.3.3 Analyses

Bayesian Inference. — Bayesian analyses of the ITS1 + ITS2, *rpS4-trnT-trnL* and combined ITS1 + ITS2 + *rpS4-trnT-trnL* data sets were performed with MrBayes software package 3.0b4 (Huelsenbeck & Ronquist, 2001). In order to select the best-fit model of substitution, the program Modeltest 3.5 was used (Posada & Crandall, 1998; 2001).

Following the results for DNA evolution of our data as indicated by ModelTest, the ML parameters in MrBayes were set as follows: Nst = 6, Rmat = ((ITS data set: A-C = 0.7720, A-G = 2.7242, A-T = 1.2057, C-G = 0.3372, C-T = 9.8048, G-T = 1.0000 (Proportion of invariable sites (I) = 0.1915; Gamma distribution shape parameter = 0.6024; Model selected: SYM + I + G)); (*rpS4-trnT-trnL* data set: A-C = 0.4777, A-G = 0.6338, A-T = 0.0968, C-G = 0.6238, C-T = 1.1010, G-T = 1.0000 (Proportion of invariable sites (I) = 0.5280; Gamma distribution shape parameter = 0.9553; Model selected: GTR + I + G)); (ITS + *rpS4-trnT-trnL* combined data set: A-C = 0.5621, A-G = 1.2123, A-T = 0.3214, C-G = 0.3810, C-T = 5.0583, G-T = 1.0000 (Proportion of invariable sites (I) = 0.5978; Gamma distribution shape parameter = 0.5788; Model selected: GTR + I + G)) and Rates = gamma.

The Markov Chain Monte Carlo process was set so that four chains ran simultaneously for 2,000,000 generations, with trees being sampled every 100 generations for a total of 20,000 trees in the initial sample. As “stationarity” was achieved by the 3,000th tree, the first 3,000 trees were discarded and the posterior probability of the phylogeny and its branches was determined from the remaining 17,000 trees. Internodes with posterior probabilities $\geq 95\%$ were considered to be well-supported.

Parsimony and Maximum Likelihood. — For the combined data set (138 taxa), a parsimony analysis and a maximum likelihood analysis (ML) were performed with PAUP Version 4.0b10 (Swofford, 2002). For the parsimony analysis, due to the impracticability of performing standard analyses on our large data set, we used the PAUPRat approach (Nixon, 1999; Sikes & Lewis, 2001), a tool for implementing Parsimony Ratchet searches using PAUP. Rather than performing many thorough and independent heuristic searches, the Ratchet performs what amounts to a single long search comprising a series of short heuristic searches. We have performed 200 iterations with TBR branch swapping. All most parsimonious trees (MPT) were saved and PAUP was used for computing a strict consensus tree. For the strict consensus tree obtained from the analysis of the combined data set, consistency index (CI), retention index (RI) and homoplasy index (HI), all excluding uninformative characters, have been calculated.

A bootstrap analysis (BS) (Felsenstein, 1985) was done to obtain support estimates for the nodes in the strict consensus tree obtained from the combined data set. The analysis was performed using the approach by Lidén & al. (1997) using 1000 replicates, random taxon addition with 10 replicates per replicate and no branch swapping.

For the ML analysis, we started with a tree generated by Neighbor Joining (NJ) and used the SYM + G (Zharkikh, 1994) evolutionary model which best fits the data according to MrModeltest 2.2 (Nylander, 2004). Because of the large size of our data set we accelerated the analysis using a ratchet approach according to the following parameters suggested by Morrison (2007): SPR branch swapping, re-weight 25% of the characters, 10 iterations of re-weighting, ApproxLim no more than 2% which indicates that approximate scores within 2% of the optimum will be evaluated fully, and MULTREES inactivated.

Partition homogeneity test. — In order to investigate whether the ITS and *rpS4-trnT-trnL* data sets can be combined, a partition homogeneity test (Farris & al., 1994; implemented in PAUP* 4.0b10; Swofford, 2002) with 10 homogeneity replicates, 10 random addition sequences, tree-bisection-reconnection (TBR) branch swapping on best only and MULTREES on was performed. In order to explore the congruency of the two data sets further, the congruency of individual clades with ≥ 0.95 PP found in the ITS and *rpS4-trnT-trnL* data sets was compared by visual inspection.

Molecular Clock Analysis. — A likelihood ratio test (Felsenstein, 1988) was performed on the tree resulting from the ML analysis (1,000 random addition sequence, TBR and MULTREES on, after Zhang & al. 2007) of the ITS data set. Modeltest 3.5 (Posada & Crandall, 1998) was used to perform the likelihood ratio test comparing the log-likelihood scores of the tree with and without enforcing a molecular clock. Degrees of freedom were equal to $s-2$ where s equals the number of taxa in the analysis. A significant difference at the 0.01 level between two scores was observed. Following this, PAUP* 4.0b10 (Swofford, 2002) was used to calculate genetic distances among taxa. After eliminating all

taxa with large genetic distances to *Saussurea elegans*, a clock-like tree with 112 taxa was obtained.

As we could not identify appropriate fossils of the study group to calibrate our molecular clock tree (but see below), published ITS substitution rates were used for calibration. According to Kay & al. (2006), ITS substitution rates in herbaceous angiosperms vary between 1.72×10^{-9} to 8.34×10^{-9} (mean = 4.13×10^{-9}) substitutions/site/year. The approximate age of seven nodes of our molecular clock tree was determined using the above three rates.

2.4 RESULTS

2.4.1 Partition homogeneity test

Significant incongruence ($p = 0.01$) between the two data sets was detected in the partition homogeneity test. Irrespective of this we decided to combine the two data sets for mainly two reasons. First, the trees resulting from the separate analysis of two data sets (Figs. 2 & 3), and particularly from the *rpS4-trnT-trnL* data set (Fig. 3), show low levels of resolution and contain few clades with high support (≥ 0.95 PP). From this we conclude that incongruency may result largely from lack of resolution. The combination of the two data sets (Fig. 4) leads to improvement of resolution and partly of branch support. Second, the MP tree from the combined data set of the Arctioid clade (Fig. 6) is very similar to the BI ITS tree of this group (Fig. 2), and all clades supported in the combined MP tree are also found in the BI ITS tree. Equally, the large majority of well-supported clades in the combined BI tree (Fig. 4) are also present in the BI ITS tree. Thus, even if combination of the two data sets should be considered suspect on the basis of the results from the partition homogeneity test, our discussion of the phylogeny of the complex would not differ greatly when based on the ITS results only.

Visual comparison of clades with ≥ 0.95 PP found in the ITS and *rpS4-trnT-trnL* trees, respectively, shows that in the majority of cases clades are not congruent among the trees (Figs. 2 & 3; Appendix 2). Thus, of the seven clades (or nested subclades) found in the *rpS4-trnT-trnL* tree, only one (clade 1) is found in the ITS tree (clade 8, containing one additional species). The remaining six clades are not present in the ITS tree, and the constituent species are separated by at least one branch with ≥ 0.95 PP. Equally, of the 28 clades found in the ITS tree, only three clades (clades 2, 9, 17) plus two species of one clade (clade 8) are recovered as clades with ≥ 0.95 PP by the *rpS4-trnT-trnL* data. The third species of clade 8 of the ITS tree, *C. gmelinii* C.Winkl., is separated from the other two species by several branches in the *rpS4-trnT-trnL* tree although none of these has ≥ 0.95 PP. The remaining 24 ITS clades are not present in the *rpS4-trnT-trnL* tree, and in 13 of these clades the species constituting the ITS clades are separated by at least one branch with ≥ 0.95 PP in the *rpS4-trnT-trnL* topology.

2.4.2 Phylogenetic analysis

The numerical results of the MP analysis of the combined ITS + *rpS4-trnT-trnL* data set are given in Table 1. The individual data sets were analyzed with Bayesian inference

(BI), and the combined data set with Maximum Parsimony (MP), Bayesian inference (BI) and Maximum Likelihood (ML). The results of the analyses of all three data sets with BI are shown in Figs. 2 – 4, the result of the MP analysis is partially shown in Fig. 6 (only the Arctioid clade) and the results of the ML analysis of the combined data set are not shown.

All analyses confirmed the monophyly of the *Arctium-Cousinia* complex. Support for this was strong in the MP and BI analyses (BS = 89%, PP = 1.00). Except for the BI analysis of *rpS4-trnT-trnL* alone, all analyses also show a clear subdivision of the complex into three groups: an Arctioid clade moderately supported by BS but well supported by PP (BS = 72%, PP = 1.00) which contains *Arctium*, *Cousinia* subg. *Cynaroides* and *Hypacanthodes*, *Hypacanthium* and *Schmalhausenia*, a Cousinioid clade with BS < 50% but with strong Bayesian support (PP = 1.00) which contains most species of *Cousinia* subg. *Cousinia*, and *C. tenella* Fisch. & C.A. Mey. as sister to the above two clades (BS = 54%, PP = 0.89). In the BI analysis of *rpS4-trnT-trnL*, *C. tenella* falls into the Arctioid clade with only low PP.

Table 1. Numerical results of the MP analysis of the combined ITS + *rpS4-trnT-trnL* data set. Tree length, CI, RI and HI were calculated for the entire tree, the tree without outgroup and for the Arctioid and the Cousinioid clades. Abbreviations: Inf., phylogenetically informative characters; tree, the entire tree including outgroup; -out., outgroup excluded; Cous., Cousinioid clade; Arct., Arctioid clade; CI, consistency index; RI, retention index; HI, homoplasy index.

	tree	-out.	Cous.	Arct.
Inf.	216	171	140	58
Tree length	1204	1076	924	139
CI	0.243	0.224	0.229	0.676
RI	0.617	0.609	0.402	0.842
HI	0.757	0.776	0.771	0.324

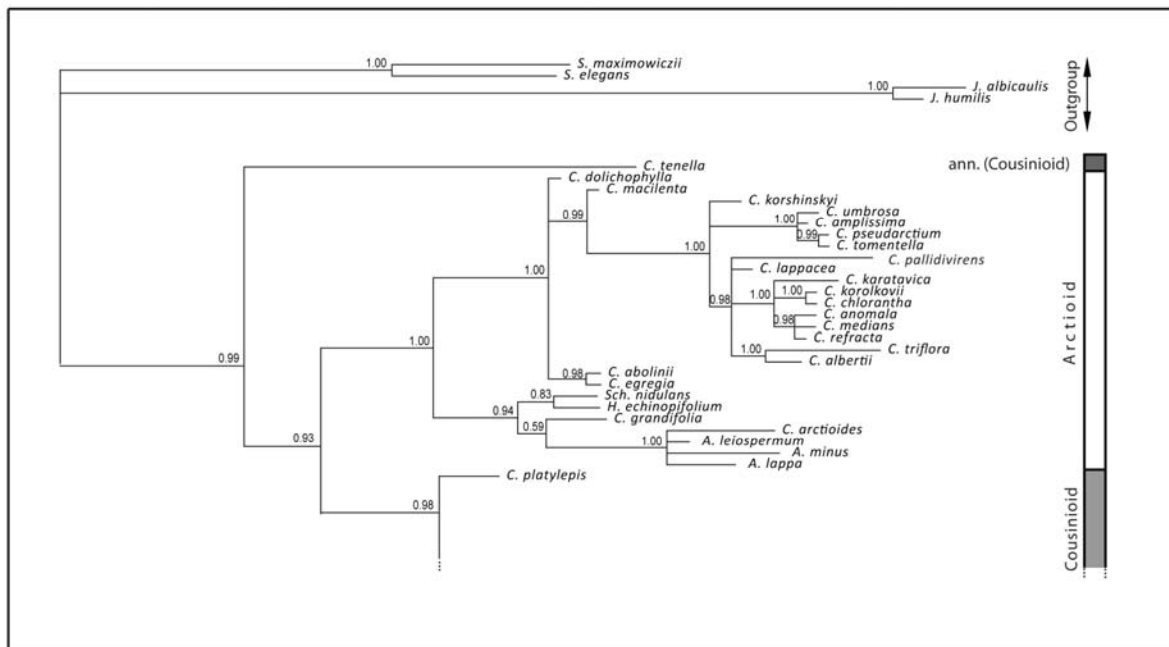


Fig. 2: 50% majority-rule consensus tree obtained from the Bayesian analysis of the ITS data set. Numbers on branches are posterior probabilities. Arctioid, Cousinioid and annual (ann.) species are indicated.

The Arctioid clade. — The description of the Arctioid clade is based on the tree obtained from the MP analysis of the combined data set (Fig. 6). This tree is essentially congruent with the BI tree but better suited for character mapping. Within the Arctioid clade relationships among species are reasonably well resolved and this clade is subdivided into two subclades (Fig. 6). The first subclade, with moderate BS (80%) but strong PP support (1.00) is formed by most species of *Cousinia* subgenera *Cynaroides* and *Hypacanthodes*. This subclade consists of an unresolved polytomy containing four species of subg. *Hypacanthodes* (*C. egregia* Juz., *C. dolichophylla* Kult., *C. abolinii* Kult. ex Tscherneva and *C. macilentata* Winkl.) in two lineages plus a well-supported clade (BS = 90%, PP = 1.00) formed by most of species of subg. *Cynaroides* which in turn fall into two unsupported subgroups. The second subclade also has good support (BS = 81%, PP = 1.00) and is formed by *Arctium* together with *C. arctioides* Schrenk of subg. *Cynaroides* (BS = 92%, PP = 1.00), *Cousinia grandifolia* Kult. of subg. *Hypacanthodes*, *Schmalhausenia* and *Hypacanthium*. Relationships in the Arctioid clade as described above are essentially similar in the BI analyses of the ITS and combined data set and in the ML analysis of the combined data set.

The Cousinioid clade. — Relationships among species in the Cousinioid clade are essentially unresolved in the MP analysis of the combined data set. Resolution is better in the BI analyses of the ITS and combined data sets and will be further discussed below (see Discussion).

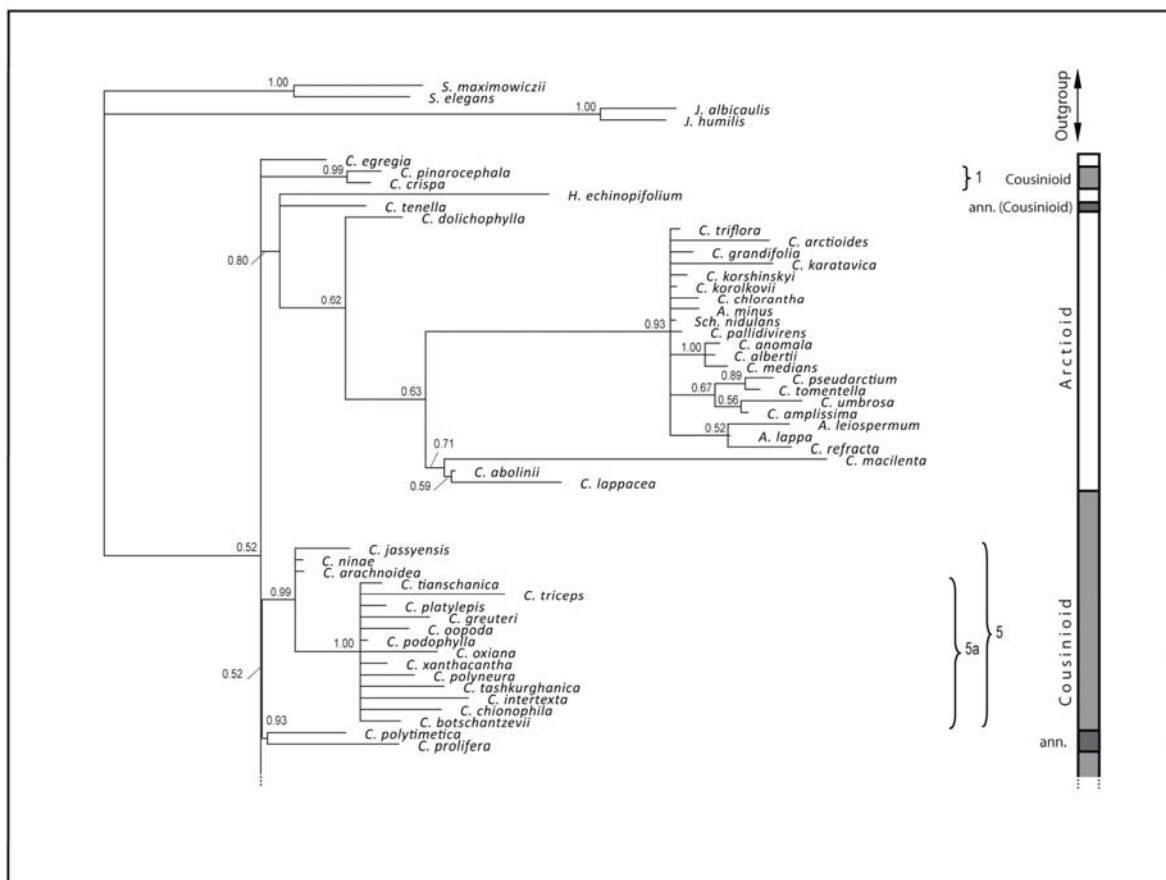


Fig. 3: 50% majority-rule consensus tree obtained from the Bayesian analysis of the *rpS4-trnT-trnL* data set. Numbers on branches are posterior probabilities. Arctioid, Cousinioid and annual (ann.) species are indicated.

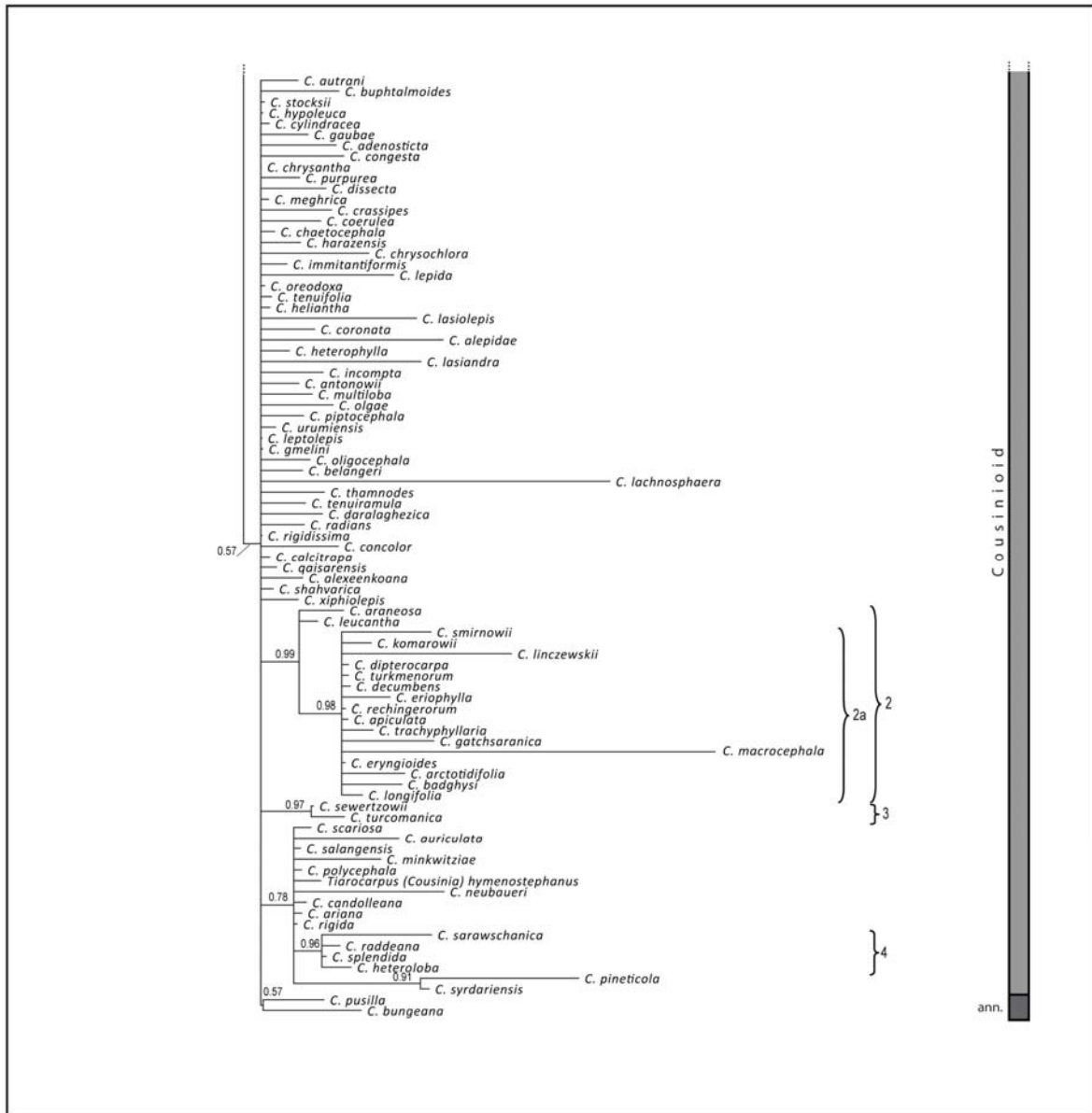


Fig. 3: ... continued from previous page.

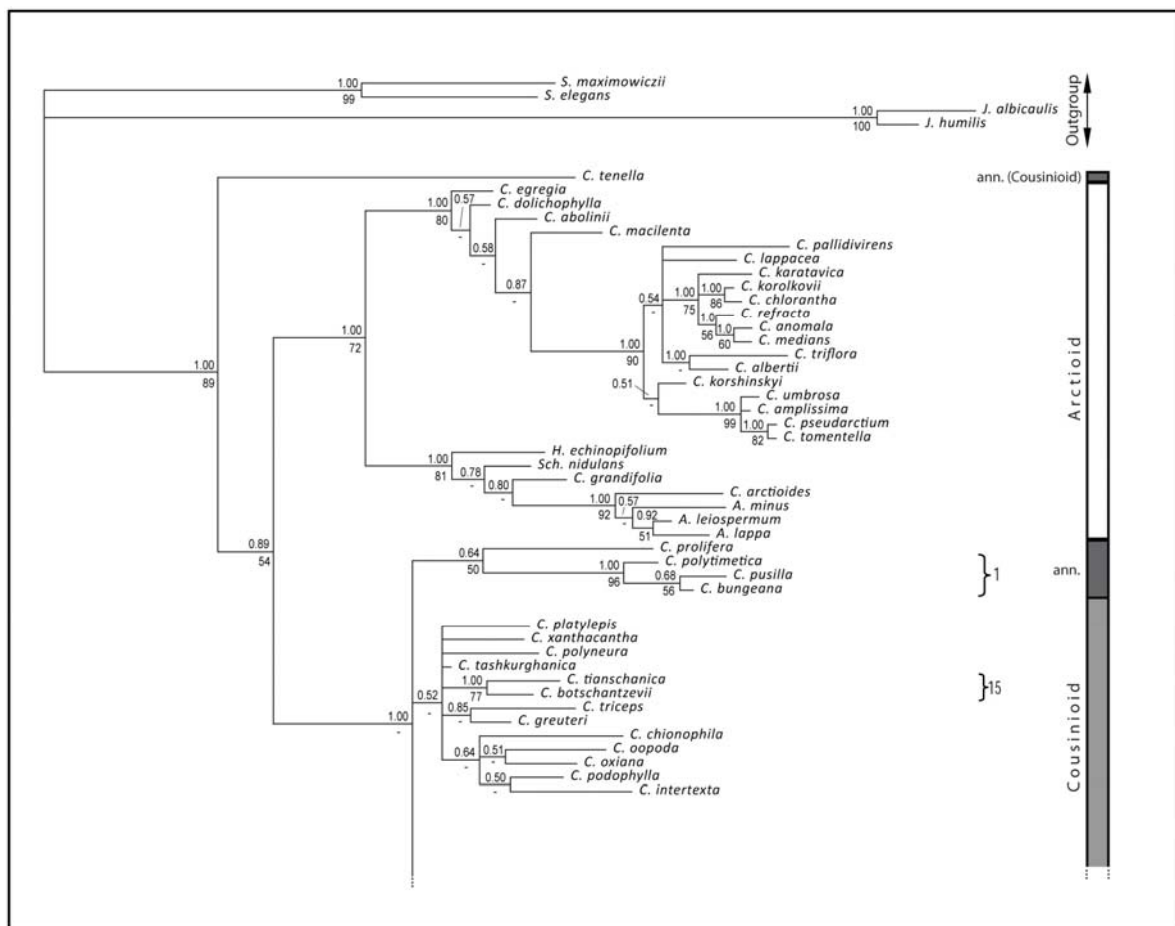


Fig. 4: 50% majority-rule consensus tree obtained from the Bayesian analysis of the combined ITS and *rp54-trnT-trnL* data set. Numbers above branches are posterior probabilities and numbers below branches are

bootstrap percentages. Bootstrap percentages > 50% are only given for clades also obtained in the MP analysis of the combined data set. Arctioid, Cousinioid and annual (ann.) species are indicated.

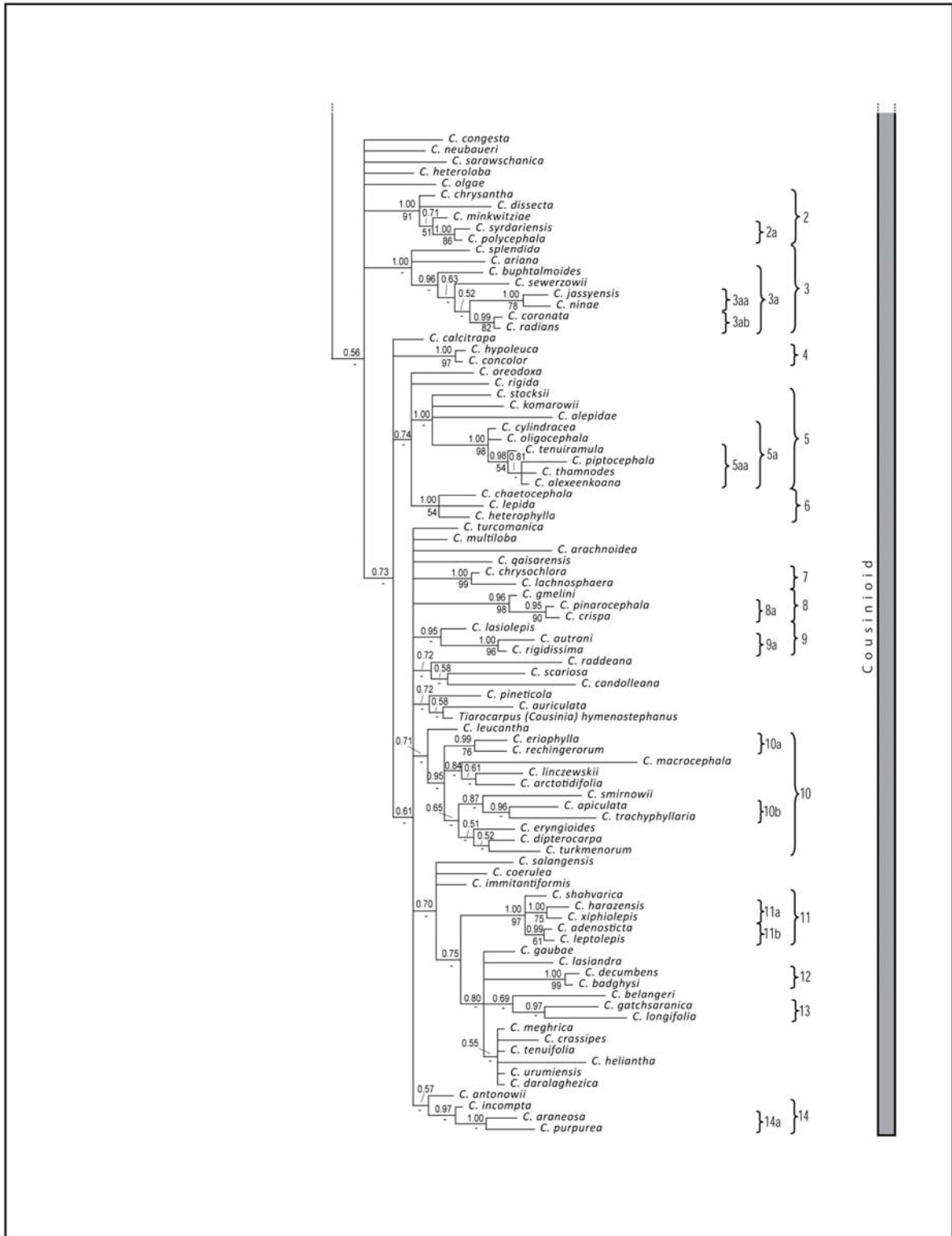


Fig. 4: ...continued from previous page.

2.4.3 Molecular Clock Analysis

The results of our molecular clock analysis are shown in Table 2 and Fig. 5. Mai (2001) reported fossil *Arctium* achenes from a German Miocene locality. The age of this fossil can be dated to 7 - 9 mya (V. Wähnert, pers. com.). Considering that the achenes of *Arctium* can not be reliably distinguished from those of the other genera of the *Arctium-Cousinia* complex, this fossil essentially is compatible with the ages calculated for the complex with all three ITS substitution rates. When considering the occurrence of this achene in Germany, and assuming that the geographical distribution of the complex in the past was similar to its distribution today, with *Arctium* being the only genus occurring in Europe, the fossil probably is best assigned to *Arctium*. This would imply that of the three ITS substitution rates used for the calibration of the molecular clock, the mean rate fits best. With this rate, the clade containing *Arctium* (node F in Fig. 5) was dated to ca. 6.3 my (crown group age). Based on the above considerations, we will refer mainly to ages obtained when using the mean ITS substitution rate in the following discussion, and these ages are also indicated in Fig. 5.

Table 2. Absolute ages in million years (my) obtained from the molecular clock analysis. * rate 1 = 1.72×10^{-9} substitutions/site/year; mean rate = 4.13×10^{-9} substitutions/site/year; rate 2 = 8.34×10^{-9} substitutions/site/year (Kay & al., 2006).

	rate 1* (my)	mean rate* (my)	rate 2* (my)
Node A	45.930	19.128	9.472
Node B	35.465	14.770	7.314
Node C	23.256	9.685	4.796
Node D	20.930	8.717	4.317
Node E	16.860	7.022	3.477
Node F	15.116	6.295	3.118
Node G	10.465	4.358	2.158

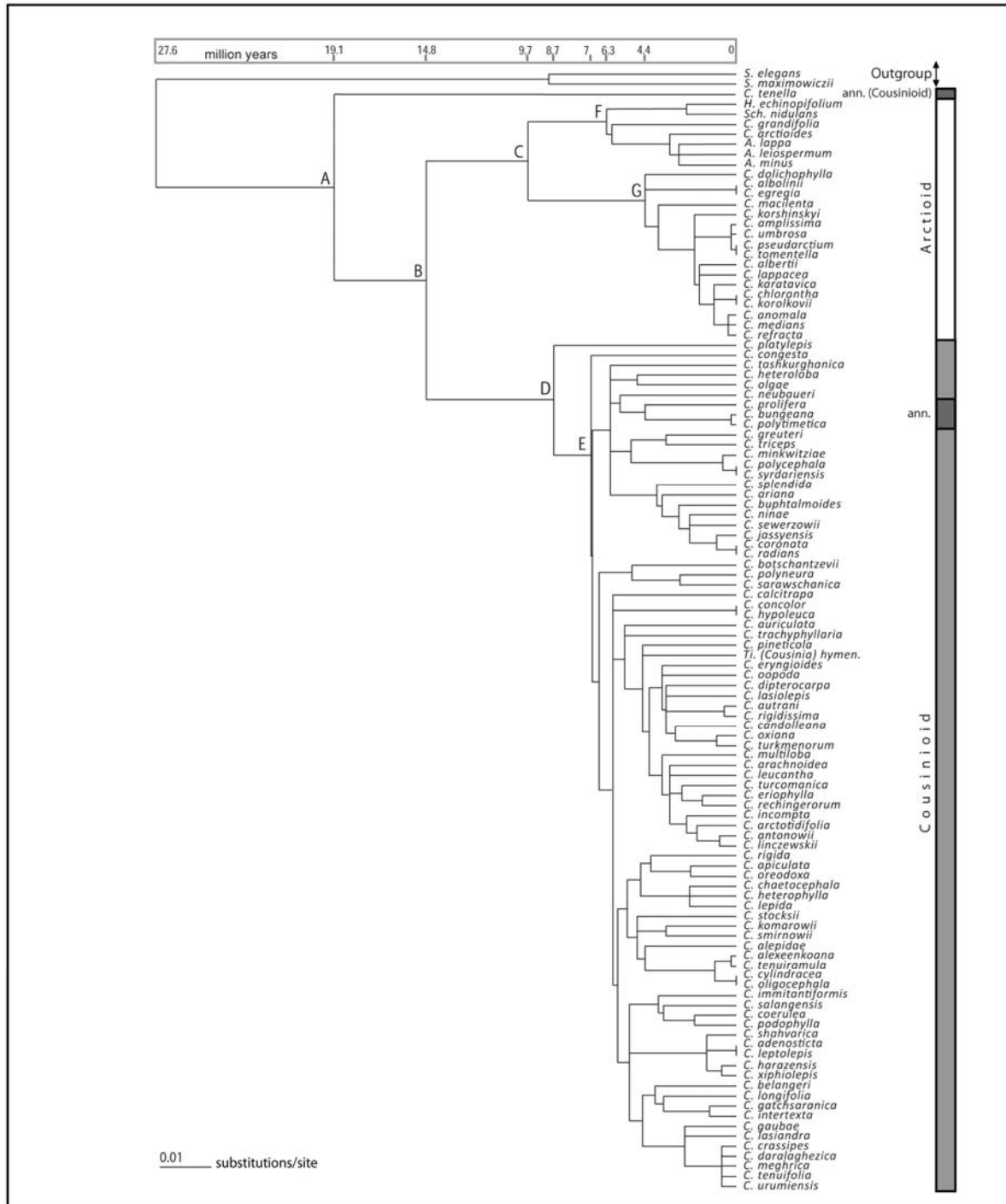


Fig. 5: Dated tree (mean rate) from the Bayesian analysis of a reduced combined ITS and *rpS4-trnT-trnL* data set. Arctioid, Cousinioid and annual (ann.) species are indicated. *Ti. (Cousinia) hymen.*: *Tiarocarpus (Cousinia) hymenostephanus*.

2.5 DISCUSSION

2.5.1 The *Arctium-Cousinia* complex

The *Arctium-Cousinia* complex, established as a monophyletic group before (see Introduction), can be divided into three groups. In all analyses except the BI analysis of *rpS4-trnT-trnL*, a division into an Arctioid clade, a Cousinioid clade and *Cousinia tenella* was found. When comparing the Arctioid and Cousinioid clades, two major differences can be observed.

First, whereas intraclade relationships are reasonably well-resolved in the Arctioid clade, very little resolution was obtained in the Cousinioid clade. Considering that the two clades are sister to each other, and that crown group diversification of the two clades started at approximately the same time (mean rate: Arctioid clade: ca. 9.7 mya, Cousinioid clade: ca. 8.7 mya; Table 2), differential age of the two groups can not be advocated as explanation for the difference in phylogenetic resolution. Instead, we believe that the striking difference in species number is responsible for the difference in phylogenetic resolution. If the Cousinioid clade were to be reduced to a random sample of species equal in number to that of the Arctioid clade, phylogenetic resolution probably would be greatly improved. Indeed, this prediction is to some extent confirmed by the data of Susanna & al. (2003a), who obtained some phylogenetic structure among the 21 species of the Cousinioid clade included in their analysis.

Second, presumably plesiomorphic and apomorphic characters are distributed unevenly across the two clades. Whereas the spiny pollen (and possibly also long stigmata) of the Arctioid clade can also be found in *Jurinea* and *Saussurea* (Punt & Hoen, 2007) as closest relatives of the *Arctium-Cousinia* complex, the short stigmata and smooth pollen of the Cousinioid clade appear to be apomorphic. In other groups of *Cardueae*, pollen morphology is associated with the pollen presentation mechanism. In Centaureinae (Garcia-Jacas & al., 2001; Vilatersana & al., 2001), basal groups have spiny pollen and long, usually dry stigmata and lack a touch-sensitive pollen presentation mechanism. More derived groups have very short, sticky stigmata and smooth pollen, and this is associated with touch-sensitive pollen presentation. We hypothesize that a similar transition of characters has taken place in the *Arctium-Cousinia* complex. As regards chromosome numbers, the Arctioid clade is rather stable with a base chromosome number of $x = 18$. Much in contrast to this, considerable descending dysploidy ($x = 9, 10, 11, 12, 13$) is found in the Cousinioid clade (Ghaffari & al., 2006). Of the closest relatives of the complex, *Jurinea* has a base chromosome number of $x = 17$ and *Saussurea* of $x = 13$ (Susanna & Garcia-Jacas, 2007). In general, basal Carduinae have higher chromosome numbers. The distribution of chromosome numbers in comparison of the Arctioid and Cousinioid clades again is paralleled in subtribe Centaureinae where an evolutionary trend from high to low chromosome numbers has been reported (Garcia-Jacas & al., 2001). Finally, it could be argued that the Arctioid and Cousinioid clades differ in habitat diversity. Whereas species of the Arctioid clade, with the obvious exception of the widespread colonizers mainly of *Arctium*, are more or less confined to high mountain habitats, species of the Cousinioid clade have diversified and grow in widely different habitats including semidesert areas,

open hilly areas, alpine ecosystems, high altitude areas transitional between humid and semiarid ecosystems, oak forest floors and rarely in lowlands. It seems possible that both descending dysploidy and pollen evolution are related to the adaptation to more extreme habitats in the Cousinioid clade. Selvi and Bigazzi (2002) suggested that in *Nonea* Med. (Boraginaceae) descending dysploidy associated with a tendency to a shorter life cycle is an adaptation to arid habitats. Watanabe *et al.* (1999) also found a relationship between low chromosome numbers, annual habit and dry habitats in *Pogonolepis* Steetz, *Sondottia* P.S. Short and *Trichantodium* Sond. & F. Muell. (Asteraceae-Gnaphalieae). The change of shape of pollen grains from spherical in *Arctium* to oblong in *Cousinia* s.str. perhaps can be interpreted as an adaptation to extreme habitats by optimizing harmomegathy (the ability for volume changes caused by desiccation; Wodehouse, 1935) as suggested for the Centaureinae by Hidalgo *et al.* (in press). Possibly the unequal distribution of plesiomorphic vs. apomorphic characters on the one hand and the differential species richness of the Arctioid and Cousinioid clades on the other hand are not only correlated but causally linked. However, whether transition to apomorphic characters in the Cousinioid clade is cause or effect of its higher species number can not be easily decided with the data available.

2.5.2 The Arctioid clade

As described in the introduction, the Arctioid clade can not be characterized morphologically beyond pollen and style morphology. Part of it (*Arctium* and four species of *Cousinia* subg. *Cynaroides*) have unarmed, large cordate leaves and involucre bracts ending in a recurved hook. Of the remainder of subg. *Cynaroides*, six species have leaves which are not cordate but involucre bracts ending in a hooked spine, and 12 species have involucre bracts ending in a straight spine. The distribution of these two characters precludes the morphological definition of a monophyletic *Arctium*. In subg. *Hypacanthodes* no species has either cordate leaves or hooked involucre bracts. The distribution of spiny leaves also runs across established generic and subgeneric boundaries. All species of *Arctium* and almost all species of *Cousinia* subg. *Cynaroides* have unarmed leaves, and only *C. alberti* Regel & Schmalh. and *C. horrescens* Juz. are spiny. In contrast to this, *Schmalhausenia*, *Hypacanthium* and *Cousinia* subg. *Hypacanthodes* (except *C. grandifolia*) have strongly spiny leaves.

A logical solution to the above character distribution would be to establish a broadly redefined *Schmalhausenia* including *Hypacanthium* and the spiny species of *Cousinia* subg. *Hypacanthodes*, and a broadly redefined *Arctium* including subg. *Cynaroides* and the unarmed *C. grandifolia* from *Cousinia* subg. *Hypacanthodes*. However, this solution clearly is not compatible with molecular evidence presented here. In fact, the tree topology (Fig. 6) suggests, as one solution, the recognition of four groups: 1) *Schmalhausenia* plus *Hypacanthium*, 2) *Cousinia grandifolia*, 3) *Arctium* incl. *Cousinia arctioides* and 4) the remaining species of *Cousinia* subgenera *Cynaroides* and *Hypacanthodes*. However, this solution is not compatible with morphological evidence (Fig. 6). In conclusion, our declared aim to revise generic limits in the Arctioid clade on the basis of a larger taxon sample could not be achieved because of the molecular placement and morphology of the species of *Cousinia* subgenera *Cynaroides* and *Hypacanthodes*. When considering the distribution of leaf and

involucral bract morphology across the phylogeny of the entire complex (Fig. 6), it is obvious that either cordate and unarmed or spiny leaves and apically hooked or straight involucral bracts – these two characters are not always correlated - evolved several times in parallel. In view of the uncertainties in our phylogeny we did not try to formally optimize the evolution of these characters.

Interestingly, the only colonizing species of the *Arctium-Cousinia* group, i.e., most species of *Arctium*, have capitula with hooked involucral bracts. Such capitula are dispersed epizoochorously and may be direct cause of the colonizing success of the genus. However, some species with hooked involucral bracts are geographically limited to the Tien-Shan. It seems possible that the biennial habit of *Arctium* – most other species of the Arctioid clade are perennial – contributed to this colonizing success as already suspected by Duistermaat (1996).

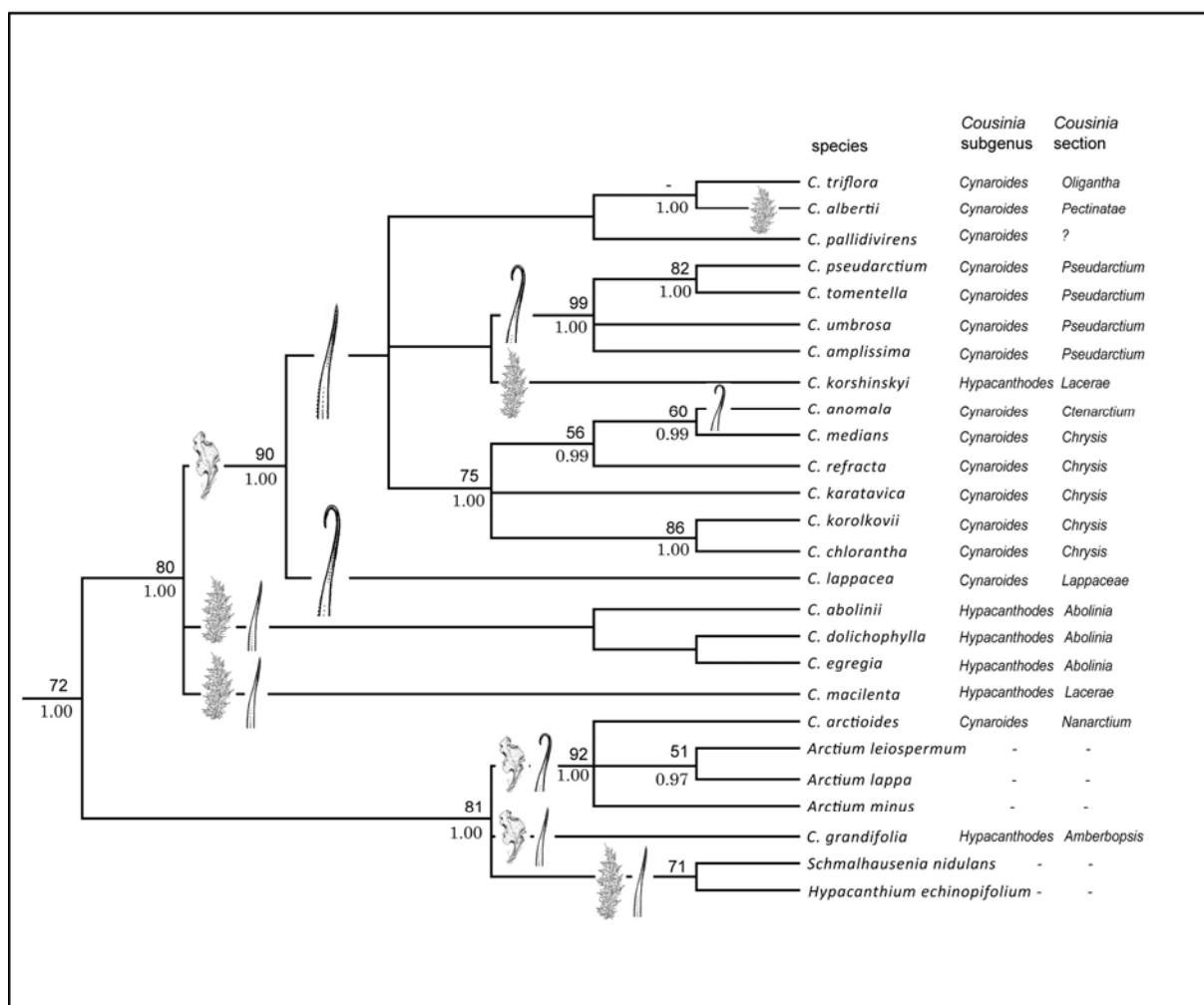


Fig. 6: Distribution of leaf (cordate, unarmed vs. lanceolate, spiny) and involucral bract (unhooked vs. hooked) morphology among species of the Arctioid clade mapped on an MP tree of the combined ITS and *rpS4-trnT-trnL* data set.

The sectional classification of *Cousinia* subg. *Cynaroides* and subg. *Hypacanthodes* is only partly supported by our results, and neither subgenus is monophyletic as presently circumscribed (Fig. 6). One species of subg. *Cynaroides*, *C. arctioides*, is placed within the

Arctium clade with good parsimony and Bayesian support (BS = 92%, PP = 1.00). This position is fully congruent with morphology as *C. arctioides* has unarmed leaves as well as involucre bracts ending in a recurved hook. We propose to follow the taxonomy of Kuntze (1891) and Duistermaat (1996) who accepted this species as *Arctium arctioides* (Schrenk) Kuntze.

Apart from this, our phylogeny is largely congruent with the current sectional classification of subg. *Cynaroides*. The species of sect. *Chrysis* (*C. medians* Juz. through *C. chlorantha*) form a clade with low BS (75%) but high PP (1.0) support. However, this clade also includes *C. anomala* Franch. of sect. *Ctenarctium*. This grouping is not supported by morphological characters as *C. anomala* has involucre bracts ending in a hook and oblong-lanceolate leaves. Section *Pseudarctium* (*C. pseudarctium* Bornm. through *C. amplissima* Boiss.) is a strongly supported clade (BS = 99%, PP = 1.00) containing species with involucre bracts with hooked spines and large, soft and slightly pubescent leaves. Sections *Oligantha* and *Pectinatae* group together with BS < 50% but strong BI support (PP = 1.00). This grouping is not supported by any morphological characters and may result from the poor representation of sect. *Pectinatae* in our sample.

Two species of subg. *Hypacanthodes* were resolved in unexpected position. Thus, *C. korshinskyi* Winkl. of sect. *Lacerae* is part of the subg. *Cynaroides* clade discussed above and separated from the other species of sect. *Lacerae* included in the analysis (*C. macilenta*). This grouping is incongruent with morphology because *C. korshinskyi* is more similar to the rest of subg. *Hypacanthodes* than to subg. *Cynaroides*. *Cousinia grandifolia* is part of the clade containing *Arctium*, *Schmalhausenia* and *Hypacanthium*. In this case, this placement is well correlated with morphology. *Cousinia grandifolia* shares the possession of large, unarmed, oblong-ovate leaves with *Arctium*, and involucre bracts ending in a spine without hook with *Schmalhausenia* and *Hypacanthium*. With these characters *C. grandifolia* is somewhat intermediate between *Arctium* on the one hand and *Schmalhausenia* and *Hypacanthium* on the other hand.

The sectional classification of subg. *Hypacanthodes* is not confirmed by our data. Although the species of sect. *Abolinia* form a clade which is homogeneous morphologically, this clade has no statistical support. *Cousinia macilenta* and *C. korshinskyi* of sect. *Lacerae* are placed in two different and strongly supported clades (see above). They had been placed in separate series of sect. *Lacerae*, series *Macilentae* and series *Pterolepideae*, by Tscherneva (1962), and differ in pubescence, height and branching of the stem, leaf size, capitulum pubescence, shape and texture of the involucre bracts and achene ornamentation.

2.5.3 The Cousinioid clade

As evident from our Bayesian analyses of the ITS, *rpS4-trnT-trnL* and combined data sets (Figs. 2, 3, 4), and also from the MP and ML analyses of the combined data set (not shown), very little phylogenetic resolution can be obtained within *Cousinia* subg. *Cousinia*. Although a varying number of mostly small species groups with high support is recognizable in the different data sets, relationships among species groups are essentially unresolved.

In the following discussion, we first will explore in detail the phylogenetic information contents of our data. This we will do by examining whether clades with ≥ 0.95

posterior probability (PP) are plausible in terms of traditional taxonomic assignment (as a proxy for morphological similarity) and/or geographical distribution by growing in the same general area. For this purpose, the following eight major centres of species diversity were defined (Fig. 1): 1) Anatolian mountains, 2) Zagros mountains, 3) Elburz mountains, 4) Kopet Dagh and mountains to the south, 5) West Hindu Kush (C & W Afghanistan), 6) East Hindu Kush (NE Afghanistan), 7) Pamir-Alay and 8) Tien-Shan (Rechinger, 1986; Knapp, 1987). Second, we will investigate possible causes for the very limited amount of phylogenetic resolution obtained.

Phylogenetic information in the *rpS4-trnT-trnL*, ITS and combined data sets. — In the *rpS4-trnT-trnL* data set, seven clades (or nested subclades) with ≥ 0.95 PP were obtained (Appendix 2). Of these, clades 3 and 4 are not plausible in terms of traditional taxonomic assignment or geographical distribution. Clade 1 is plausible in both terms, and clades 2 – 2a and 5 – 5a, with few exceptions (2 – 2a: *C. araneosa* DC., *C. macrocephala* C. A. Mey., *C. gatchsaranica* Mehregan, Assadi & Attar; 5 – 5a: *C. oxiana* Tscherneva, *C. intertexta* Freyn & Sint.), contain species from the Kopet Dagh area (S Turkmenistan, NE & E Iran and NW Afghanistan) and Central Asia, respectively, but of different sections of *Cousinia* subg. *Cousinia*. In the ITS data set, 28 clades (or nested subclades) with ≥ 0.95 PP were obtained (Appendix 2). Of these, 16 are plausible both in terms of taxonomic assignment and geographical distribution, two are plausible in terms of taxonomic assignment only, four are plausible in terms of geographical distribution only, and the remaining six clades are not plausible in either terms. In the combined data set, 28 clades (or nested subclades) with ≥ 0.95 PP were obtained (Appendix 2). Of these, 13 are plausible both in terms of taxonomic assignment and geographical distribution, four are plausible in terms of taxonomic assignment only, four in terms of geographical distribution only, and the remaining seven clades are not plausible in either terms.

To summarize the above considerations, our phylogenetic trees do appear to contain some plausible phylogenetic information mainly in their distal branches. When considering the two criteria of clade plausibility, it also appears that geographical distribution is a more reliable criterion for recognizing phylogenetic relatedness than traditional taxonomic assignment as also found in other studies (e.g. González-Albaladejo & al., 2005).

Most interestingly, and in support of the above conclusion, the annual species (except *C. pygmaea* C. Winkl. - not contained in the trees shown - and *C. tenella*; for discussion of these two species see below) group in one clade in the majority of our analyses. In the ITS data set (Fig. 2), *C. bungeana*, *C. polytimetica* and *C. pusilla* form one clade with 1.0 PP which is part of a polytomy also containing *C. prolifera*. In the *rpS4-trnT-trnL* data set (Fig. 3), *C. prolifera* Jaub. & Spach and *C. polytimetica* Tscherneva form one clade (0.93 PP) widely separated (although by no branch with ≥ 0.95 PP) from *C. pusilla* C. Winkl. and *C. bungeana* Regel & Schmalh. which are part of a large polytomy. In the Bayesian analysis of the combined data set (Fig. 4) these four annual species form one clade with 0.64 PP, of which *C. bungeana*, *C. polytimetica* and *C. pusilla* form a subclade with 1.0 PP. These four annual species are also recovered as a monophyletic group in the MP analysis of the combined data set (50% BS; *C. bungeana*, *C. polytimetica*, *C. pusilla*: 96% BS; not shown), and *C. bungeana*, *C. polytimetica* and *C. pusilla* are recovered in the ML analysis of the combined data set (not shown). The monophyly of the annual species (except *C. pygmaea* and *C. tenella*) in the combined data set even more than the above considerations implies that our

ITS and *rpS4-trnT-trnL* sequence data do contain limited but valuable phylogenetic information.

Possible causes for lack of phylogenetic resolution in *Cousinia* subg. *Cousinia* — The first obvious reason for the lack of phylogenetic resolution obtained in the analyses of the ITS, *rpS4-trnT-trnL* and combined data sets is the small number of characters available in relation to the number of taxa analysed. For the 108 species included of *Cousinia* subg. *Cousinia*, the *rpS4-trnT-trnL* data set yielded 21, the ITS data set 119 and the combined data set 140 parsimony informative characters (see Table 1 for combined data set). Although in theory the number of parsimony informative characters in the ITS and combined data sets would be sufficient to resolve a phylogeny of 108 species, they are not because the characters show considerable homoplasy. Thus, CI (0.229) and RI (0.402) are low for the MP tree obtained from the combined data set (Table 1). The most likely reason for the lack of characters in *Cousinia* subg. *Cousinia* is its comparatively young age (Table 2, Fig. 5) in combination with its high species number. Thus, using the average substitution rate for ITS for herbaceous perennials (Kay & al., 2006) as to some extent justified by the age of the fossil *Arctium* achene by Mai (2001; see above), a crown group age of ca. 8.7 my (node D) was found for *Cousinia* subg. *Cousinia*, and its major diversification started only ca. 7 mya (node E).

Considering the existence of a large number of closely related and often sympatric species with no obvious mechanism of reproductive isolation in *Cousinia* subg. *Cousinia*, hybridization and hybrid speciation seems possible and clearly would confound the reconstruction of phylogeny (Nieto-Feliner & al., 2001; Font & al., 2002; Vriesendorp & Bakker, 2005; Suárez-Santiago & al., 2007). Based on the examination of literature reports of hybrids and intermediate forms and the morphological and molecular examination of some suspected hybrids, Mehregan & Kadereit (2006) concluded that although hybridization does occur in *Cousinia*, it seems to be comparatively rare in the genus. Thus, only 28 hybrids and 11 intermediate forms in *Cousinia* subg. *Cousinia* have been published (Tscherneva, 1962; Rechinger, 1972, 1979; Mehregan & Kadereit, 2006). These hybrids and intermediate forms involve ca. 11% of the currently recognized species of *Cousinia* subg. *Cousinia*. The two hybrids examined in detail (*C. shahvarica* x *C. decumbens*, *C. eryngioides* x *C. chrysochlora*), confirmed by additivity of their ITS sequences, showed reduced pollen fertility. It is possible that hybridization is much more frequent but undetected because of lack of sufficiently detailed taxonomic knowledge and the existence of several morphologically very similar species. However, the complete absence of polyploid chromosome numbers in *Cousinia* subg. *Cousinia* among the 148 species analyzed (Watanabe, 2007) implies that polyploid hybrid speciation played no role in the evolution of *Cousinia* subg. *Cousinia*. Nothing can be said about the evolutionary significance of homoploid hybrid speciation in this group.

In summary, there is little evidence that hybridization and/or hybrid speciation are important factors hindering the reconstruction of the phylogeny of *Cousinia* subg. *Cousinia*.

The phylogeny and evolution of *Cousinia* subg. *Cousinia*. — As evident from the above discussion, very little can be said about the phylogeny of *Cousinia* subg. *Cousinia*. Although a number of species groups can be recognized which may well represent monophyletic lineages as judged from their taxonomic assignment and/or geographical distribution, relationships among species groups are entirely unclear and no major

subdivision of *Cousinia* subg. *Cousinia* is evident from our data. This is most likely the result of paucity of phylogenetic informative characters contained in our ITS and *rpS4-trnT-trnL* data sets in relation to species number. This in turn is the result of the comparatively young geological age of the group in combination with its species richness. Apart from the recovery of a number of probably monophyletic species groups, our data contain valuable information about the evolution of annuality, a rare condition in *Cousinia* subg. *Cousinia*. It appears that annuality originated twice in *Cousinia* subg. *Cousinia*. The first lineage of annuals, comprising *C. bungeana*, *C. polytimetica*, *C. pusilla* and *C. prolifera* has been discussed above and is well-nested within *Cousinia* subg. *Cousinia*. The second lineage comprises *C. tenella* and *C. pygmaea* and will be discussed further below.

With its comparatively young age and high species number *Cousinia* subg. *Cousinia* represents a massive radiation which is quite unusual because it took place in a comparatively small geographical area. The high diversity of *Cousinia* subg. *Cousinia* is concentrated in the rather limited territory of the Irano-Turanian area of the Ancient Mediterranean subkingdom in Takhtajan's (1986) delimitation (Tscherneva, 1974; Rechinger, 1986; Knapp, 1987). Within this area, two main regions can be recognized, each with its own specific set of sections as traditionally recognized. The first of these expands from lowland Iraq and east Turkey to the Kopet Dag Mts. and Iranian Baluchestan (regions 1 to 4 in Fig. 1). The second ranges from the Hindu Kush through the Pamir-Alay to north Tien Shan and the deserts of north Kazakhstan (regions 5 to 8 in Fig. 1). The border between these two regions is a principal plant biogeographical frontier in the Irano-Turanian region, separating two main types of mountain floras (Kamelin, 1973). Only 16 species of *Cousinia* cross this border. In the western region there are four centres of diversity of *Cousinia* (Tscherneva, 1974) corresponding to floristic regions recognized by Popov (1950). In the eastern region another four diversity centres exist for *Cousinia*. Sectional and specific richness in the region is quickly diminishing towards Central Asia and the Himalaya. The highest diversity is observed in the middle and high mountain belts and in arid areas in the foothills.

Based on the results of an ongoing taxonomic revision of part of *Cousinia* subg. *Cousinia* (sect. *Cynaroides*; Mehregan & Kadereit, in prep.), mainly two conclusions can be drawn about the evolution of this group. First, it seems possible that the number of species described (c. 600) vastly overestimates the number of existing species. Thus, our revision will reduce the number of species in sect. *Cynaroides* from > 90 to ca. 30. Second, of the ca. 30 species recognized by Mehregan & Kadereit (in prep.), only two are geographically widespread, namely *C. calocephala* Jaub. & Spach and *C. onopordioides* Ledeb. The remaining species have rather narrow and, most importantly, allo- or parapatric geographical ranges where species boundaries are marked by prominent topographical barriers. This may imply that the predominant speciation process in *Cousinia* subg. *Cousinia* may be geographical speciation. Today, the group is found mainly (but not exclusively) in vegetation types classified as 'Kurdo-Zagrosian and other steppe-forest climaxes' by Zohary (1973). When this type of vegetation is considered essentially identical with 'Mediterranean to sub-mediterranean *Artemisia-Ephedra-Juniperus-Compositae* steppe of mountainous regions' as defined by Frenzel & al. (1992), the reconstruction of vegetation during the last glacial maximum (20.000 to 18.000 years ago) by Frenzel & al. (1992) suggests that the geographical range of *Cousinia* subg. *Cousinia* in the last glacial maximum was compressed in only the

northern parts of its extant range. This in turn implies substantial changes in geographical distribution of species during the Quaternary. Considering the age of the crown group diversification of *Cousinia* subg. *Cousinia* (c. 8.7 mya; Table 2) and the age of species which in most cases is older than the onset of the Quaternary (Fig. 5), the climatic oscillations of the Quaternary do not appear to have resulted in widespread extinction of the group. Whether these climatic oscillations instead were a stimulus for speciation (through changes in geographical distribution), as found for, e.g., *Primula* L. sect. *Auricula* and *Epimedium* L. (Kadereit & al., 2004; Zhang & al., 2007), we can not say without further analysis.

2.5.4 *Cousinia tenella*

In all our analyses except the BI analysis of the *rpS4-trnT-trnL* data set alone, *C. tenella* is sister to the Arctioid and Cousinioid clades. Support for the sister group relationship between the Arctioid and Cousinioid clades increases (BS = 94%, PP = 1.00; tree not shown) when *C. tenella* is removed from the data matrix.

Although only *C. tenella* was included in the data sets shown here, an enlarged ITS data set of 216 species (not shown) shows *C. pygmaea* to be sister to *C. tenella* with 0.84 PP. Such relationship is plausible considering the great similarity between the two species which differ only in flower colour, relative length of corolla tube and limb and achene shape (Rechinger, 1972). The placement of *C. tenella* in most of our analyses might suggest segregation of *C. tenella* and *C. pygmaea* from *Cousinia* subg. *Cousinia*. On the basis of karyology, pollen type and stigma morphology, however, *C. tenella* (and probably *C. pygmaea*) clearly falls into the Cousinioid clade. *Cousinia tenella* has $2n = 26$ chromosomes according to Aryavand (1975) and Susanna & al. (2003b), the Cousinioid pollen type and stigma morphology (Susanna, pers. com.). The fact that this species is resolved as sister to the rest of the *Arctium-Cousinia* complex probably is due to its annuality, autogamy and probably increased mutation rate. There exist other examples for unexpected placements of annuals in tribe Cardueae. In *Echinops* L., annual species together with the annual *Acantholepis* Less. are sister to the rest of the genus (Garnatje & al., 2005); in *Ptilostemon* Cass., the only annual species, *Ptilostemon stellatus* (L.) Greuter, is sister to the rest of the genus (R. Vilatersana & al., in prep.); and in subtribe *Centaureinae* the annual *Schischkinia* Iljin and *Stizolophus* Cass. are successive sisters to the rest of the subtribe (Susanna & al., 2006). In all these cases, the position of annuals as sister to the remainder of their respective groups is not congruent with morphology. Several authors have pointed out that annual plants often have an elevated rate of molecular evolution compared with perennials, explained by generation time, population size and speciation rate (Bousquet & al., 1992; Laroche & al., 1997; Andreasen & Baldwin, 2001). If this indeed should be the explanation for the unexpected placement of *C. tenella* (it should be noted that, e.g., *C. lachmospaera* and *C. macrocephala* group as expected irrespective of their long branches in the *rpS4-trnT-trnL* tree; Fig. 3), it is interesting to observe that this problem does not appear to exist for the equally annual *C. bungeana*/*C. polytimetica*/*C. pusilla*/*C. prolifera* lineage which clearly falls into the Cousinioid clade as expected from morphology.

2.6 ACKNOWLEDGEMENTS

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2.8 APPENDIX 1

Species included in the molecular analysis with voucher information and GenBank accession numbers. For all species of *Cousinia* the subgeneric classification is given. As part of this dissertation, ITS sequences for species 1-113 were newly generated in Mainz.

Hypacanthium echinopifolium* (Bornm.) Juz.**, Kyrgyzstan: Sine loc., *Iljin* (LE). ***Jurinea albicaulis* Bunge**, Greece: Makedonia, Halkidiki, between Arnea and Paleokastro, *Susanna 1957 & al.* (BC). ***Jurinea humilis* DC.**, Spain: Huesca, Plan, La Barana, *P. Montserrat* (JACA). ***Saussurea elegans* Ledeb.**, Kazakhstan: Aksu-Dzabagly reservation, 1800 m, *Susanna 2179 & al.* (BC). ***Saussurea maximowiczii* Herder**, Japan: Ofuna Botanical Garden. ***Schmalhausenia nidulans* (Regel) Petrak**, Kazakhstan: Almatinskaya oblast, Alatau mt., above Almaty, *Susanna 2088 & al.* (BC). ¹Arctium lappa* L.**, Iran: NNE, Khorassan: 25 SW Bodjnour, 1500 m, *Mehregan 140* (JGM). ***Arctium leiospermum* Juz. & C. Serg.**, Kazakhstan: Zambylskaya oblast, Kurdai pass, 900 m, *Susanna 2154 & al.* (BC). ***Arctium minus* (Hill.) Bernh.**, Belgium: Lovaina Botanical Garden. ²***Tiarocarpus* (*Cousinia*) *hymenostephanus* Rech. f.** (subg. *Cousinia*, unassigned to section), Afghanistan: W, Herat, Band-e Farsi, 10 SW Farsi, 3200 m, *Freitag 6841* (KAS). ³***Cousinia neubaueri* Rech. f.** (subg. *Cousinia*, unassigned to section), Afghanistan: C, Bamian, Band-i Amir, Hochfächen, 3000 m, *Dieterle 896* (M). ⁴***Cousinia oopoda* Juz.** (subg. *Cousinia* sect. *Actinia* Bunge), Tajikistan: South Tajikistan, west mountainside, Khodzha-Kazjyan range, Koy-Pjez-Tau mt., limestone outcrops, 1240 m, *Kinzikaeva 3585* (LE). ⁵***Cousinia tashkurghanica* Rech. f.** (subg. *Cousinia* sect. *Actinia* Bunge), Afghanistan: N, Mazar Sharif, Tang-e Sayyad, S of Tashkurghan, 600 m, *Freitag 3905* (KAS). ⁶***Cousinia oligocephala* Boiss.** (subg. *Cousinia* sect. *Albidae* Rech. f.), Iran: Fars, Inter Shiraz and Sepidan, Shoul pass, 2000 m, *Mehregan 218* (JGM). ***Cousinia chrysantha* Kult.** (subg. *Cousinia* sect. *Alpinae* Bunge), Kazakhstan: Shimkientskaya oblast, Aksu Dzabagly reservation, Darbassa canyon, 1840 m, *Susanna 2198 & al.* (BC). ⁷***Cousinia dipterocarpa* Bornm. & Rech. f.** (subg. *Cousinia* sect. *Alpinae* Bunge), Iran: Khorassan, 27 km from Ghouchan to Bajgiran, Alam Ali pass, 1820 m, *Mehregan 167* (JGM). ⁸***Cousinia lasiolepis* Boiss.** (subg. *Cousinia* sect. *Alpinae* Bunge), Iran: Yasoudj, Dena mts., Bizhan Pass, 3300 m, *Mehregan 202* (JGM). ⁹***Cousinia multiloba* DC.** (subg. *Cousinia* sect. *Alpinae* Bunge), Iran: Khorassan, SW Bodjnour, Salouk mt., 2200 m, *Mehregan 189* (JGM). ¹⁰***Cousinia serawschanica* C. Winkl.** (subg. *Cousinia* sect. *Alpinae* Bunge), Tajikistan: Voru, 2000-2300 m, *Susanna 2516 & al.* (BC). ¹¹***Cousinia splendida* C. Winkl.** (subg. *Cousinia* sect. *Alpinae* Bunge), Tajikistan: Fan mountains, road above Iskandar-Kul, 2300 m, *Susanna 2507 & al.* (BC). ¹²***Cousinia badghysi* Kult.** (subg. *Cousinia* sect. *Badghysia* Tschern.), Turkmenistan: Badghys, Eroylanduz lake, SE "sopki" Kazan, *Kamelin 360* (LE). ¹³***Cousinia piptocephala* Bunge** (subg. *Cousinia* sect. *Badghysia* Tschern.), Iran: Isfahan, 5km from Mourchekhort towards Natanz, 1500 m, *Mehregan 188* (JGM). ¹⁴***Cousinia ariana* Bornm.** (subg. *Cousinia* sect. *Carduncellus* (Juz.) Rech. f.), Afghanistan: E, Kabul, N Salang, 3150 m, *Freitag 3494* (KAS). ¹⁵***Cousinia buphthalmoides* Regel** (subg. *Cousinia* sect. *Carduncellus* (Juz.) Rech. f.), Afghanistan: Unai-Pass, E side, 3050 m, *Freitag 6268* (KAS). ***Cousinia tianschanica* Kult.** (subg. *Cousinia* sect. *Carduncellus* (Juz.) Rech. f.), Kazakhstan: Shimkientskaya oblast, Aksu Dzabagly reservation, Aksu canyon, *Susanna 2191 & al.* (BC). ***Cousinia dissecta* Kar. & Kir.** (subg. *Cousinia* sect. *Chrysoptera* Tschern.), Kazakhstan: Almatinskaya oblast, Sugati mts., Kokpekti narrows, *Susanna 2137 & al.* (BC). ¹⁶***Cousinia oxiana* Tschern.** (subg. *Cousinia* sect. *Chrysoptera* Tschern.), Afghanistan: NW, Herat, 34 km N of Shindand, 1320 m, *Amin 5252* (KAS). ¹⁷***Cousinia turkmenorum* Bornm.** (subg. *Cousinia* sect. *Chrysoptera* Tschern.), Iran: Khorassan, 20 km from Mashhad to Neishabour, 1150 m, *Mehregan 197* (JGM). ¹⁸***Cousinia greuteri* Rech. f.** (subg. *Cousinia* sect. *Congesta* Bunge), Afghanistan: N, Robatak pass between Haibak and Puli-Khumri, 1400 m, *Tonchev 2200* (KAS). ***Cousinia coronata* Franch.** (subg. *Cousinia* sect. *Coronophora* (Juz.) Rech. f.), Uzbekistan: road Tashkent–Samarkand, 10 km from the crossroads to Jizzak, 400 m, *Susanna 2039 & al.* (BC). ¹⁹***Cousinia radians* Bunge** (subg. *Cousinia* sect. *Coronophora* (Juz.) Rech. f.), Iran: Khorassan, 66 km from Mashhad to Kalat-Naderi, 1000 m, *Ghahreman & al.* (TUH). ***Cousinia congesta* Bunge** (subg. *Cousinia* sect. *Cousinia*), Uzbekistan: between Samarkand and Kitov, Takhta–Karachi pass, 1600 m, *Susanna 2059 & al.* (BC). ²⁰***Cousinia daralaghezica* Takht.** (subg. *Cousinia* sect. *Cousinia*), Armenia: Vajots Dzor, Eghegnadzor distr., Eghegnadzor town, *Tamanian s.n.* (ERE). ²¹***Cousinia intertexta* Freyn & Sint.** (subg. *Cousinia* sect. *Cousinia*), Turkey: Sivas, Divrigi–Arapkir, 20 km S Divrigi, 1410 m, *Nydegger 17154* (M). ²²***Cousinia meghrica* Takht.** (subg. *Cousinia* sect. *Cousinia*), Armenia: Sjunik, Meghri distr., Agarak village, *Tamanian s.n.* (ERE). ***Cousinia minkwitziae* Bornm.** (subg. *Cousinia* sect. *Cousinia*), Kazakhstan: Zambylskaya oblast, Talaski Alatau, 6 km W from Il Tai, 1000 m, *Susanna 2183 & al.* (BC). ***Cousinia polycephala* Rupr.** (subg. *Cousinia* sect. *Cousinia*), Kazakhstan: Zambylskaya

oblast, 30 km from the Kurdai pass, *Susanna 2161 & al.* (BC). ***Cousinia syrdariensis* Kult.** (subg. *Cousinia* sect. *Cousinia*), Kazakhstan: Zambylskaya oblast, 30 km from the Kurdai pass, *Susanna 2159 & al.* (BC). ²³***Cousinia tenuifolia* C. A. Mey.** (subg. *Cousinia* sect. *Cousinia*), Iran: Azerbaijan, 10 km from Sarab to Ardebil, 1400 m, *Mehregan 186* (JGM). ²⁴***Cousinia urumiensis* Bornm.** (subg. *Cousinia* sect. *Cousinia*), Iran: Azerbaijan, Urmia, inter Silvana and Razhan, 1650 m, *Mehregan 201* (JGM). ²⁵***Cousinia araneosa* DC.** (subg. *Cousinia* sect. *Cynaroideae* Bunge), Iran: Hamedan, Alvand mt., 10 km from Hamedan to Toiserkan, Ganjnameh Valley, 2400 m, *Mehregan 219* (JGM). ²⁶***Cousinia macrocephala* C. A. Mey.** (subg. *Cousinia* sect. *Cynaroideae* Bunge), Iran: Azerbaijan, Arasbaran, Molouk pass, 1500 m, *Mehregan 212* (JGM). ***Cousinia purpurea* C. A. Mey. in DC.** (subg. *Cousinia* sect. *Cynaroideae* Bunge), Armenia: Ararat, near the village of Shahap, roadsides, *Tamanian s.n.* (ERE). ²⁷***Cousinia decumbens* Rech. f.** (subg. *Cousinia* sect. *Decumbentes* Rech. f.), Iran: Semnan, Shahroud, mt. Shahvar, SW Slopes, 3600 m, *Mehregan 110* (JGM). ²⁸***Cousinia bungeana* Regel & Schmalh.** (subg. *Cousinia* sect. *Dichotomae* Bunge), Sine loc.: *Ovczinnikov 16104* (TAD). ²⁹***Cousinia polytimitica* Tschern.** (subg. *Cousinia* sect. *Dichotomae* Bunge), Uzbekistan: Bukharskaya reg., deserted left bank of Zeravshan river, to SE from Uzliskent vil., *Kryakin* (LE). ³⁰***Cousinia pusilla* C. Winkl.** (subg. *Cousinia* sect. *Dichotomae* Bunge), Tajikistan: S Tajikistan, spackled rock mountains to the S from Besharcha mts. to Babatag range, *Botschantzev 117* (LE). ³¹***Cousinia auriculata* Boiss.** (subg. *Cousinia* sect. *Eriocousinia* Tschern.), Afghanistan: E, Parvan, Ghowrband, Sorkh-Parsa, 2050 m, *Freitag 1128* (KAS). ³²***Cousinia chionophila* Rech. & Koeie** (subg. *Cousinia* sect. *Eriocousinia* Tschern.), Afghanistan: SE, Ghazni, mts. SE of Dashti Nawor (Sperlu Buli), 3850 m, *Freitag 1478* (KAS). ³³***Cousinia gmelini* C. Winkl.** (subg. *Cousinia* sect. *Eriocousinia* Tschern.), Iran: Kandevar to Yoush, *Djavadi* (IRAN). ³⁴***Cousinia polyneura* Rech. f.** (subg. *Cousinia* sect. *Eriocousinia* Tschern.), Afghanistan: E, Kabul, mts. above Paghman, 4000 m, *Freitag 3555* (KAS). ³⁵***Cousinia xanthacantha* Regel** (subg. *Cousinia* sect. *Eriocousinia* Tschern.), Afghanistan: Kabul, in dec. orient. jugi Unai, *Breckle 2286* (M). ³⁶***Cousinia harazensis* Rech. f.** (subg. *Cousinia* sect. *Harazensis* Rech. f.), Iran: Mazandaran, Haraz road, Rineh, 1900 m, *Mehregan 175* (JGM). ³⁷***Cousinia gatchsaranica* I. Mehregan, Assadi & Attar** (subg. *Cousinia* sect. *Hausknechtii* Rech. F.), Iran: Gachsaran, N slopes of Khami mt., above Tol Chegah, 2100 m, *Mehregan 83246* (JGM). ³⁸***Cousinia heliantha* Bunge** (subg. *Cousinia* sect. *Helianthae* Bunge), Iran: Khorassan, 30 km from Sabzevar to Esferaien, 1550 m, *Mehregan 170* (JGM). ³⁹***Cousinia coerulea* Kult. ex Tschern.** (subg. *Cousinia* sect. *Homalochaete* C. Winkl.), Tajikistan: Vorzov canyon, Kudratov, *Susanna 2459 & al.* (BC). ⁴⁰***Cousinia crassipes* Kult.** (subg. *Cousinia* sect. *Homalochaete* C. Winkl.), Iran: Khorassan, Kalat-e Naderi, Ghareh-Sou, 1400 m, *Mehregan 144* (JGM). ⁴¹***Cousinia podophylla* Tschern.** (subg. *Cousinia* sect. *Homalochaete* C. Winkl.), Sine loc., *Ouchinniku 258* (TAD). ⁴²***Cousinia raddeana* C. Winkl.** (subg. *Cousinia* sect. *Hoplophylla* Tschern.), Iran: Khorassan, Mashhad, Kalat-e Naderi road, Sanganeh, Chahchaheh, 1600 m, *Ghahreman & al. 27315* (TUH). ⁴³***Cousinia immitantiformis* Rech.f** (subg. *Cousinia* sect. *Immitantes* Rech. f.), Afghanistan: NW, Sabzak pass, NE Herat, 2400 m, *Freitag 6784* (KAS). ⁴⁴***Cousinia salangensis* Rech. f.** (subg. *Cousinia* sect. *Immitantes* Rech. f.), Afghanistan: E, Kabul, S Salang valley, marble area, 2500 m, *Freitag 3490* (KAS). ⁴⁵***Cousinia jassyensis* C. Winkl.** (subg. *Cousinia* sect. *Jurineopsis* (Juz.) Tschern.), Kyrgyzstan: SW, Jalal Abad Oblast, Toktogul Rayoh, 790 m, *Martins 872* (JE). ⁴⁶***Cousinia smirnowii* Trautv.** (subg. *Cousinia* sect. *Kopetdagia* Tschern.), Iran: Khorassan, SW Bodjnourd, Salouk mt., 2300 m, *Mehregan 152* (JGM). ⁴⁷***Cousinia chrysochlora* Rech. f. & Koeie** (subg. *Cousinia* sect. *Lachnosphaerae* Rech. f.), Iran: Khorassan, 30 km from Sedeh to Asad Abad, Mahousak, 2000 m, *Mehregan 198* (JGM). ⁴⁸***Cousinia lachnosphaera* Bunge** (subg. *Cousinia* sect. *Lachnosphaerae* Rech. f.), Iran: Khorassan, 40 km from Gonabad to Ferdous, 1900 m, *Mehregan 145* (JGM). ⁴⁹***Cousinia alepideae* Boiss.** (subg. *Cousinia* sect. *Lasiandrae* Bunge), Afghanistan: SW, Ghazni, Jamroud, 45 km SW of Ghazni, 2010 m, *Freitag 2008* (KAS). ⁵⁰***Cousinia lasiandra* Bunge** (subg. *Cousinia* sect. *Lasiandrae* Bunge), Iran: Khorassan, 3 km from Doust Abad to Birjand, 1500 m, *Mehregan 127* (JGM). ⁵¹***Cousinia triceps* Kult.** (subg. *Cousinia* sect. *Leiacanthos* Tschern.), Uzbekistan: Kughitang range, Tanghydevol canyon, rocky area, 870 m, *Kamelin 870* (LE). ⁵²***Cousinia antonowii* C. Winkl.** (subg. *Cousinia* sect. *Leiocaules* Bunge), Iran: Khorassan, 10 km from Tivan to Bajgiran, 1590 m, *Mehregan 196* (JGM). ⁵³***Cousinia arctotidifolia* Bunge** (subg. *Cousinia* sect. *Leiocaules* Bunge), Iran: Khorassan, Shirvan, 10 km from Ziarat to Lojelli, 1215 m, *Mehregan 120* (JGM). ⁵⁴***Cousinia heterophylla* Boiss.** (subg. *Cousinia* sect. *Lepidae* Bunge), Afghanistan: W, N-Kattawz, between Kotanni-Kotal and Patanna, 2150 m, *Freitag 3345* (KAS). ⁵⁵***Cousinia lepida* (Bunge ex) Boiss.** (subg. *Cousinia* sect. *Lepidae* Bunge), Iran: Khorassan, Esferaien, 5 km Dahaneh Ojagh to Esferaien, 1420 m, *Mehregan 114* (JGM). ⁵⁶***Cousinia linczewskii* Juz.** (subg. *Cousinia* sect. *Leucocaulon* Tschern.), Iran: Khorassan, Inter Mashhad and Sarakhs, Mazd-Avand pass, 1000 m, *Mehregan 138* (JGM). ⁵⁷***Cousinia turcomanica* C. Winkl.** (subg. *Cousinia* sect. *Leucocaulon* Tschern.), Iran: Khorassan, 110 km W of Bojnourd, between Spakhou and Kastan, 2000 m, *Mehregan 105* (JGM). ⁵⁸***Cousinia rigida* Kult.** (subg. *Cousinia* sect. *Lopholepis* Tschern.), Kyrgyzstan:

Talasskaya reg., north mountainside of Talassky Alatau, Kur-Bokair canyon, south rocky slope, *Popova* (LE). ***Cousinia arachnoidea* Fisch. & C. A. Mey.** (subg. *Cousinia* sect. *Microcarpae* Bunge), Kazakhstan: Almatinskaya oblast, Malai Sary pass, 700 m, *Susanna 2140 & al.* (BC). ⁵⁹***Cousinia ninae* Juz.** (subg. *Cousinia* sect. *Microcarpae* Bunge), Kyrgyzstan: Oshskaya, Torgulsky reg., Oitaya area north from Shoporovo vil., speckled soils, *Sultanova* (LE). ***Cousinia platylepis* Schrenk. ex Fisch. & C. A. Mey.** (subg. *Cousinia* sect. *Microcarpae* Bunge), Kazakhstan: Zambylskaya oblast, 30 km from the Kurdai pass, *Susanna 2158 & al.* (BC). ***Cousinia sewertzowii* Regel** (subg. *Cousinia* sect. *Microcarpae* Bunge), Kazakhstan: Aksu-Dzabagly reservation, 1800 m, *Susanna 2178 & al.* (BC). ⁶⁰***Cousinia prolifera* Jaub. & Spach** (subg. *Cousinia* sect. *Microcousinia* Tschern.), Iran: Khorassan, 110 km from Birjand to Ferdous, 1500 m, *Mehregan 233* (JGM). ⁶¹***Cousinia heteroloba* Rech. f.** (subg. *Cousinia* sect. *Molles* Schrenk.), Afghanistan: NE, Andarab valley below Khinjan, near Ghazan, 1000 m, *Freitag 3043* (KAS). ⁶²***Cousinia candolleana* Jaub. & Spach.** (subg. *Cousinia* sect. *Myriotemae* Rech. f.), Iran: Ghazvin, 10 km from Abgarm to Avadj, 1950 m, *Mehregan 239* (JGM). ⁶³***Cousinia olgae* Regel. & Schmalh.** (subg. *Cousinia* sect. *Olgaeanthe* Tschern.), Iran: Khorassan, 40 km from Torbat-e Djam to Saleh Abad, 1550 m, *Mehregan 194* (JGM). ⁶⁴***Cousinia eriophylla* (Kult.) Bornm.** (subg. *Cousinia* sect. *Platyacanthae* Rech. f.), Iran: Khorassan, Inter Ghouchan and Bajgiran, 5 km S of Dorbadam, 1500 m, *Mehregan 190* (JGM). ⁶⁵***Cousinia rechingerorum* Bornm.** (subg. *Cousinia* sect. *Platyacanthae* Rech. f.), Iran: Khorassan: 30 km W of Torbat-e Djam, E slopes of Bezd mt., 2000 m, *Mehregan 163* (JGM). ⁶⁶***Cousinia trachyphyllaria* Bornm. & Rech. f.** (subg. *Cousinia* sect. *Platyacanthae* Rech. f.), Iran: Khorassan, Neishabour, Khorw, 2100 m, *Mehregan 217* (JGM). ⁶⁷***Cousinia apiculata* Tschern.** (subg. *Cousinia* sect. *Pseudactinia* Tschern.), Iran: Khorassan, Shirvan, Sarani, 2300 m, *Ghahreman & Attar* (JGM). ⁶⁸***Cousinia oreodoxa* Bornm. & Sint.** (subg. *Cousinia* sect. *Pseudactinia* Tschern.), Iran: Khorassan, Inter Bodjnour and Raz, 7 km from Tangeh Torkeman to Ashkhaneh, 1000 m, *Mehregan 150* (JGM). ⁶⁹***Cousinia belangeri* DC.** (subg. *Cousinia* sect. *Pugioniferae* Bunge), Iran: Tehran, 15 km to Karaj, 1200 m, *Mehregan* (JGM). ⁷⁰***Cousinia calcitrapa* DC.** (subg. *Cousinia* sect. *Pugioniferae* Bunge), Iran: Fars, pass inter Sepidan and Yassoudj, 20 km from Sepidan, 2400 m, *Mehregan 203* (JGM). ⁷¹***Cousinia incompta* DC.** (subg. *Cousinia* sect. *Pugioniferae* Bunge), Iran: 20 km Borujen to Isfahan, 2400 m, *Mehregan 128* (JGM). ⁷²***Cousinia pineticola* Rech. f. & Gilli** (subg. *Cousinia* sect. *Racemosae* Rech. f.), Afghanistan: E, Kabul, Korogh Koh, SW of Kabul, 2600 m, *Freitag 1568* (KAS). ⁷³***Cousinia botschantzevii* Juz. ex Tschern.** (subg. *Cousinia* sect. *Regelianae* (Juz.) Tschern.), Uzbekistan: Kuramit mt., Koitash range, S slope above the Koitash village, 1850 m, *Kamelin 29* (LE). ⁷⁴***Cousinia autranii* C. Winkl.** (subg. *Cousinia* sect. *Rigidissimae* Rech. f.), Afghanistan: W, Herat, Ghorat, Bande Frasi, 15 km SSE Farsi, 2400-2500 m, *Freitag 6831* (KAS). ⁷⁵***Cousinia rigidissima* Rech. f.** (subg. *Cousinia* sect. *Rigidissimae* Rech. f.), Afghanistan: W, Herat, Ghorat, in summo jugo 5 km S Dahan-e Kaftarkhan ad viam inter Tulak et Farsi, 2350 m, *Podlech 19193* (M). ⁷⁶***Cousinia scariosa* Regel** (subg. *Cousinia* sect. *Scariosae* Rech. f.), Afghanistan: N, Sar-e Pol, Sangcharak, 40 km SSW mts. above Damdaran, 1900-2500 m, *Freitag 6594* (KAS). ⁷⁷***Cousinia eryngioides* Boiss.** (subg. *Cousinia* sect. *Sciadocousinia* Tschern.), Iran: Khorassan, 50 km from Mashhad to Neishabour, 1500 m, *Mehregan 168* (JGM). ⁷⁸***Cousinia concolor* Bunge** (subg. *Cousinia* sect. *Serratuloides* Bunge), Iran: Semnan, Shahroud, S slopes of Shahvar mt., above Nekarmann, 2500 m, *Mehregan 158* (JGM). ⁷⁹***Cousinia crispa* Jaub. & Spach.** (subg. *Cousinia* sect. *Serratuloides* Bunge), Iran: Chalous road, 10 km from Kandavan to Chalous, 2000 m, *Mehregan 185* (JGM). ⁸⁰***Cousinia hypoleuca* Boiss.** (subg. *Cousinia* sect. *Serratuloides* Bunge), Iran: Tehran, Inter Firouzkouh and Polur, 5 km W of Lasem, 2500 m, *Mehregan 177* (JGM). ⁸¹***Cousinia pinarocephala* Boiss.** (subg. *Cousinia* sect. *Serratuloides* Bunge), Iran: Tehran, Firouzkouh, Gadouk pass, 2200 m, *Mehregan 192* (JGM). ⁸²***Cousinia adenosticta* Bornm.** (subg. *Cousinia* sect. *Sphaerocephalae* Bunge), Iran: Tehran, between Shemshak and Dizin, 3000 m, *Mehregan 165* (JGM). ⁸³***Cousinia leptolepis* (Bornm. & Gauba) Rech. f.** (subg. *Cousinia* sect. *Sphaerocephalae* Bunge), Iran: Tehran, Karadj, Kuh Dashteh, S slopes, 2200 m, *Mehregan 111* (JGM). ⁸⁴***Cousinia shahvarica* Rech.f.** (subg. *Cousinia* sect. *Sphaerocephalae* Bunge), Iran: Semnan, Shahroud, mt. Shahvar, S slopes, 3000 m, *Mehregan 117* (JGM). ⁸⁵***Cousinia xiphiolepis* Boiss.** (subg. *Cousinia* sect. *Sphaerocephalae* Bunge), Iran: Tehran, inter Firouzkouh and Polur, 5 km W of Lasem, 2600 m, *Mehregan 179* (JGM). ⁸⁶***Cousinia longifolia* C. Winkl. & Bornm.** (subg. *Cousinia* sect. *Spinuliferae* Rech. f.), Iran: Kerman, Laleh zar to Rabor, *Attar 226* (JGM). ⁸⁷***Cousinia qaisarensis* Rech. f.** (subg. *Cousinia* sect. *Spinuliferae* Rech.f.), Afghanistan: NW, Fariab, Maimana, Qaisar, 20 km, mts. above Shakh (Gala Shakh), 2200 m, *Freitag 6745* (KAS). ⁸⁸***Cousinia alexeenkoana* Bornm.** (subg. *Cousinia* sect. *Stenocephalae* Bunge), Iran: Isfahan, 10 km from Khaansaar to Boein, 2500 m, *Mehregan 132* (JGM). ⁸⁹***Cousinia cylinracea* Boiss.** (subg. *Cousinia* sect. *Stenocephalae* Bunge), Iran: Fars, inter Shiraz and Sepidan, Shoul pass, 2000 m, *Mehregan 213* (JGM). ⁹⁰***Cousinia gaubae* Bornm.** (subg. *Cousinia* sect. *Stenocephalae* Bunge), Iran: Ghazvin, Karadj, in declivibus lapidosis, 1400 m, *Rechinger 5504* (M). ⁹¹***Cousinia tenuiramula* Rech. f.** (subg. *Cousinia* sect.

Stenocephalae Bunge), Iran: Bakhtiari, Rokh pass, 2200 m, *Mehregan* 206 (JGM). ⁹²***Cousinia thamnoides* Boiss. & Hausskn.** (subg. *Cousinia* sect. *Stenocephalae* Bunge), Iran: Gachsaran, Khami mt. above Tol Chegah, 3170 m, *Mehregan* 237 (JGM). ⁹³***Cousinia komarovii* (O. Kuntze) C. Winkl.** (subg. *Cousinia* sect. *Stenoloma* Juz.), Iran: Khorassan, 15 km Bajgiran to Ghouchan, 1700 m, *Mehregan* 156 (JGM). ⁹⁴***Cousinia leucantha* Bornm. & Sint.** (subg. *Cousinia* sect. *Stenoloma* Juz.), Iran: Golestan Nat. Park, 12 km ENE of Tange Gol, 1900-2100 m, *Akhani* 11357 (M). ⁹⁵***Cousinia stocksii* C.Winkl.** (subg. *Cousinia* sect. *Stocksianae* Rech. f.), Afghanistan: W, Farah, Schucht, 1 km nördlich Hakumate Purchaman, 1880 m, *Podlech* 21787 (M). ⁹⁶***Cousinia tenella* Fisch. & C. A. Mey.** (subg. *Cousinia* sect. *Tenellae* Bunge), Iran: Golestan Nat. Park, between Sharlegh and Cheshmeh Khan, *Akhani* 243 (JGM). ⁹⁷***Cousinia chaetocephala* Kult.** (subg. *Cousinia* sect. *unknown*), Iran: Khorassan, Tchenaran, 3km from Meritchehan to Radekan, 1500 m, *Mehregan* 115 (JGM). ⁹⁸***Cousinia pallidivirens* Kult.** (subg. *Cynaroides* Tschern. unassigned to section), Uzbekistan: Sine loc., *Botschantzev* (LE). ⁹⁹***Cousinia chlorantha* Kult.** (subg. *Cynaroides* Tschern. sect. *Chrysis* Juz.), Uzbekistan: Malguzar mt., S slope, by Tashkesken "say", *Kamelin* 199 (LE). ***Cousinia karatavica* Regel et Schmalh.** (subg. *Cynaroides* Tschern. sect. *Chrysis* Juz.), Kazakhstan: Zambylskaya oblast, Karatau mt., Kuyuk pass, 1000 m, *Susanna* 2162 & al. (BC). ¹⁰⁰***Cousinia korolkowii* Regel & Schmalh.** (subg. *Cynaroides* Tschern. sect. *Chrysis* Juz.), Uzbekistan: N macro-mountaininside, Nuratau range, Sintob kishlak surroundings, rocky slopes, *Botschantzev* 427 (LE). ¹⁰¹***Cousinia medians* Juz.** (subg. *Cynaroides* Tschern. sect. *Chrysis* Juz.), Uzbekistan: S, Supkhandarbinskaya reg., between kishlaks Sajrob and Shurob, 121-122 km of the road from Termez, Speckled rock outcrops, *Botschantzev* 240 (LE). ¹⁰²***Cousinia refracta* (Bornm.) Juz.** (subg. *Cynaroides* Tschern. sect. *Chrysis* Juz.), Tajikistan: Kondara river canyon, Varzowski Rayon reservation, *Susanna* 2456 & al. (BC). ¹⁰³***Cousinia anomala* Franch.** (subg. *Cynaroides* Tschern. sect. *Ctenarctium* Juz.), Tajikistan: Slopes above Voru, about 300 m above Kishlak, 2200-2300 m, *Susanna* 2521 & al. (BC). ***Cousinia lappacea* Schrenk** (subg. *Cynaroides* Tschern. sect. *Lappaceae* Bunge), Kazakhstan: Zambylskaya oblast, Kurdai pass, 900 m, *Susanna* 2150 & al. (BC). ¹⁰⁴***Cousinia arctioides* Schrenk** (subg. *Cynaroides* Tschern. sect. *Nanarctium* Juz. ex. Tschern.), Kazakhstan: Dzhezkazganskaya reg., Turgajskaya lowland, 49 km to SW from Dzhezkazgana, right bank of Kumula river, Tamarix bushland, *Kamelin* 6434 (LE). ¹⁰⁵***Cousinia triflora* Schrenk** (subg. *Cynaroides* Tschern. sect. *Oligantha* Juz.), Iran: Golestan Nat. Park, Yakhbala pass, *Akhani* 102 (JGM). ***Cousinia albertii* Regel et Schmalh.** (subg. *Cynaroides* Tschern. sect. *Pectinatae* C. Winkl.), Kazakhstan: Shimkientskaya oblast, Mashat canyon, 1840 m, *Susanna* 2206 & al. (BC). ¹⁰⁶***Cousinia amplissima* (Boiss.) Boiss.** (subg. *Cynaroides* Tschern. sect. *Pseudarctium* Juz.), Iran: Dena, 15 km from Meimand to Yassoudj, 2500 m, *Mehregan* 174 (JGM). ¹⁰⁷***Cousinia pseudarctium* Bornm.** (subg. *Cynaroides* Tschern. sect. *Pseudarctium* Juz.), Tajikistan: Vorzov valley, 2 km N kishlak Ziddy, *Susanna* 2477 & al. (BC). ¹⁰⁸***Cousinia tomentella* C. Winkl.** (subg. *Cynaroides* Tschern. sect. *Pseudarctium* Juz.), Tajikistan: S mountainside of Guissar range, left bank of Varzob river, Deamalik kishlak surroundings, 1800 m, *Tschukavina* 10512 (LE). ***Cousinia umbrosa* Bunge** (subg. *Cynaroides* Tschern. sect. *Pseudarctium* Juz.), Kazakhstan: Almatinskaya oblast, Alatau mt. above Almaty, 1200 m, *Susanna* 2100 & al. (BC). ¹⁰⁹***Cousinia abolinii* Kult. ex Tscherneva** (subg. *Hypacanthodes* Tschern. sect. *Abolinia* Tschern.), Kyrgyzstan: SW, Jalal Abad Oblast, Kara Saj Tal, Aksy Rayan, 1030 m, *Lazkov s.n.* (JE). ¹¹⁰***Cousinia dolichophylla* Kult.** (subg. *Hypacanthodes* Tschern. sect. *Abolinia* Tschern.), Uzbekistan: Ugamsky range above Nanaj, right edge of Pskem valley, "shiblyak", *Kamelin* 265 (LE). ¹¹¹***Cousinia egregia* Juz.** (subg. *Hypacanthodes* Tschern. sect. *Abolinia* Tschern.), Uzbekistan: Angren valley, rise to Kamchik pass, rubby slope, *Kamelin* 420 (LE). ***Cousinia grandifolia* Kult.** (subg. *Hypacanthodes* Tschern. sect. *Amberbopsis* Tschern.), Kazakhstan: Zambylskaya oblast, Talaski Alatau, 6 km W from Il Tai, 1000 m, *Susanna* 2181 & al. (BC). ¹¹²***Cousinia korshinskyi* C. Winkl.** (subg. *Hypacanthodes* Tschern. sect. *Lacerae* C. Winkl.), Kyrgyzstan: isolated terrain feature Kanka, upper waters of river Kanka, near snow pot, h. 2300 m, *E.M. Il'ina* (LE). ¹¹³***Cousinia macilenta* C. Winkl.** (subg. *Hypacanthodes* Tschern. sect. *Lacerae* C. Winkl.), Tajikistan: SW, Jugum Hissaricum (Gissar), divorticum aquarum inter flumina Ljucjob et Unou, 3000 m, *Zaprojagae* s.n. (M).

2.9 APPENDIX 2

Geographical distribution and taxonomic composition of clades found in the BI analyses of the ITS, *rps4-trnT-trnL* and combined ITS + *rps4-trnT-trnL* data sets. Numbers refer to clades or subclades of the Cousinioid group with posterior probabilities ≥ 0.95 in Figs. 2, 3 and 4. Geographical distribution according to the eight main centres of diversity of *Cousinia* as shown in Fig. 1.

rps4-trnT-trnL

CLADE 1: *C. pinarocephala*, Sect. *Serratuloides*, Reg. 3; *C. crispa*, Sect. *Serratuloides*, Reg. 3.

CLADE 2: *C. araneosa*, Sect. *Cynaroideae*, Reg. 2; *C. leucantha*, Sect. *Stenoloma*, Reg. 4; (NESTED SUBCLADE 2a: *C. smirnowii*, Sect. *Kopetdagia*, Reg. 4; *C. komarowii*, Sect. *Stenoloma*, Reg. 4; *C. linczewskii*, Sect. *Leucocaulon*, Reg. 4; *C. dipterocarpa*, Sect. *Alpinae*, Reg. 4; *C. turkmenorum*, Sect. *Chrysoptera*, Reg. 4; *C. decumbens*, Sect. *Decumbentes*, Reg. 4; *C. eriophylla*, Sect. *Platyacanthae*, Reg. 4; *C. rechingerorum*, Sect. *Platyacanthae*, Reg. 4; *C. apiculata*, Sect. *Pseudactinia*, Reg. 4; *C. trachyphyllaria*, Sect. *Platyacanthae*, Reg., 4; *C. gatchsaranica*, Sect. *Hausknechtii*, Reg. 2; *C. macrocephala*, Sect. *Cynaroideae*, Reg. 1; *C. eryngioides*, sect. *Sciadocousinia*, Reg. 3, 4; *C. arctotidifolia*, sect. *Leiocaules*, Reg. 4; *C. badghysi*, sect. *Badghysia*, Reg. 4; *C. longifolia*, sect. *Spinuliferae*, Reg. 4).

CLADE 3: *C. sewertzowii*, sect. *Microcarpae*, Reg. 7; *C. turcomanica*, sect. *Leucocaulon*, Reg. 4.

CLADE 4: *C. serawschanica*, sect. *Alpinae*, Reg. 7; *C. raddeana*, sect. *Hoplophylla*, Reg. 4, 5, 7; *C. splendida*, sect. *Alpinae*, Reg. 7; *C. heteroloba*, sect. *Molles*, Reg. 5, 6.

CLADE 5: *C. jassyensis*, sect. *Jurineopsis*, Reg. 8; *C. ninae*, sect. *Microcarpae*, Reg. 7, 8; *C. arachnoidea*, sect. *Microcarpae*, Reg. 8; (NESTED SUBCLADE 5a: *C. tianschanica*, sect. *Carduncellus*, Reg. 8; *C. triceps*, sect. *Leiacanthos*, Reg. 7; *C. platylepis*, sect. *Microcarpae*, Reg. 5, 7, 8; *C. greuteri*, sect. *Congesta*, Reg. 5, 6; *C. oopoda*, sect. *Actinia*, Reg. 7; *C. podophylla*, sect. *Homalochaete*, Reg. 7; *C. oxiana*, sect. *Chrysoptera*, Reg. 4; *C. xanthacantha*, sect. *Eriocousinia*, Reg. 6; *C. polyneura*, sect. *Eriocousinia*, Reg. 6; *C. tashkurghanica*, sect. *Actinia*, Reg. 5; *C. intertexta*, sect. *Cousinia*, Reg. 1; *C. chionophila*, sect. *Eriocousinia*, Reg. 5; *C. botschantzevii*, sect. *Regeliana*, Reg. 7).

ITS

CLADE 1: *C. splendida*, sect. *Alpinae*, Reg. 7; *C. ariana*, sect. *Carduncellus*, Reg. 5, 6; *C. bupthalmoides*, sect. *Carduncellus*, Reg. 5, 6, 7; *C. sewertzowii*, sect. *Microcarpae*, Reg. 7; *C. ninae*, sect. *Microcarpae*, Reg. 8, 7; *C. jassyensis*, sect. *Jurineopsis*, Reg. 8; (NESTED SUBCLADE 1a: *C. coronata*, sect. *Coronophora*, Reg. 7; *C. radians*, sect. *Coronophora*, Reg. 4).

CLADE 2: *C. tianschanica*, sect. *Carduncellus*, Reg. 8; *C. botschantzevii*, sect. *Regeliana*, Reg. 7.

CLADE 3: *C. polytimetica*, sect. *Dichotomae*, Reg. 7; *C. pusilla*, sect. *Dichotomae*, Reg. 7; *C. bungeana*, sect. *Dichotomae*, Reg. 8.

CLADE 4: *C. minkwitziae*, sect. *Cousinia*, Reg. 8; *C. chrysantha*, sect. *Alpinae*, Reg. 8; *C. dissecta*, sect. *Chrysoptera*, Reg. 8; (NESTED SUBCLADE 4a: *C. syrdariensis*, sect. *Cousinia*, Reg. 8; *C. polycephala*, sect. *Cousinia*, Reg. 7, 8).

CLADE 5: *C. serawschanica*, sect. *Alpinae*, Reg. 7; *C. polyneura*, sect. *Eriocousinia*, Reg. 6.

CLADE 6: *C. hypoleuca*, sect. *Serratuloides*, Reg. 3; *C. concolor*, sect. *Serratuloides*, Reg. 3, 4.

CLADE 7: *C. rigida*, sect. *Lopholepis*, Reg. 8; (NESTED SUBCLADE 7a: *C. stocksii*, sect. *Stocksiana*, Reg. 4, 5; (NESTED SUBCLADE 7aa: *C. tenuiramula*, sect. *Stenocephalae* s.l., Reg. 2; *C. piptocephala*, sect. *Badghysia*, Reg. 2; *C. thamnodes*, sect. *Stenocephalae* s.l., Reg. 2; *C. alexeenkoana*, sect. *Stenocephalae* s.l., Reg. 2; *C. cylindracea*, sect. *Stenocephalae* s.l., Reg. 2; *C. oligocephala*, sect. *Stenocephalae* s.l., Reg. 2)); (NESTED SUBCLADE 7b: *C. apiculata*, sect. *Pseudactinia*, Reg. 4; *C. oreodoxa*, sect. *Pseudactinia*, Reg. 4); (NESTED SUBCLADE 7c: *C. chaetocephala*, sect. unknown, Reg. 4; *C. lepida*, sect. *Lepidae*, Reg. 4; *C. heterophylla*, sect. *Lepidae*, Reg. 4, 5).

CLADE 8: *C. gmelinii*, sect. *Serratuloides*, Reg. 3; *C. pinarocephala*, sect. *Serratuloides*, Reg. 3; *C. crispa*, sect. *Serratuloides*, Reg. 3.

CLADE 9: *C. eriophylla*, sect. *Platyacanthae*, Reg. 4; *C. rechingerorum*, sect. *Platyacanthae*, Reg. 4.

CLADE 10: *C. salangensis*, sect. *Immitantes*, Reg. 6; *C. immitantiformis*, sect. *Immitantes*, Reg. 5; (NESTED SUBCLADE 10a: *C. coerulea*, sect. *Homalochaete*, Reg. 7; *C. podophylla*, sect. *Homalochaete*, Reg. 7).

- CLADE 11:** *C. incompta*, sect. *Pugioniferae*, Reg. 2; (NESTED SUBCLADE 11a: *C. purpurea*, sect. *Cynaroideae*, Reg. 1; *C. araneosa*, sect. *Cynaroideae*, Reg. 2; *C. macrocephala*, sect. *Cynaroideae*, Reg. 1).
- CLADE 12:** *C. chrysochlora*, sect. *Lachnosphaerae*, Reg. 4; *C. lachnosphaera*, sect. *Lachnosphaerae*, Reg. 4, 5.
- CLADE 13:** *C. turkmenorum*, sect. *Chrysoptera*, Reg. 4; *C. oxiana*, sect. *Chrysoptera*, Reg. 4.
- CLADE 14:** *C. autranii*, sect. *Rigidissimae*, Reg. 5; *C. rigidissimae*, sect. *Rigidissimae*, Reg. 5.
- CLADE 15:** *C. auriculata*, sect. *Eriocousinia*, Reg. 5, 6, 7; *C. chionophila*, sect. *Eriocousinia*, Reg. 5.
- CLADE 16:** *C. shahvarica*, sect. *Sphaerocephalae*, Reg. 3; (NESTED SUBCLADE 16a: *C. harazensis*, sect. *Sphaerocephalae*, Reg. 3; *C. xiphiolepis*, sect. *Sphaerocephalae*, Reg. 3); (NESTED SUBCLADE 16b: *C. adenosticta*, sect. *Sphaerocephalae*, Reg. 3; *C. leptolepis*, sect. *Sphaerocephalae*, Reg. 3).
- CLADE 17:** *C. decumbens*, sect. *Decumbentes*, Reg. 3; *C. badphysi*, sect. *Badghysia*, Reg. 4.
- CLADE 18:** *C. gatchsaranica*, sect. *Hausknechtii*, Reg. 2; *C. intertexta*, sect. *Cousinia*, Reg. 1.

Combined ITS + *rps4-trnT-trnL*

- CLADE 1:** *C. polytimitica*, sect. *Dichotomae*, Reg. 7; *C. pusilla*, sect. *Dichotomae*, Reg. 7; *C. bungeana*, sect. *Dichotomae*, Reg. 8.
- CLADE 2:** *C. chrysantha*, sect. *Alpinae*, Reg. 8; *C. dissecta*, sect. *Chrysoptera*, Reg. 8; (NESTED SUBCLADE 2a: *C. minkwitziae*, sect. *Cousinia*, Reg. 8; *C. syrdariensis*, sect. *Cousinia*, Reg. 8; *C. polycephala*, sect. *Cousinia*, Reg. 7, 8).
- CLADE 3:** *C. splendida*, sect. *Alpinae*, Reg. 7; *C. ariana*, sect. *Carduncellus*, Reg. 6, 5; (NESTED SUBCLADE 3a: *C. bupthalmoides*, sect. *Carduncellus*, Reg. 5, 6, 7; *C. sewertzowii*, sect. *Microcarpae*, Reg. 7; (NESTED SUBCLADE 3aa: *C. jassyensis*, sect. *Jurineopsis*, Reg. 8; *C. ninae*, sect. *Microcarpae*, Reg. 7, 8); (NESTED SUBCLADE 3ab: *C. coronata*, sect. *Coronophora*, Reg. 7; *C. radians*, sect. *Coronophora*, Reg. 4)).
- CLADE 4:** *C. hypoleuca*, sect. *Serratuloides*, Reg. 3; *C. concolor*, sect. *Serratuloides*, Reg. 3, 4.
- CLADE 5:** *C. stocksii*, sect. *Stocksianae*, Reg. 4, 5; *C. komarowii*, sect. *Stenoloma*, Reg. 4; *C. alepideae*, sect. *Lasiandrae*, Reg. 5; (NESTED SUBCLADE 5a: *C. cylindracea*, sect. *Stenocephalae* s.l., Reg. 2; *C. oligocephala*, sect. *Stenocephalae* s.l., Reg. 2; (NESTED SUBCLADE 5aa: *C. tenuiramula*, sect. *Stenocephalae* s.l., Reg. 2; *C. piptocephala*, sect. *Badghysia*, Reg. 2; *C. thamnodes*, sect. *Stenocephalae* s.l., Reg. 2; *C. alexeenkoana*, sect. *Stenocephalae* s.l., Reg. 2)).
- CLADE 6:** *C. chaetocephala*, sect. unknown, Reg. 4; *C. lepida*, sect. *Lepidae*, Reg. 4; *C. heterophylla*, sect. *Lepidae*, Reg. 4, 5.
- CLADE 7:** *C. chrysochlora*, sect. *Lachnosphaerae*, Reg. 4; *C. lachnosphaera*, sect. *Lachnosphaerae*, Reg. 4, 5.
- CLADE 8:** *C. gmelinii*, sect. *Serratuloides*, Reg. 3; (NESTED SUBCLADE 8a: *C. pinarocephala*, sect. *Serratuloides*, Reg. 3; *C. crispa*, sect. *Serratuloides*, Reg. 3).
- CLADE 9:** *C. lasiolepis*, sect. *Alpinae*, Reg. 2, 4, 5; (NESTED SUBCLADE 9a: *C. autranii*, sect. *Rigidissimae*, Reg. 5; *C. rigidissimae*, sect. *Rigidissimae*, Reg. 5).
- CLADE 10:** *C. araneosa*, sect. *Cynaroideae*, Reg. 2; *C. linczewskii*, sect. *Leucocaulon*, Reg. 4; *C. arctotidifolia*, sect. *Leiocaulon*, Reg. 4; *C. smirnowii*, sect. *Kopetdagia*, Reg. 4; *C. eryngioides*, sect. *Sciadocousinia*, Reg. 3, 4; *C. dipterocharpa*, sect. *Alpinae*, Reg. 4; *C. turkmenorum*, sect. *Chrysoptera*, Reg. 4.; (NESTED SUBCLADE 10a: *C. eriophylla*, sect. *Platyacanthae*, Reg. 4; *C. rechingerorum*, sect. *Platyacanthae*, Reg. 4); (NESTED SUBCLADE 10b: *C. apiculata*, sect. *Pseudactinia*, Reg. 4; *C. trachyphyllaria*, sect. *Platyacanthae*, Reg. 4).
- CLADE 11:** *C. shahvarica*, sect. *Sphaerocephalae*, Reg. 3; (NESTED SUBCLADE 11a: *C. harazensis*, sect. *Sphaerocephalae*, Reg. 3; *C. xiphiolepis*, sect. *Sphaerocephalae*, Reg. 3); (NESTED SUBCLADE 11b: *C. adenosticta*, sect. *Sphaerocephalae*, Reg. 3; *C. leptolepis*, sect. *Sphaerocephalae*, Reg. 3).
- CLADE 12:** *C. decumbens*, sect. *Decumbentes*, Reg. 3; *C. badphysi*, sect. *Badghysia*, Reg. 4.
- CLADE 13:** *C. gatchsaranica*, sect. *Hausknechtii*, Reg. 2; *C. longifolia*, sect. *Spinuliferae*, Reg. 4.
- CLADE 14:** *C. incompta*, sect. *Pugioniferae*, Reg. 2; (NESTED SUBCLADE 14a: *C. araneosa*, sect. *Cynaroideae*, Reg. 2; *C. purpurea*, sect. *Cynaroideae*, Reg. 1).
- CLADE 15:** *C. tianschanica*, sect. *Carduncellus*, Reg. 8; *C. botschantzevii*, sect. *Regelianae*, Reg. 7.

CHAPTER 3

THE ROLE OF HYBRIDIZATION IN THE EVOLUTION OF *COUSINIA* S.S.

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3.1 ABSTRACT

In order to assess the possible role of interspecific hybridization for the evolution of the high diversity of *Cousinia* subg. *Cousinia* (*Cousinia* s.s., ca. 600 spp.), we examined the frequency of hybridization in this taxon. For this, hypothetical hybrid combinations published in the past were critically examined, and morphological and molecular evidence for two hybrids identified by ourselves is presented. To examine relationships among hybridizing species, a Bayesian analysis of nuclear-ribosomal ITS of 216 species of *Cousinia* and related genera was performed. Twenty-eight putative hybrids and 11 intermediate forms have been published. Two intermediate specimens collected by us were identified as hybrids by their morphological intermediacy, additivity of ITS sequences and reduced pollen fertility. Neither hybrids between *Cousinia* s.s. and other main clades of the '*Arctium-Cousinia* complex', nor between annual and perennial species of *Cousinia* s.s. have been observed. Our results clearly show that hybridization in *Cousinia* is possible and that ca. 10.7 % of the species of this taxon appear to be involved in interspecific hybridization. This figure together with the complete absence of polyploids in *Cousinia* s.s. leads to the conclusion that the role of interspecific hybridization for the evolution and diversity of the group is likely to have been minor.

Keywords: *Cousinia*, *C.* subg. *Cousinia*, hybridization, phylogeny

3.2 INTRODUCTION

Cousinia Cass. is the largest genus of Asteraceae-Cardueae and contains about 630 species in SW and C Asia (*Cousinia* subg. *Cousinia* ca. 600 spp.; *Cousina* subg. *Hypacanthodes* Tschern. 10 spp.; *Cousina* subg. *Cynaroides* Tschern. ca. 20 spp.). Within Cardueae, *Cousinia* belongs to the 'Arctium-Cousinia complex'. The genus is exceptional in containing a large number of species in a comparatively small geographical area. Eight areas of exceptionally high diversity can be observed. These are the western Tien-Shan (ca. 60 spp.), Pamir-Alay (ca. 170 spp.), NE Afghanistan (East Hindu Kush; ca. 80 spp.), NW Afghanistan (West Hindu Kush; ca. 45 spp.), Kopetdagh (ca. 70 spp. in Iran, 30 spp. in Turkmenistan), Elburz mountains (N Iran, ca. 70 spp.), N Zagros mountains (W Iran, ca. 45 spp.) and E Anatolian mountains and Azerbaijan (W Turkey and NW Iran, ca 40 spp.; Rechinger 1986, Knapp 1987, Tscherneva 1988, 1990).

Monophyly of the *Arctium-Cousinia* complex has been demonstrated in previous studies based on nuclear and chloroplast DNA sequences (Susanna et al. 2003a). The complex consists of two distinct groups supported by characters such as stigma morphology, pollen type and chromosome number: the Arctioid group including *Arctium* L., *Hypacanthium* Juz., *Schmalhausenia* C. Winkl. and *Cousinia* subgg. *Cynaroides* and *Hypacanthodes*, this group always has a diploid chromosome number of $2n = 36$, and the Cousinioid group with only *Cousinia* subg. *Cousinia* (= *Cousinia* s.s.) with chromosome numbers of $2n = 18, 20, 22, 24$ and 26 (Kuprianova & Tscherneva 1982, Duistermaat 1996, Susanna et al. 2003b, Ghaffari et al. 2006, López-Vinyallonga & et al., in press).

Interspecific hybridization plays an important role in plant and animal evolution (Arnold 1997), and can result in the formation of new taxa via introgressive hybridization and homoploid and polyploid hybrid speciation (Stebbins 1950, 1959, Abbott 1992, Rieseberg 1997, Ramsey & Schemske 1998). Based on a detailed analysis of five floras of Europe (British Isles, Scandinavia), North America (Great Plains, Intermountain West) and the Hawaiian Islands, Ellstrand et al. (1996) estimated the frequency and taxonomic distribution of interspecific hybridization. They suggested that the number of hybrids (expressed as a percentage of the total number of species in these floras) ranged between ca. 6 and 21.8%. They also found hybridization to be nonrandomly distributed among taxa, and in all five floras analyzed Asteraceae are among the six families with the highest number of hybrids. According to Rieseberg (1997), the above figures may substantially underestimate true hybrid frequency because a large number of hybrids may be undetected due to the inadequacy of taxonomic knowledge in certain groups and some of the floras analyzed. In the flora of the British Isles, one of the best-known floras in the world, 61 (ca. 22.8%) of 268 species of Asteraceae (excl. *Hieracium* and *Taraxacum*) are involved in the formation of 43 hybrids. In British Cardueae, 12 (35%) of 40 spp. form 14 different hybrids (Stace 1991). According to Duistermaat (1996), five of six species belonging to *Arctium* s.s. are involved in hybridization.

On this background, we here examine the frequency of interspecific hybridization in *Cousinia* s.s. and try to assess its possible role in the evolution of the high specific diversity of this taxon. Many species of *Cousinia* s.s. are distributed sympatrically, and there exist no obvious mechanisms of prezygotic reproductive isolation between sympatric species.

Hybridization between the Arctioid species of *Cousinia* has been analyzed by Duistermaat (1996).

3.3 MATERIAL AND METHODS

Published accounts of *Cousinia* were critically examined for reports of hybrids or intermediate forms. Two specimens found by us with clearly intermediate characters were examined both morphologically and molecularly along with their suspected parents (Fig. 1, Tab. 2). For DNA extraction, silica-gel dried leaves of these two specimens were used. Pollen fertility was determined by aceto-carmin staining and light microscopy (Tyagi & Singh 1998), and the total number of pollen grains per flower was counted.

Phylogenetic relationships between hypothetical parents of hybrids were also determined. For this, we constructed an ITS phylogeny of 216 species representing 63 sections of *Cousinia* (out of ca. 70 described by Rechinger (1972) and Tscherneva (1988)), three species of *Arctium*, one species each of *Hypacanthium* and *Schmalhausenia* and two outgroups (*Jurinea albicaulis* Bunge and *Saussurea elegans* Ledeb.). The material used for DNA extraction is listed in Appendix 1.

Total genomic DNA extraction, ITS (ITS1 & ITS2) amplification and sequencing were performed as described by López-Vinyallonga et al (in press). Bayesian analyses of the ITS1 + ITS2 data sets were performed with MrBayes software package 3_0b4 (Huelsenbeck and Ronquist 2001). In order to select the best-fit model of substitution, the program ModelTest 3.5 was used (Posada & Crandall 1998, 2001). Following the results for DNA evolution of our data as indicated by ModelTest, the ML parameters in MrBayes were set as follows: Nst = 6, rates=gamma, Rmat = (A-C = 0.7998, A-G = 2.8343, A-T = 1.5745, C-G = 0.2990, C-T = 11.8505, G-T = 1.0000), proportion of invariable sites (I) = 0.1818, gamma distribution shape parameter = 0.6192 and model selected: SYM+I+G. The number of generations was set to 2.000.000, with trees being sampled every 100 generations for a total of 20.000 trees in the initial sample. The first 3.000 trees were discarded and the posterior probability of the phylogeny and its branches was determined from the remaining 17.000 trees.

ITS sequences of the suspected hybrids collected by ourselves and their parents were examined for additivity of diagnostic nucleotide positions.

3.4 RESULTS

Twenty-eight hybrids and 11 intermediate forms in *Cousinia* s.s. have been published (Tscherneva 1962, Rechinger 1972, 1979, Kamelin 1973) and are compiled in Tab. 1. Both intermediate specimens found by us were confirmed to be hybrids by their morphological intermediacy (Fig. 1) and additivity of ITS sequences (Tab. 2). They represent hybrids between *C. shahvarica* and *C. decumbens* and between *C. eryngioides* and *C. chrysochlora*, respectively. Pollen fertility of the hybrid individuals was clearly reduced (*C. shahvarica*: 95.4%, *C. decumbens*: 92.3%, hybrid: 77%; *C. eryngioides*: 96.3%, *C. chrysochlora*: 95%, hybrid: 86%; Tab. 3). The hybrid between *C. shahvarica* and *C. decumbens*, but not that between *C. eryngioides* and *C. chrysochlora*, also showed a reduced number of pollen grains (Tab. 3).

Tab. 1. Published *Cousinia* s.s. hybrids (designated with H-) and intermediate forms of possible hybrid origin (designated with I-).

	confirmed or possible parents	nothospecies	evidence	position in tree	position in traditional taxonomy	reference
H-1	<i>C. decumbens</i> Rech. f. <i>C. shahvarica</i> Rech. f.	-	intermediate characters, ITS	between clades	sect. <i>Decumbentes</i> sect. <i>Sphaerocephalae</i>	inter sections current paper
H-2	<i>C. chrysochlora</i> Rech. f. & Koeie <i>C. eryngioides</i> Boiss.	-	intermediate characters, ITS	between clades	sect. <i>Lachnosphaerae</i> sect. <i>Sciadocousinia</i>	inter sections current paper
H-3	<i>C. crispa</i> Jaub. & Spach <i>C. gmelini</i> C. Winkler	<i>C. × kamarbandensis</i> Rech. f.	intermediate characters	within clade	sect. <i>Serratuloides</i> sect. <i>Eriocousinia</i>	inter sections Rechinger 1950
H-4	<i>C. crispa</i> Jaub. & Spach <i>C. sphaerocephala</i> Jaub. & Spach	<i>C. × hybrida</i> Rech. f.	intermediate characters	-	sect. <i>Serratuloides</i> sect. <i>Sphaerocephalae</i>	inter sections Rechinger 1950
H-5	<i>C. behboudiana</i> Rech. f. & Esfand. <i>C. belangeri</i> DC.	<i>C. × mesomorpha</i> Rech. f.	intermediate characters	between clades	sect. <i>Cynaroideae</i> sect. <i>Pugioniferae</i>	inter sections Rechinger 1979
H-6	<i>C. chlorosphaera</i> Bornm. <i>C. orthoclada</i> Hausskn. & Bornm.	<i>C. × subinflata</i> Bornm.	intermediate characters	between clades	sect. <i>Cynaroideae</i> sect. <i>Pugioniferae</i>	inter sections Rechinger 1972
H-7	<i>C. turkestanica</i> (Tegel) Juz. <i>C. scabrida</i> Juz.	-	intermediate characters	-	sect. <i>Cousinia</i> sect. <i>Cousinia</i>	within section Tscherneva 1962
H-8	<i>C. resinosa</i> Juz. <i>C. maracandica</i> Juz.	-	intermediate characters	-	sect. <i>Cousinia</i> sect. <i>Cousinia</i>	within section Tscherneva 1962
H-9	<i>C. coronata</i> Franch. <i>C. microcarpa</i> Boiss.	<i>C. × atripurpurea</i> Juz.	intermediate characters	within clade	sect. <i>Coronophora</i> sect. <i>Microcarpae</i>	inter sections Tscherneva 1962
H-10	<i>C. radians</i> Bunge <i>C. microcarpa</i> Boiss.	<i>C. × paraatripurpurea</i> Kamelin	intermediate characters	within clade	sect. <i>Coronophora</i> sect. <i>Microcarpae</i>	inter sections Kamelin 1973
H-11	<i>C. alpestris</i> Bornm. <i>C. submutica</i> Franch.	<i>C. × heteromorpha</i> Bornm.	intermediate characters	-	sect. <i>Coronophora</i> sect. <i>Jurineopsis</i>	inter sections Tscherneva 1962
H-12	<i>C. alpina</i> Bunge <i>C. submutica</i> Franch.	<i>C. × iskanderi</i> Bornm.	intermediate characters	-	sect. <i>Carduncellus</i> sect. <i>Jurineopsis</i>	inter sections Tscherneva 1962
H-13	<i>C. microcarpa</i> Boiss. <i>C. submutica</i> Franch.	-	intermediate characters	-	sect. <i>Microcarpae</i> sect. <i>Jurineopsis</i>	inter sections Tscherneva 1962
H-14	<i>C. outichaschensis</i> Franch. <i>C. microcarpa</i> Boiss.	-	intermediate characters	-	sect. <i>Carduncellus</i> sect. <i>Microcarpae</i>	inter sections Tscherneva 1962
H-15	<i>C. outichaschensis</i> Franch. <i>C. pulchella</i> Bunge	<i>C. × heterogenetos</i> Bornm.	intermediate characters	-	sect. <i>Carduncellus</i> sect. <i>Pulchellae</i>	inter sections Tscherneva 1962
H-16	<i>C. microcarpa</i> Boiss. <i>C. pulchella</i> Bunge	-	intermediate characters	within clade	sect. <i>Microcarpae</i> sect. <i>Pulchellae</i>	inter sections Tscherneva 1962
H-17	<i>C. microcarpa</i> Boiss. <i>C. sewertzowii</i> Regel	-	intermediate characters	within clade	sect. <i>Microcarpae</i> sect. <i>Pulchellae</i>	inter sections Tscherneva 1962

H-18	<i>C. ninae</i> Juz.	<i>C. × cana</i> Juz.	intermediate characters	within clade	sect. <i>Microcarpae</i>	inter sections	Tscherneva 1962
	<i>C. sewertzowii</i> Regel				sect. <i>Pulchellae</i>		
H-19	<i>C. jassyensis</i> C. Winkl.	-	intermediate characters	within clade	sect. <i>Jurineopsis</i>	inter sections	Tscherneva 1962
	<i>C. ninae</i> Juz.				sect. <i>Microcarpae</i>		
H-20	<i>C. xanthina</i> Bornm.	-	intermediate characters	-	sect. <i>Alpinae</i>	within section	Tscherneva 1962
	<i>C. laetevirens</i> C. Winkl.				sect. <i>Alpinae</i>		
H-21	<i>C. trichophora</i> Kult.	-	intermediate characters	-	sect. <i>Alpinae</i>	within section	Tscherneva 1962
	<i>C. newesskyana</i> C. Winkl.				sect. <i>Alpinae</i>		
H-22	<i>C. verticillaris</i> Bunge	-	intermediate characters	-	sect. <i>Alpinae</i>	within section	Tscherneva 1962
	<i>C. laetevirens</i> C. Winkl.				sect. <i>Alpinae</i>		
H-23	<i>C. myrioglochis</i> Rech. f.	-	intermediate characters	-	sect. <i>Alpinae</i>	within section	Rechinger 1972
	<i>C. kataghanica</i> Rech. f.				sect. <i>Alpinae</i>		
H-24	<i>C. ramulosa</i> Rech. f.	-	intermediate characters	-	sect. <i>Alpinae</i>	within section	Rechinger 1972
	<i>C. schugnanica</i> Juz.				sect. <i>Alpinae</i>		
H-25	<i>C. auriculata</i> Boiss.	-	intermediate characters	within clade	sect. <i>Eriocousinia</i>	within section	Rechinger 1972
	<i>C. chionophila</i> Rech. f.				sect. <i>Eriocousinia</i>		
H-26	<i>C. urumiensis</i> Bornm.	-	intermediate characters	within clade	sect. <i>Cousinia</i>	within section	Rechinger 1972
	<i>C. tenuifolia</i> C. A. Mey.				sect. <i>Cousinia</i>		
H-27	<i>C. aggregata</i> DC.	-	intermediate characters	-	sect. <i>Stenocephalae</i>	within section	Rechinger 1972
	<i>C. cylindracea</i> Boiss.				sect. <i>Stenocephalae</i>		
H-28	<i>C. ecbatanensis</i> Bornm.	-	intermediate characters	-	sect. <i>Cynaroideae</i>	within section	Rechinger 1972
	<i>C. kopi-karadaghensis</i> Rech. f. or				sect. <i>Cynaroideae</i>		
	<i>C. inflata</i> Boiss. & Hauskn.						
I-1	<i>C. hypopolia</i> Bornm.	-	intermediate characters	-	sect. <i>Stenocephalae</i>	within section	Tscherneva 1962
	<i>C. albiflora</i> (Bornm. & Sient.) Bornm.				sect. <i>Stenocephalae</i>		
I-2	<i>C. oxiana</i> Tschern.	-	intermediate characters	within clade	sect. <i>Chrysoptera</i>	within section	Tscherneva 1962
	<i>C. turkmenorum</i> Bornm.				sect. <i>Chrysoptera</i>		
I-3	<i>C. lomakinii</i> C. Winkl.	-	intermediate characters	-	sect. <i>Cousinia</i>	within section	Tscherneva 1962
	<i>C. erivanensis</i> Bornm.				sect. <i>Cousinia</i>		
I-4	<i>C. fetissowii</i> C. Winkl.	-	intermediate characters	-	sect. <i>Carduncellus</i>	within section	Tscherneva 1962
	<i>C. schischkinii</i> Juz.				sect. <i>Carduncellus</i>		
I-5	<i>C. verticillaris</i> Bunge	-	intermediate characters	-	sect. <i>Alpinae</i>	within section	Rechinger 1972
	<i>C. blepharobasis</i> Rech. f. & Gilli				sect. <i>Alpinae</i>		

I-6	<i>C. heterophylla</i> Boiss.	-	intermediate characters	-	sect. <i>Lapidae</i>	within section	Rechinger 1972
	<i>C. miserabilis</i> Rech. f.				sect. <i>Lapidae</i>		
I-7	<i>C. lachnosphaera</i> Bunge	-	intermediate characters	between clades	sect. <i>Lachnosphaerae</i>	within section	Rechinger 1972
	<i>C. myriolepis</i> Rech. f.				sect. <i>Lachnosphaerae</i>		
I-8	<i>C. polyneura</i> Rech. f.	-	intermediate characters	between clades	sect. <i>Eriocousinia</i>	inter sections	Rechinger 1972
	<i>C. multiloba</i> DC.				sect. <i>Alpinae</i>		
I-9	<i>C. carduchorum</i> C. Winkl. & Bornm.	-	intermediate characters	-	sect. <i>Cynaroideae</i>	within section	Rechinger 1972
	<i>C. algurdina</i> Rech. f.				sect. <i>Cynaroideae</i>		
I-10	<i>C. macrolepis</i> Boiss. & Hausskn.	-	intermediate characters	-	sect. <i>Cynaroideae</i>	within section	Rechinger 1972
	<i>C. phyllocephala</i> Bornm. & Gauba				sect. <i>Cynaroideae</i>		
I-11	<i>C. odontolepis</i> DC.	-	intermediate characters	-	sect. <i>Cynaroideae</i>	within section	Rechinger 1972
	<i>C. leatherdalei</i> Rech. f.				sect. <i>Cynaroideae</i>		

A 50% majority rule consensus tree from the Bayesian analysis of the ITS data set is shown in Fig. 2. Posterior probabilities (PP) are given above branches. This analysis of the ITS region supports previous studies and confirms the monophyly of the group and shows a clear subdivision into an Arctioid group (*Arctium*, *Cousinia* subgg. *Cynaroides* and *Hypacanthodes*, *Hypacanthium*, *Schmalhausenia*) and a Cousinioid group (*Cousinia* subg. *Cousinia*). Relationships among species in the Cousinioid clade are essentially unresolved. Phylogenetic relationships within the *Arctium-Cousinia* complex have been discussed in detail by López-Vinyallonga et al. (in press).

The position of suspected or conclusively identified hybrid parents in the phylogenetic tree is indicated (Fig. 2). Hybrids or intermediate forms result from parents of both the same and different sections following the traditional system of the genus (Tab. 1), and from parents of the same and of different clades in our phylogeny (Fig. 2). Seventeen of the reported 28 hybrids are suspected or known (H1, H2) to have parents belonging to different sections of *Cousinia* s.s., and, as far as species were included in our ITS analysis, four hybrids are known (H1, H2) or suspected to have parents belonging into different clades, and nine hybrids to have parents which belong into the same clade (Tab. 1). All but one of the intermediate forms refer to species of the same section, but two of the species pairs for which intermediate forms have been reported fall into different clades. Neither hybrids between *Cousinia* s.s. and other main clades of the '*Arctium-Cousinia* complex' nor between annual and perennial species of *Cousinia* s.s. have been reported.

3.5 DISCUSSION

Our results, particularly those related to the two hybrids identified by ourselves, clearly show that hybridization in *Cousinia* is possible. These two hybrids have parents which belong to different sections and to different clades in our phylogeny (Tab. 1, Fig. 2). This picture is supported by hybrid combinations reported in the literature, which involve species belonging to the same and different sections and to the same and different clades. As regards exact phylogenetic relationships in those instances where hybrid parents belong to different clades, the basally largely unresolved topology of *Cousinia* s.s. does not allow us to draw any firm conclusions. Our results also show that those hybrids which could be examined in detail show reduced pollen fertility, indicating the presence of postzygotic reproductive barriers. The major radiation of *Cousinia* s.s. has been estimated to have started ca. seven million years ago (López-Vinyallonga et al. submitted). Although divergence times between different parental species are not known and can not be estimated, the observation of postzygotic reproductive barriers, probably a by-product of divergent evolution, perhaps is not surprising in any way considering the age of the entire group.

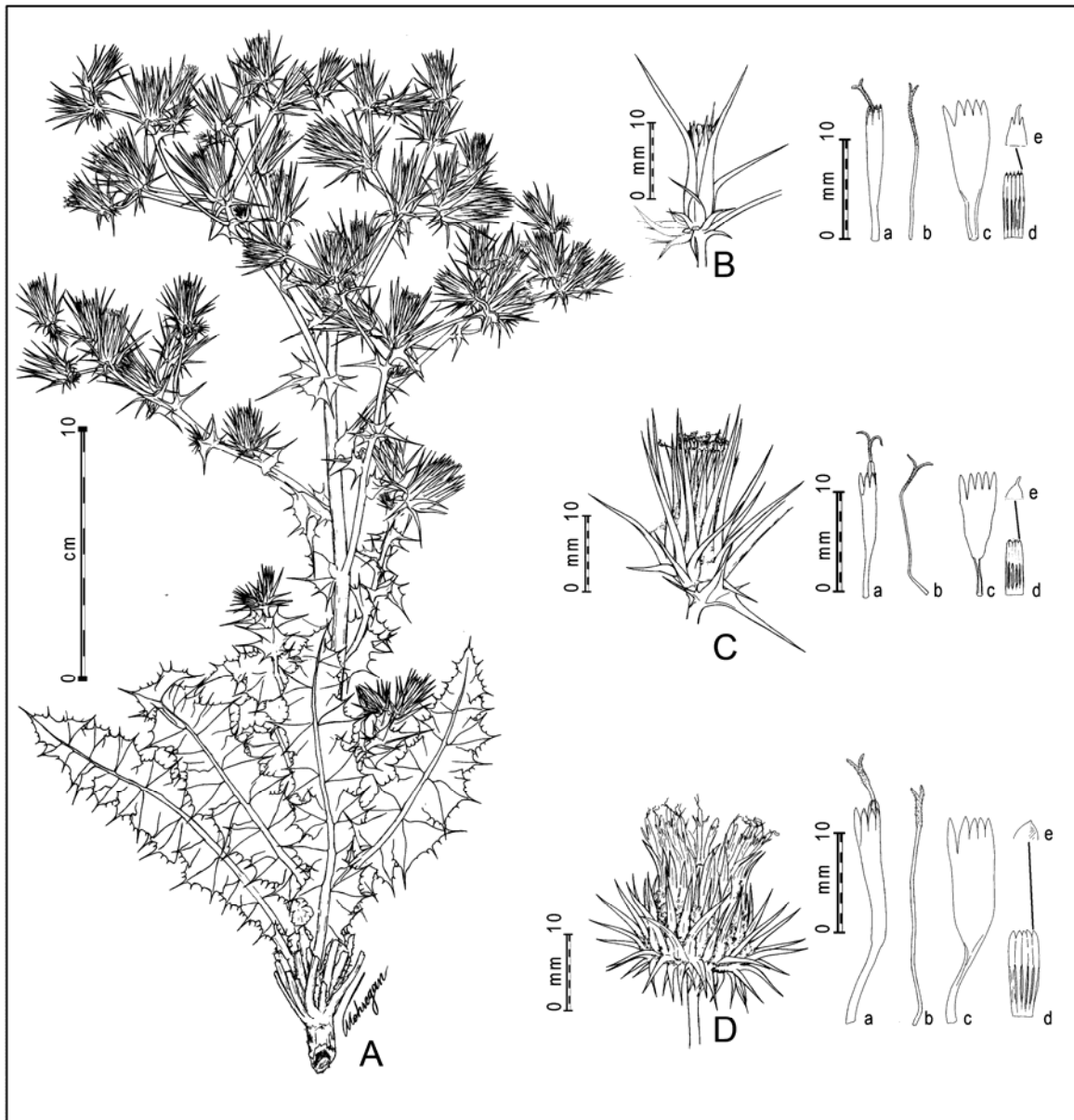


Fig. 1. Morphological intermediacy of the hybrid between *C. eryngioides* and *C. chrysochlora*; A. Habit of *C. eryngioides* x *chrysochlora*. Capitulum and flower morphology of B. *C. eryngioides*, C. *C. eryngioides* x *chrysochlora*, D. *C. chrysochlora*. (a. flower. b. style. c. opened and flattened corolla. d. opened anther tube. e. anther apex).

Tab. 2. ITS positions showing sequence additivity in the hybrids between *C. eryngioides* and *C. chrysochlora* and *C. shahvarica* and *C. decumbens*.

<i>species or hybrid</i>	<i>nucleotide position</i>																				
	4	5	6	8	8	1	1	1	1	2	2	2	2	3	3	3	4	4	4	4	
	5	1	8	0	1	1	2	4	8	0	0	2	8	9	0	0	0	1	6	6	6
					4	0	1	9	6	7	2	8	0	4	7	8	3	2	3	4	
<i>C. eryngioides</i>	C	G	Y	C	T	C	A	T	C	Y	Y	T	Y	G	T	C	T	Y	T	G	Y
hybrid	Y	S	Y	Y	Y	Y	R	Y	M	Y	Y	Y	Y	K	Y	Y	Y	Y	Y	K	Y
<i>C. chrysochlora</i>	Y	C	C	T	C	Y	G	C	A	T	C	C	Y	K	C	T	C	Y	C	T	T
	9	1	1	1	1	1	1	2	2	2	3	3	3	3	4	4	4	4	4	4	4
	1	0	2	2	3	4	9	7	8	9	0	0	4	9	4	4	4	5	6	6	7
		4	1	7	8	3	8	4	7	1	7	8	1	7	0	1	4	2	2	4	0
<i>C. shahvarica</i>	C	G	G	T	G	G	A	C	T	T	C	T	C	C	C	A	G	T	Y	C	T
hybrid	Y	R	R	Y	R	R	R	Y	Y	Y	Y	Y	Y	N	Y	R	R	Y	Y	Y	Y
<i>C. decumbens</i>	T	A	A	C	A	A	G	Y	C	C	T	C	T	A	T	G	A	C	C	T	C

Tab. 3. Number of pollen grains per flower and percentage of fertile pollens (pollen fertility) in *C. eryngioides*, *C. chrysochlora*, *C. shahvarica* and *C. decumbens* and their hybrids.

<i>Species/hybrid</i>	<i>no. of pollen grains per flower (x 10³)</i>	<i>pollen fertility (%)</i>
<i>C. shavarica</i>	9.1	95.4
<i>C. shahvarica</i> x <i>C. decumbens</i>	4.4	77
<i>C. decumbens</i>	11.6	92.3
<i>C. eryngioides</i>	7	96.3
<i>C. eryngioides</i> x <i>C. chrysochlora</i>	6.2	86
<i>C. chrysochlora</i>	5.4	95

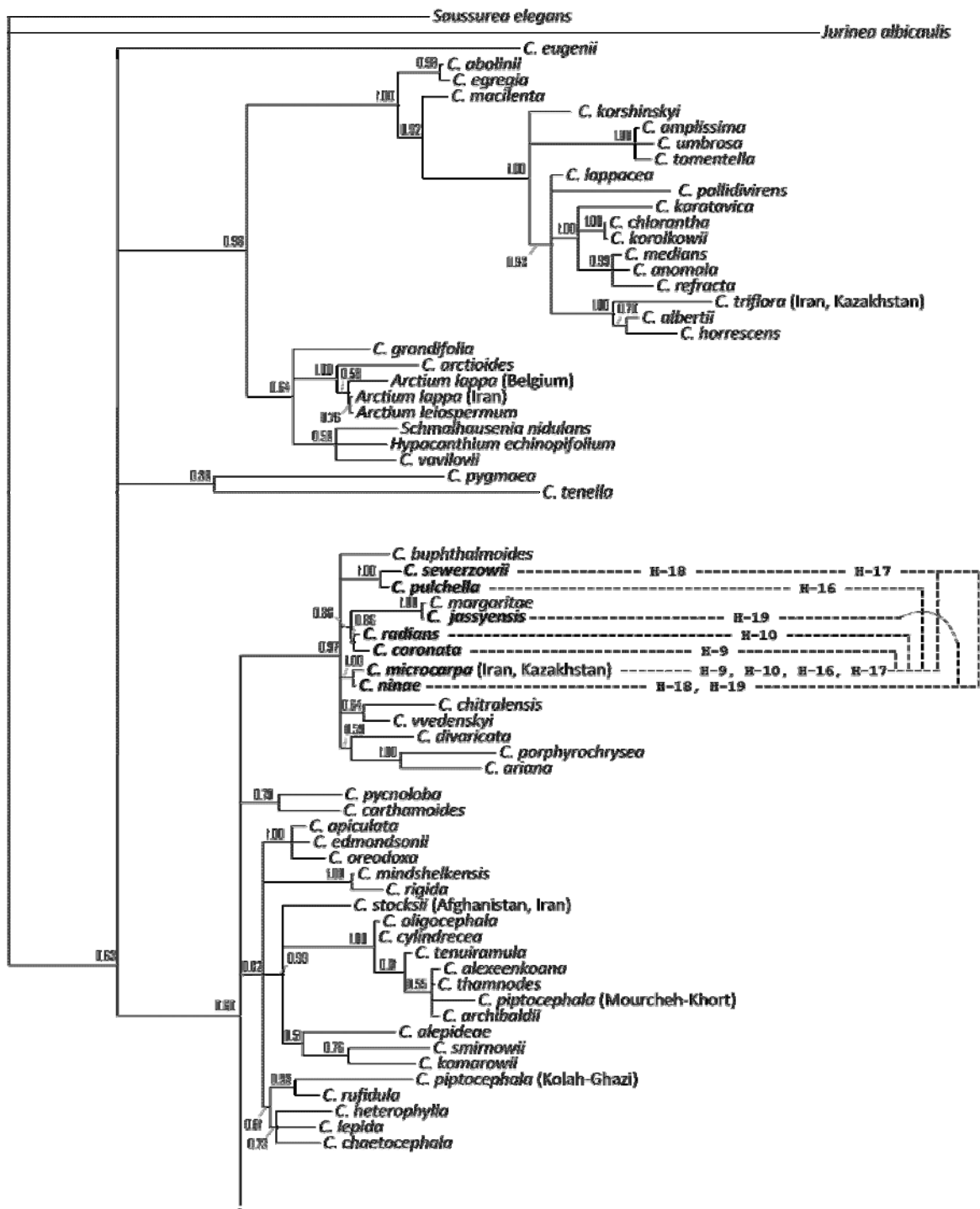


Fig. 2. 50% majority rule consensus tree from the Bayesian analysis of the ITS data set. Posterior probabilities (PP) are given above branches. The positions in the phylogenetic tree of suspected or conclusively identified hybrid parents are indicated by lines. The numbers above lines refer to hybrids or intermediate forms compiled in Tab. 1.

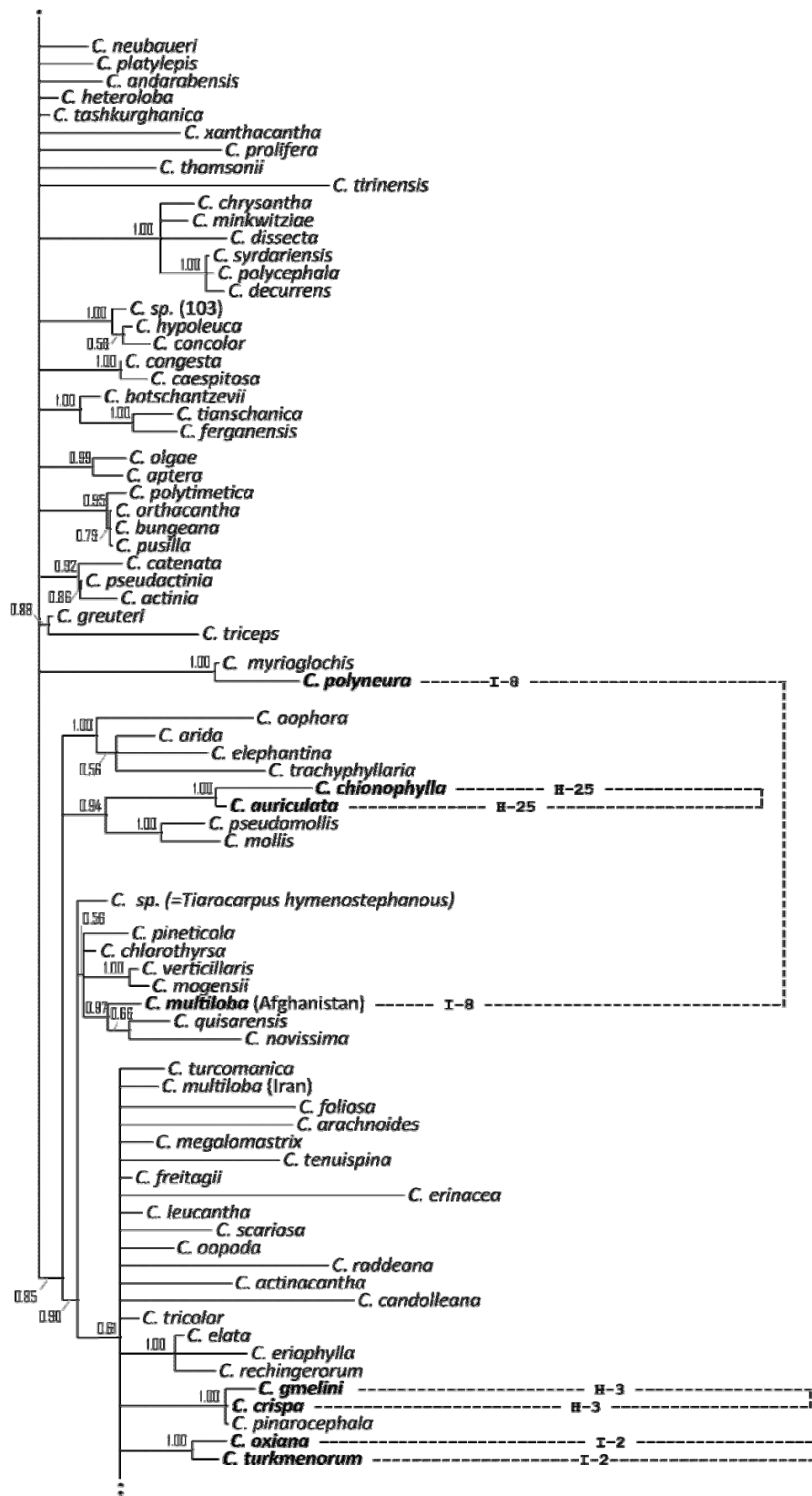


Fig. 2. ... continued from previous page.

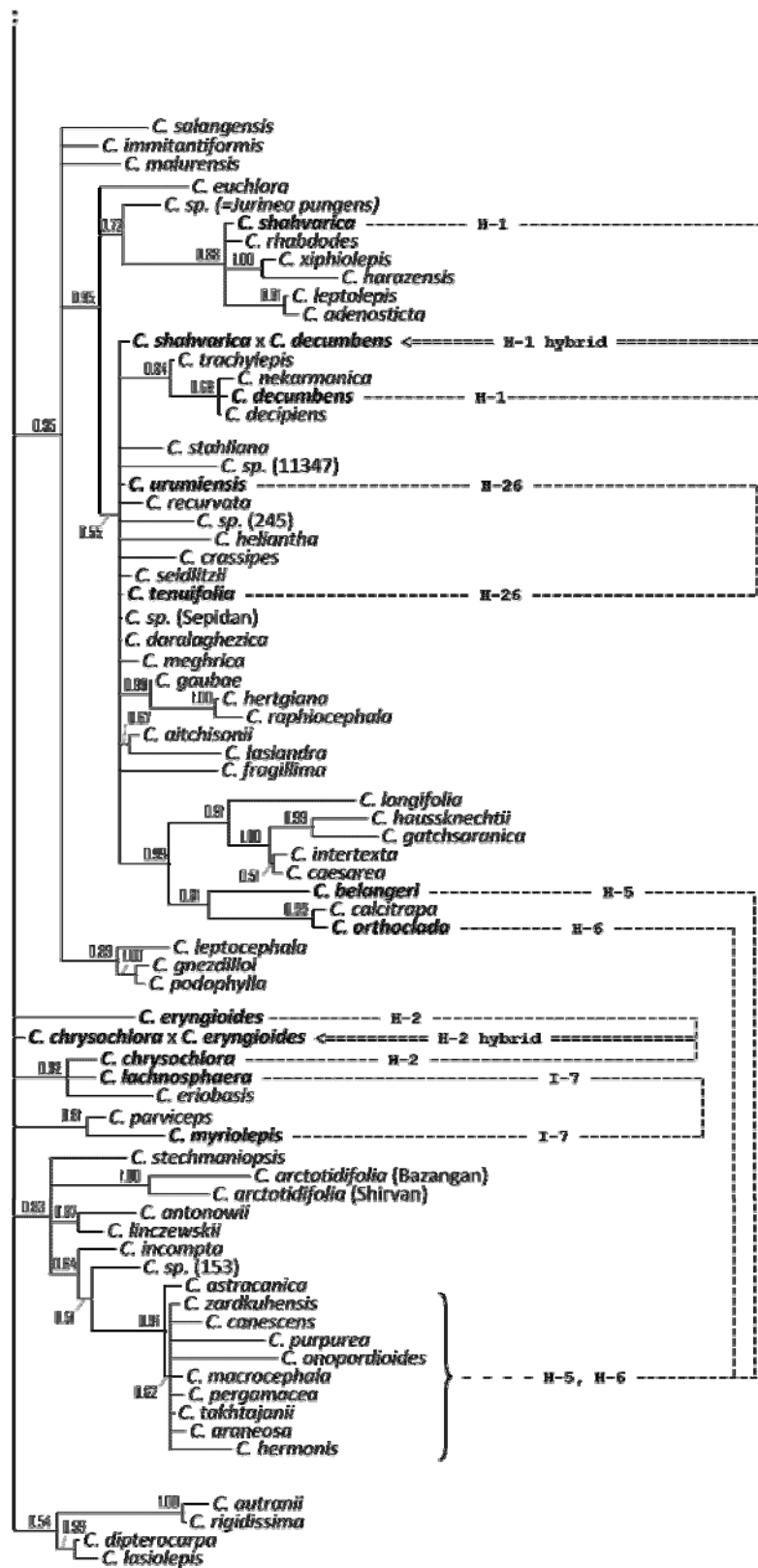


Fig. 2. ... continued from previous page.

In case all reported hybrids should have been correctly identified, and the intermediate forms reported should also be hybrids, altogether 64 of ca. 600 species of *Cousinia* s.s., i.e. ca. 10.7 %, are involved in interspecific hybridization. If this count is limited to only the 28 hybrids reported, the number of species involved is 42 or ca. 7 %. Both figures are more or less the same as those average figures across different floras reported by Ellstrand et al. (1996), but much lower than those found in Asteraceae and Cardueae of the British Isles or found in *Arctium* s.s. by Duistermaat (1996). *Cousinia* s.s. is a large group of often rather similar and partly not well-known species, and the figures presented here may be either over- or underestimates. If the estimated frequency of hybrids should be correct, however, it would illustrate that interspecific hybridization is not more frequent in this group than expected from average values, and substantially less frequent than in Asteraceae and Cardueae in the British Isles.

In *Cousinia* the chromosome numbers of 148 species have been determined (<http://www-asteraceae.cla.kobe-u.ac.jp/search.html>), and not a single polyploid chromosome number has been reported to date. As polyploidy probably more often than not arises from allopolyploid hybrid speciation (Levin 2002), the apparent absence of polyploids in conjunction with the above observation of average rates of interspecific hybridization may indicate that the role of interspecific hybridization for the evolution and diversity of the group has been minor.

Our ongoing revision of *Cousinia* s.s. sect. *Cynaroideae* (Mehregan & Kadereit in press) indicates that the very large majority of the ca. 30 species of this group are distributed allo- or parapatrically, and that species ranges often are separated by prominent geographical barriers. This, if true for other clades of *Cousinia* s.s., might explain the apparently minor evolutionary role of interspecific hybridization in this taxon, although, as shown above, hybridization between clades is possible.

3.6 ACKNOWLEDGEMENTS

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2.8 APPENDIX 1

List of taxa and their localities included in this study. In some cases the Genebank codes for previously published sequences are given.

Arctium lappa L., Belgium: AF319048, AF319102. *Arctium lappa* L., Iran: NNE, Khorassan, 25 SW Bodjnourd, 1500m, Mehregan 140 (JGM). *Arctium leiospermum* Juz. & C. Serg., Kazakhstan: AY373720, AY373687. *Cousinia abolinii* Kult. ex Tschern., (subg. *Hypacanthodes* Tschern., sect. *Abolinia* Tschern.), Kyrgyzstan: SW, Jalal Abad Oblast, Kara Saj Tal, Aksy Rayan, 1030m, Lazkov s.n. (JE). *Cousinia actinacantha* Rech. f., (subg. *Cousinia*, sect. -), Afghanistan: NW, Fariab, Maimana, 20 km SSE, at road to Sare Hauz, 1100m, Freitag 6693 (KAS). *Cousinia actinia* Boiss., (subg. *Cousinia*, sect. *Actinia* Bunge), Afghanistan: E, Kabul, Korogh Koh, SW of Kabul, 2600m, Freitag 1570 (KAS). *Cousinia adenosticta* Bornm., (subg. *Cousinia*, sect. *Sphaerocephalae* Bunge), Iran: Tehran, Between Shemshak and Dizin, 3000m, Mehregan 165 (JGM). *Cousinia aitchisonii* C. Winkl., (subg. *Cousinia*, sect. *Lasiandrae* Bunge), Afghanistan: W, 70 km WNW Herat, near Tirpul, 780m, Freitag 5461 (KAS). *Cousinia albertii* Regel et Schmalh., (subg. *Cynaroides* Tschern., sect. *Pectinatae* C. Winkl.), Kazakhstan: AY373721, AY373688. *Cousinia alepideae* Boiss., (subg. *Cousinia*, sect. *Lasiandrae* Bunge), Afghanistan: SW, Ghazni, Jamroud, 45 km SW of Ghazni, 2010m, Freitag 2008 (KAS). *Cousinia alexeenkoana* Bornm., (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: C, Isfahan, 10 km from Khaansaar to Boein, 2500 m, Mehregan 132 (JGM). *Cousinia amplissima* (Boiss.) Boiss., (subg. *Cynaroides* Tschern., sect. *Pseudarctium* Juz.), Iran: CSW, Dena, 15 km from Meimand to Yassoudj, 2500m, Mehregan 174 (JGM). *Cousinia andarabensis* Rech. f., (subg. *Cousinia*, sect. -), Afghanistan: NE, Baghlan, Mittleres Andarab-Tal, Oberes Darreh-i Shahsan, 2600m, Podlech 11984 (M). *Cousinia anomala* Franch., (subg. *Cynaroides* Tschern., sect. *Ctenarctium* Juz.), Tajikistan: Slopes above Voru, about 300 m above Kishlak, 2200-2300 m, Susanna 2521 (BC). *Cousinia antonowii* C. Winkl., (subg. *Cousinia*, sect. *Leiocaules* Bunge), Iran: NE, Khorassan, 10 km from Tivan to Bajgiran, 1590m, Mehregan 196 (JGM). *Cousinia apiculata* Tschern., (subg. *Cousinia*, sect. *Pseudactinia* Tschern.), Iran: NE, Khorassan, Shirvan, Sarani, 2300m, Ghahreman et al. TUH-27664 (JGM). *Cousinia aptera* Aitch. & Hemsl., (subg. *Cousinia*, sect. *Olgaeanthe* Tschern.), Afghanistan: C, Ghazni, Upper Sari Ab Valley, 44 km NW of Ghazni, 2780m, Freitag 1408 (KAS). *Cousinia arachnoides* Fisch. & C. A. Mey., (subg. *Cousinia*, sect. *Microcarpae* Bunge), Kazakhstan: AY373722, AY373689. *Cousinia araneosa* DC., (subg. *Cousinia*, sect. *Cynaroideae* Bunge), Iran: Hamedan, Alvand mnt., 10 km from Hamedan to Toiserkan, Ganjnameh Valley, 2400m, Mehregan 219 (JGM). *Cousinia archibaldii* Rech. f., (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: Nahavand to Malayer, 28 km S of Nahavand, Kouhaye Garrow, 1800 - 2400 m, Terme & Moussavi 33893-E (IRAN). *Cousinia arctioides* Schrenk., (subg. *Cynaroides* Tschern., sect. *Nanarctium* (Juz. ex.) Tschern.), Kazakhstan: Dzhezkazganskaya reg., Turgajskaya lowland, 49 km to SW from Dzhezkazgana, right bank of Kumula river, Tamarix bushland, Kamelin 6434 (LE). *Cousinia arctotidifolia* Bunge, (subg. *Cousinia*, sect. *Leiocaules* Bunge), Iran: NE, Khorassan, Inter Mashhad and Sarakhs, Bazangan lake, 750m, Mehregan 119 (JGM). *Cousinia arctotidifolia* Bunge, (subg. *Cousinia*, sect. *Leiocaules* Bunge), Iran: NE, Khorassan, Shirvan, 10 km from Ziarat to Lojelli, 1215m, Mehregan 120 (JGM). *Cousinia ariana* Bornm., (subg. *Cousinia*, sect. *Carduncellus* (Juz.) Rech. f.), Afghanistan: E, Kanul, N Salang, 3150m, Freitag 3494 (KAS). *Cousinia arida* C. Winkl., (subg. *Cousinia*, sect. *Neurocentrae* Bunge), Afghanistan: Herat, 70 km WNW, near Torpul, 780m, Freitag 5455 (KAS). *Cousinia astracanica* (Spreng.) Tamamsch., (subg. *Cousinia*, sect. *Leiocaules* Bunge), Kazakhstan: AY373723, AY373690. *Cousinia auriculata* Boiss., (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Afghanistan: E, Parvan, Ghowrband, Sorkh-Parsa, 2050m, Freitag 1128 (KAS). *Cousinia autranii* C. Winkl., (subg. *Cousinia*, sect. *Rigidissimae* Rech. f.), Afghanistan: W, Herat, Ghorat, Bande Frasi, 15 km SSE Farsi, 2400-2500m, Freitag 6831 (KAS). *Cousinia belangeri* DC., (subg. *Cousinia*, sect. *Pugioniferae* Bunge), Iran: N, Tehran, 15 km to Karaj, 1200m, Mehregan s.n. (JGM). *Cousinia botschantzevii* Juz. ex Tschern., (subg. *Cousinia*, sect. *Regelianae* (Juz.) Tschern.), Uzbekistan: Kuramit mount., Koitash range, south slope above the Koitash village, 1850 m, Kamelin 29 (LE). *Cousinia bungeana* Regel & Schmalh., (subg. *Cousinia*, sect. *Dichotomae* Bunge), Sine loc.: Ovczinnikov 16104 (TAD). *Cousinia bupthalmoides* Regel, (subg. *Cousinia*, sect. *Carduncellus* (Juz.) Rech. f.), Afghanistan: Unai-Pass, E side, 3050m, Freitag 6268 (KAS). *Cousinia caesarea* Boiss. & Bal., (subg. *Cousinia*, sect. *Cousinia*), Turkey: Sivas, Kangal-Sincan, 58km E Kangal, 1280m, Nydegger 17136 (M). *Cousinia caespitosa* C. Winkl., (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Kazakhstan: AY373724, AY373691. *Cousinia calcitrapa* Boiss., (subg. *Cousinia*, sect. *Pugioniferae* Bunge), Iran: CSW, Fars, Pass inter Sepidan and Yassoudj, 20 km from Sepidan, 2400m, Mehregan 203 (JGM). *Cousinia*

candolleana Jaub. & Spach, (subg. *Cousinia*, sect. *Myriotomae* Rech. f.), Iran: C, Ghazvin, 10 km from Abgarm to Avadj, 1950m, Mehregan 239 (JGM). *Cousinia canescens* DC., (subg. *Cousinia*, sect. *Cynaroideae* Bunge, Iran: NW AF319068, AY319122. *Cousinia carthamoides* Aitch. & Hemsl., (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Afghanistan: E, Paktia, Jaji, W side of Shotor Gardan Pass, 2950m, Freitag 5737 (KAS). *Cousinia catenata* Rech. f., (subg. *Cousinia*, sect. *Actinia* Bunge), Afghanistan: N, Sar-Pol, Sangcharak, SE Sar-e-Pol, 10 km S, Darreh Angoshte Shah, 1330m, Freitag 6565 (KAS). *Cousinia chaetocephala* Tschern., (subg. *Cousinia*, sect. -), Iran: NE, Khorassan, Tchenaran, 3km from Meritchehan to Radekan, 1500m, Mehregan 115 (JGM). *Cousinia chionophylla* Rech. & Koeie, (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Afghanistan: SE, Ghazni, Mnts. SE of Dashti Nawor (Sperlu Buli), 3850m, Freitag 1478 (KAS). *Cousinia chitralensis* Rech. f., (subg. *Cousinia*, sect. -), Afghansitan: NE, Badakhshan, Wakhan, Darya-e Ptukh Tal, 3400m, Anders 7248 (M). *Cousinia chlorantha* Kult., (subg. *Cynaroides* Tschern., sect. *Chrysis* Juz.), Uzbekistan: Malguzar mount., south slope, by Tashkesken "say", Kamelin 199 (LE). *Cousinia chlorothyrsa* Rech. f. & Koeie, (subg. *Cousinia*, sect. *Racemosae* Rech. f.), Afghanistan: E, Kabul, 12 km WNW, 1950m, Freitag 1983 (KAS). *Cousinia chrysantha* Kult., (subg. *Cousinia*, sect. *Alpinae* Bunge), Kazakhstan: AY373725, AY373692. *Cousinia chrysochlora* Rech. f. & Koeie, (subg. *Cousinia*, sect. *Lachnosphaerae* Rech. f.), Iran: E, Khorassan, 30 km from Sedeh to Asad Abad, Mahousak, 2000m, Mehregan 198 (JGM). *Cousinia chrysochlora* Rech. f. & Koeie x *C. eryngioides* Boiss., (subg. *Cousinia*, hybrid), Iran: E, Khorassan, 30 km from Sedeh to Asad Abad, Mahousak, 2000m, Mehregan 238 (JGM). *Cousinia concolor* Bunge, (subg. *Cousinia*, sect. *Serratuloides* Bunge), Iran: Semnan, Shahroud, S slopes of Shahvar mnt, above Nekarmann, 2500m, Mehregan 158 (JGM). *Cousinia congesta* Bunge, (subg. *Cousinia*, sect. *Congestae* Bunge), Uzbekistan: AY373726, AY373693. *Cousinia coronata* Franch., (subg. *Cousinia*, sect. *Coronophora* (Juz.) Rech. f.), Uzbekistan: AY373727, AY373694. *Cousinia crassipes* Kult., (subg. *Cousinia*, sect. *Homalochaete* C. Winkl.), Iran: NE, Khorassan, Kalat-e Naderi, Ghareh-Sou, 1400m, Mehregan 144 (JGM). *Cousinia crispa* Jaub. & Spach, (subg. *Cousinia*, sect. *Serratuloides* Bunge), Iran: N, Chalous road, 10 km from Kandavan to Chalous, 2000m, Mehregan 185 (JGM). *Cousinia cylindracea* Boiss., (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: CSW, Fars, Inter Shiraz and Sepidan, Shoul pass, 2000m, Mehregan 213 (JGM). *Cousinia daralaghezica* Takht., (subg. *Cousinia*, sect. *Cousinia*), Armenia: Vajots Dzor, Eghegnadzor distr., Eghegnadzor town, Tamanian s.n. (ERE). *Cousinia decipiens* Boiss. & Buhse, (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: NNE, Mazandaran, 50 km S of Kord-Koui, inter Deraznou and Radekan, 2000m, Mehregan 131 (JGM). *Cousinia decumbens* Rech. f., (subg. *Cousinia*, sect. *Decumbentes* Rech. f.), Iran: NNE, Semnan, Shahroud, mnt. Shahvar, SW Slopes, 3600m, Mehregan 110 (JGM). *Cousinia decurrens* Regel, (subg. *Cousinia*, sect. *Congestae* Bunge), Afghanistan: E, Ghazni, 10 km NW, near road to Nawor, 2400m, Freitag 1371 (KAS). *Cousinia dipterocarpa* Bornm. & Rech. f., (subg. *Cousinia*, sect. *Alpinae* Bunge), Iran: Khorassan, 27 km from Ghouchan to Bajgiran, Alam Ali pass, 1820m, Mehregan 167 (JGM). *Cousinia dissecta* Kar. & Kir., (subg. *Cousinia*, sect. *Chrysoptera* Tschern.), Kazakhstan: AY373728, AY373695. *Cousinia divaricata* C. Winkl., (subg. *Cousinia*, sect. *Leiacanthos* Tschern.), Tadjikistan: Darvaz, southern macroslope between villages Zikar and former village Yovgar, Kamelin 656 (LE). *Cousinia edmondsonii* Rech. f., (subg. *Cousinia*, *Pseudactinia* Tschern.), Iran: NNE, Khorassan, Bojnourd, N Slopes of mnt. Kourkhoud, between Zard and Hastan, 2500m, Assadi 101 (JGM). *Cousinia egregia* Juz., (subg. *Hypacanthodes* Tschern., sect. *Abolinia* Tschern.), Uzbekistan: Angren valley, rise to Kamchik pass, rubby slope, Kamelin 420 (LE). *Cousinia elata* Boiss. & Buhse, (subg. *Cousinia*, sect. -), Iran: NE, Khorassan, between Kadkan and Esfiz, 1900m, Mehregan s.n. (JGM). *Cousinia elephantina* Rech. f., (subg. *Cousinia*, sect. *Leiocaules* Bunge), Afghanistan: NW, Between Herat and Karakh, 1300m, Freitag 6809 (KAS). *Cousinia erinacea* Jaub. & Spach, (subg. *Cousinia*, sect. -), Iran: NNW, Guilan, Deylaman, Saeedi 18814 (TUH). *Cousinia eriobasis* Bunge, (subg. *Cousinia*, sect. *Lachnosphaerae* Rech. f.), Iran: AY373729, AY373696. *Cousinia eriophylla* (Kult) Bornm., (subg. *Cousinia*, sect. *Platyacanthae* Rech. f.), Iran: Khorassan, NE, Inter Ghouchan and Bajgiran, 5 km S of Dorbadam, 1500m, Mehregan 190 (JGM). *Cousinia eryngioides* Boiss., (subg. *Cousinia*, sect. *Sciadocousinia* Tschern.), Iran: NE, Khorassan, 50 km from Mashhad to Neishabour, 1500m, Mehregan 168 (JGM). *Cousinia euchlora* Bornm. & Rech. f., (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Iran: ENE, Khorassan, 30 km W of Torbat-e Djam, E slopes of Bezd mnt., 1800m, Mehregan 136 (JGM). *Cousinia eugenii* Kult., (subg. *Cousinia*, sect. *Dichotomae* Bunge), Uzbekistan: E, arenae Kyzylkum, in arenis salsis prope pueum Baskara, Poretzky 4643 (M). *Cousinia ferganensis* Bornm., (subg. *Cousinia*, sect. *Cousinia*), Tadjikistan: Fergana Valley, Ouczinnikov 102, 22.v.1967 (TAD). *Cousinia foliosa* Boiss., (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Turkey: Malatya, Pötürge, 14 km nach Abzweigung gegen Kube Dag, 1680m, Nydegger 17205 (M). *Cousinia fragillima* Rech. f., (subg. *Cousinia*, sect. *Fragillimae* Rech. f.), Iran: Khorassan, Khaur (Khaus ?), 7000 ft., Koelz 16834 (W). *Cousinia freitagii* Rech. f., (subg. *Cousinia*, sect. *Leucocaulon* Tschern.), Afghanistan: N, Baghlan, Kataghan, in valley Ribat (Robatak), inter Pol-e Khumri

and Samnangan, 1410m, Freitag 3147 (KAS). *Cousinia gatchsaranica* Mehregan, Assadi & Attar, (subg. *Cousinia*, sect. *Hausknechtianae* Rech. f.), Iran: SW, Gachsaran, N. slopes of Khami mnt., above Tol Chegah, 2100m, Mehregan 83246 (JGM). *Cousinia gaubae* Bornm., (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: N, Ghazvin, Karadj, in declivibus lapidosis, 1400m, Rechinger 5504 (M). *Cousinia gmelini* C. Winkl., (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Iran: N, Kandevar to Yoush, Djavadi (IRAN). *Cousinia gnezdilloi* Tschern., (subg. *Cousinia*, sect. *Homalochaete* C. Winkl.), Uzbekistan, range Kugitang, near village Hodzha-fil'-ata, gorge Emerdara, Coll. Trans-Caucasian - Middle-Asian group 798 (LE). *Cousinia grandifolia* Kult., (subg. *Hypacanthodes* Tschern., sect. *Amberbopsis* Tschern.), Kazakhstan: AY373730, AY373697. *Cousinia greuteri* Rech. f., (subg. *Cousinia*, sect. *Congestae* Bunge), Afghanistan: N, Robatak pass between Haibak and Pulikhumri, 1400m, Tonchev 2200 (KAS). *Cousinia harazensis* Rech. f., (subg. *Cousinia*, sect. *Sphaerocephalae* Bunge.), Iran: Mazandaran, Haraz road, Rineh, 1900m, Mehregan 175 (JGM). *Cousinia hausknechtii* C. Winkl., (subg. *Cousinia*, sect. *Hausknechtianae* Rech. f.), Iran: W, Kuhe Gerri, Strauss, s.n. (JE). *Cousinia heliantha* Bunge, (subg. *Cousinia*, sect. *Helianthae* Bunge), Iran: Khorassan, 30 km from Sabzevar to Esferaien, 1550m, Mehregan 170 (JGM). *Cousinia hergtiana* Boiss., (subg. *Cousinia*, sect. *Hausknechtianae* Rech. f.), Iran: Isfahan, Mnt. Karkas, from Tameh, 2300m, Mehregan 240 (JGM). *Cousinia hermonis* Boiss., (subg. *Cousinia*, sect. *Cynaroideae* Bunge), Israel: N, Mt. Hermon, 1700 m, Fragmom-Sapir s. n. (dried Achenes, planted at JGM). *Cousinia heteroloba* Rech. f., (subg. *Cousinia*, sect. *Molles* Schrenk.), Afghanistan: NE, Andarab valley below Khinjan, near Ghazan, 1000m, Freitag 3043 (KAS). *Cousinia heterophylla* Boiss., (subg. *Cousinia*, sect. *Lepidae* Bunge), Afghanistan: W, N-Kattawz, between Kotanni-Kotal and Patanna, 2150m, Freitag 3345 (KAS). *Cousinia horrescens* Juz., (subg. *Cynaroides* Tschern., sect. *Pectinatae* C. Winkl.), Kazakhstan: Tian-schan occidentalis, ad declivia saxoso-argillosa secus canalem Bos-su prope pagum Niazbek, Granitov s. n. (TAD). *Cousinia hypoleuca* Boiss., (subg. *Cousinia*, sect. *Serratuloides* Bunge), Iran: Tehran, Inter Firouzkouh and Polur, 5 km W of Lasem, 2500m, Mehregan 177 (JGM). *Cousinia immitantiformis* Rech.f., (subg. *Cousinia*, sect. *Immitantes* Rech. f.), Afghanistan: NW, Sabzak pass, NE Heart, 2400m, Freitag 6784 (KAS). *Cousinia incompta* DC., (subg. *Cousinia*, sect. *Pugioniferae* Bunge), Iran: C, 20 km Borujen to Isfahan, 2400m, Mehregan 128 (JGM). *Cousinia intertexta* Freyn & Sint., (subg. *Cousinia*, sect. *Cousinia*), Turkey: Sivas, Divrigi-Arapkir, 20 km S Divrigi, 1410, Nydegger 17154 (M). *Cousinia jassyensis* C. Winkl., (subg. *Cousinia*, sect. *Jurineopsis* (Juz.) Tschern.), Kyrgyzstan: SW, Jalal Abad Oblast, Toktogul Rayoh, 790m, Martins 872 (JE). *Cousinia karatavica* Regel & Schmalh., (subg. *Cynaroides* Tschern., sect. *Chrysis* Juz.), Kazakhstan: AY373732, AY373699. *Cousinia komarowii* (O. Kuntze) C. Winkl., (subg. *Cousinia*, sect. *Stenoloma* Juz.), Iran: NE, Khorassan, 15 km Bajgiran to Ghouchan, 1700m, Mehregan 156 (JGM). *Cousinia korolkowii* Regel & Schmalh., (subg. *Cynaroides* Tschern., sect. *Chrysis* Juz.), Uzbekistan: North macro-mountainside, Nuratau range, Sintob kishlak surroundings, rocky slopes, Botschantzev 427 (LE). *Cousinia korshinskyi* C. Winkl., (subg. *Hypacanthodes* Tschern., sect. *Lacerae* C. Winkl.), Kirgizstan: Isolated terrain feature Kanka, Upper waters of river Kanka. Near snow pot, h. 2300 m, E.M. Il'ina (LE). *Cousinia lachnosphaera* Bunge, (subg. *Cousinia*, sect. *Lachnosphaerae* Rech. f.), Iran: E, Khorassan, 40 km from Gonabad To Ferdous, 1900m, Mehregan 145 (JGM). *Cousinia lappacea* Schrenk., (subg. *Cynaroides* Tschern., sect. *Lappaceae* Bunge), Kazakhstan: AY373733, AY373700. *Cousinia lasiandra* Bunge, (subg. *Cousinia*, sect. *Lasiandrae* Bunge), Iran: E, Khorassan, 3 km from Doust Abad to Birjand, 1500m, Mehregan 127 (JGM). *Cousinia lasiolepis* Boiss., (subg. *Cousinia*, sect. *Alpinae* Bunge), Iran: CSW, Yasoudj, Dena mnts., Bizhan Pass, 3300m, Mehregan 202 (JGM). *Cousinia lepida* (Bunge ex) Boiss., (subg. *Cousinia*, sect. *Lepidae* Bunge), Iran: NNE, Khorassan, Esferaien, 5 km. Dahaneh Ojagh to Esferajen, 1420m, Mehregan 114 (JGM). *Cousinia leptcephala* Fisch. et C. A. Mey., (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Turkmenistan: W, Krasnovodsk, Inter Basch mygura et Bala-Ischen, Korovin s.n. (B). *Cousinia leptolepis* (Bornm. & Gauba) Rech. f., (subg. *Cousinia*, sect. *Sphaerocephalae* Bunge), Iran: N, Tehran, Karadj, Kuh Dashteh, S slopes, 2200m, Mehregan 111 (JGM). *Cousinia* sp. (11347), (subg. *Cousinia*, sect. *Sphaerocephalae* Bunge), Iraq: N, Kurdistan, Erbil, Mons Helgurd ad confines Persiae, 2000-2600m, Rechinger 11347 (M). *Cousinia leucantha* Bornm. & Sint., (subg. *Cousinia*, sect. *Stenoloma* Juz.), Iran: NNE, Golestan Nat. Park, 12 km ENE of Tange Gol, 1900-2100m, Akhani 11357 (M). *Cousinia linczewskii* Juz., (subg. *Cousinia*, sect. *Leucocaulon* Tschern.), Iran: NE, Khorassan, Inter Mashhad and Sarakhs, Mazd-Avand pass, 1000m, Mehregan 138 (JGM). *Cousinia longifolia* C. Winkl. & Bornm., (subg. *Cousinia*, sect. *Spinuliferae* Rech.f), Iran: SE, Kerman, Laleh zar to Rabor, Attar 226 (JGM). *Cousinia macilenta* C. Winkl., (subg. *Hypacanthodes* Tschern., sect. *Lacerae* C. Winkl.), Tadjikistan: SW, Jugum Hissaricum (Gissar), divorticum aquarum inter flumina Ljuczob et Unou, 3000 m, Zaprojagaev s.n. (M). *Cousinia macrocephala* C. A. Mey., (subg. *Cousinia*, sect. *Cynaroideae* Bunge), Iran: Azerbaijan, Arasbaran, Molouk pass, 1500m, Mehregan 212 (JGM). *Cousinia malurensis* Rech. f., (subg. *Cousinia*, sect. -), Afghanistan: NW, Fariab, Maimana, 45 km S,

mnts. Around Sare hauz, >1700m, Freitag 6721 (KAS). *Cousinia margaritae* Kult., (subg. *Cousinia*, sect. *Jurineopsis* (Juz.) Tschern.), Kyrgyzstan: SW, Talas Oblast, 25 km SW Talas, 1600m, Martins 909 (JE). *Cousinia medians* Juz., (subg. *Cynaroides* Tschern., sect. *Chrysis* Juz.), Uzbekistan: South, Supkhandarbinskaya reg., between kishlaks Sajrob and Shurob, 121-122 km of the road from Termez, Speckled rock outcrops, Botschantzev 240 (LE). *Cousinia megalomatrix* Rech. f., (subg. *Cousinia*, sect. -), Afghanistan: NW, Khesht Pol, between Bale Murghab and Maimana, 800m, M. Amin 6223 (KAS). *Cousinia meghrica* Takht., (subg. *Cousinia*, sect. *Cousinia*), Armenia: Sjunik, Meghri distr., Agarak village, Tamanian s.n. (ERE). *Cousinia microcarpa* Boiss., (subg. *Cousinia*, sect. *Microcarpae* Bunge), Iran: NE, Khorassan, 50 km from Mashhad to Neishabour, 1500m, Mehregan 169 (JGM). *Cousinia microcarpa* Boiss., (subg. *Cousinia*, sect. *Microcarpae* Bunge), Kazakhstan: AY373734, AY373701. *Cousinia mindshelkensis* B. Fedtsch., (subg. *Cousinia*, sect. *Lopholepis* Tschern.), Kazakhstan: S, mnt. Karatan, Rustem-Mazar, Bolchovitina s. n. (M). *Cousinia minkwitziae* Bornm., (subg. *Cousinia*, sect. *Cousinia*), Kazakhstan: AY373735, AY373702. *Cousinia mogensii* Rech. f., (subg. *Cousinia*, sect. *Alpinae* Bunge), Afghanistan: SE, Ghazni, Hajigak-pass, N-side, 3300m, Freitag 6376 (KAS). *Cousinia mollis* Schrenk., (subg. *Cousinia*, sect. *Molles* Schrenk.), Afghanistan: N, Mazar Sharif, in declivibus occidentalibus jugi Shibaghlan, 600m, Rechinger 34270 (M). *Cousinia multiloba* DC., (subg. *Cousinia*, sect. *Alpinae* Bunge), Afghanistan: N, Sar-e Pol, Sangcharak, 40 km SSE, mnts. Above Damardan, 2600-2800m, Freitag 6645 (KAS). *Cousinia multiloba* DC., (subg. *Cousinia*, sect. *Alpinae* Bunge), Iran: NNE, Khorassan, SW Bodjournour, Salouk mnt., 2200m, Mehregan 189 (JGM). *Cousinia myrioglochis* Rech. f., (subg. *Cousinia*, sect. *Alpinae* Bunge), Afghanistan: E, Kabul, upper S Salang valley, >3700m, Freitag 3647 (KAS). *Cousinia myriolepis* Rech. & Koie, (subg. *Cousinia*, sect. *Lachnosphaerae* Rech. f.), Afghanistan: E, Parvan, Ghowrband valley, 49 km W of Charikar bridge, near Pol-i Rango, 1920m, Freitag 1088 (KAS). *Cousinia nekermanica* Rech. f., (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: NNE, Semnan, Shahroud, S slopes of Shahvar mnt, above Nekarmann, 2100m, Mehregan 137 (JGM). *Cousinia neubaueri* Rech. f., (subg. *Cousinia*, sect. -), Afghanistan: C, Bamian, Band-i Amir, Hochfächen, 3000m, Dieterle 896 (M). *Cousinia ninae* Juz., (subg. *Cousinia*, sect. *Microcarpae* Bunge), Kyrgyzstan: Oshskaya, Torgulsky reg., Oitaya area north from Shoporovo vil., speckled soils, Sultanova (LE). *Cousinia novissima* Rech. f., (subg. *Cousinia*, sect. -), Afghanistan: W, Herat, 15 km SSE Farsi, 2400-2700m, Freitag 6822 (KAS). *Cousinia olgae* Regel. & Schmalh., (subg. *Cousinia*, sect. *Olgaeanthae* Tschern.), Iran: Khorassan, 40 km from Torbat-e Djam to Saleh Abad, 1550m, Mehregan 194 (JGM). *Cousinia oligocephala* Boiss., (subg. *Cousinia*, sect. *Albidae* Rech. f.), Iran: CSW, Fars, Inter Shiraz and Sepidan, Shoul pass, 2000m, Mehregan 218 (JGM). *Cousinia onopordioides* Ledeb., (subg. *Cousinia*, sect. *Cynarioideae* Bunge), Iran: AF319070, AF319122. *Cousinia oophora* Rech. f., (subg. *Cousinia*, sect. *Leiocaules* Bunge), Afghanistan: NW, Fariab, Qaisar, 20 km SW mnts. Above Shakh, 1850-2500m, Freitag 6742 (KAS). *Cousinia oopoda* Juz., (subg. *Cousinia*, sect. *Actinia* Bunge), Tadjikistan: South Tadjikistan, west mountainside, Khodzha-Kazjyan range, Koy-Pjez-Tau mount., limestone outcrops, 1240 m, 07. V. 1976, Kinzikaeva 3585 (LE). *Cousinia oreodoxa* Bornm. & Sint., (subg. *Cousinia*, sect. *Pseudactinia* Tschern.), Iran: NE, Khorassan, Inter Bodjournour and Raz, 7 km from Tangeh Torkeman to Ashkhaneh, 1000m, Mehregan 150 (JGM). *Cousinia orthacantha* Tschern., (subg. *Cousinia*, sect. *Dichotomae* Bunge), Afghanistan: N, 20 km E of Mazar-i-Sharif, 330 m, Uotila 16964 (W). *Cousinia orthoclada* Hausskn. & Bornm., (subg. *Cousinia*, sect. *Pugioniferae* Bunge), Iran: CSW, Bakhtiari, Farsan, Dehnou, 10 km from Dehnou to Shahreiarri, 2100m, Mehregan 147 (JGM). *Cousinia oxiana* Tschern., (subg. *Cousinia*, sect. *Chrysoptera* Tschern.), Afghanistan: NW, Herat, 34 km N of Shindand, 1320m, M. Amin 5252 (KAS). *Cousinia pallidivirens* Kult., (subg. *Cynaroides* Tschern., sect. -), Uzbekistan: Sine loc., Botschantzev (LE). *Cousinia parvicipes* Rech. f. & Koie, (subg. *Cousinia*, sect. *Parvicipites* Rech. f.), Afghanistan: C, Ghazni, Bimi Dara-ak Kotal, 50 km WNW of Ghazni, E side near road to Nawor, 2960m, Freitag 1412 (KAS). *Cousinia pergamacea* Boiss. & Hausskn., (subg. *Cousinia*, sect. *Cynarioideae* Bunge), Iran: W, Kurdistan, Mnt. E of Baneh, 2200m, Mehregan 208 (JGM). *Cousinia pinarocephala* Boiss., (subg. *Cousinia*, sect. *Serratuloides* Bunge), Iran: N, Tehran, Firouzkouh, Gadouk pass, 2200m, Mehregan 192 (JGM). *Cousinia pineticola* Rech. f. & Gilli, (subg. *Cousinia*, sect. *Racemosae* Rech. f.), Afghanistan: E, Kabul, Korogh Koh, SW of Kabul, 2600m, Freitag 1568 (KAS). *Cousinia piptocephala* Bunge, (subg. *Cousinia*, sect. *Badghysia* Tschern.), Iran: C, Isfahan, 5km from Mourcheh-Khort to Natanz, 1500m, Mehregan 188 (JGM). *Cousinia piptocephala* Bunge, (subg. *Cousinia*, sect. *Badghysia* Tschern.), Iran: Isfahan, Kolah-Ghazi, AY373736, AY373703. *Cousinia platylepis* Schrenk., (subg. *Cousinia*, sect. *Microcarpae* Bunge), Kazakhstan: AY373737, AY373704. *Cousinia podophylla* Tschern., (subg. *Cousinia*, sect. *Homalochaete* C. Winkl.), Sine loc., Ouchinniku 258 (TAD). *Cousinia polycephala* Rupr., (subg. *Cousinia*, sect. *Cousinia*), Kazakhstan: AY373738, AY373705. *Cousinia polyneura* Rech. f., (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Afghanistan: E, Kabul, Mnts. Above Paghman, 4000m, Freitag 3555 (KAS). *Cousinia polytimetica* Tschern.,

(subg. *Cousinia*, sect. *Dichotomae* Bunge), Uzbekistan: Bukharskaya reg., deserted left bank of Zeravshan river, to SE from Uzliskent vil., Kryakin (LE). ***Cousinia porphyrochrysea* Rech. f.**, (subg. *Cousinia*, sect. *Pulchellae* (Juz.) Rech. f.), Afghanistan: NE, Badakhshan, Yawarzag, 30km S of Qeshm, 500m, Hedge, Wendelbo & Ekberg 9288 (B). ***Cousinia prolifera* Jaub. & Spach**, (subg. *Cousinia*, sect. *Microcousinia* Tschern.), Iran: E, Khorassan, 110 km from Birjand to Ferdous, 1500m, Mehregan 233 (JGM). ***Cousinia pseudactinia* Rech. f.**, (subg. *Cousinia*, sect. *Actinia* Bunge), Afghanistan: N, Samangan, 10 km E, 1200m, Freitag 3159 (KAS). ***Cousinia pseudomollis* C. Winkl.**, (subg. *Cousinia*, sect. *Molles* Schrenk.), Afghanistan: N, Kataghan, Kalate Robatak, NW Pole Khumrie, 1410m, Freitag 3147 (KAS). ***Cousinia pulchella* Bunge**, (subg. *Cousinia*, sect. *Pulchellae* (Juz.) Rech. f.), Afghanistan: NE, Badakhshan, Kuhe Chungar, NW Pole Khumrie, 2000-2400m, Freitag 6497 (KAS). ***Cousinia purpurea* C. A. Mey.**, (subg. *Cousinia*, sect. *Cynaroideae* Bunge), Armenia: AY373739, AY373706. ***Cousinia pusilla* C. Winkl.**, (subg. *Cousinia*, sect. *Dichotomae* Bunge), Tadjikistan: South Tadjikistan, spackled rock mountains to the South from Besharcha mounts to Babatag range, Botschantzev 117 (LE). ***Cousinia pycnoloba* Boiss.**, (subg. *Cousinia*, sect. *Alpinae* Bunge), Afghanistan: E, Paktia, Gardez, SE side of Altimur Kotal, 2600m, Freitag 1611 (KAS). ***Cousinia pygmaea* C. Winkl.**, (subg. *Cousinia*, sect. *Chrysantha* Tschern.), Afghanistan: NE, Kataghan, Baghlan, Dashte Gawar, 700-750m, Tonchev 2230 (KAS). ***Cousinia qaisarensis* Rech. f.**, (subg. *Cousinia*, sect. *Spinuliferae* Rech.f), Afghanistan: NW, Fariab, Maimana, Qaisar, 20 km, mnts. Above Shakh (Gala Shakh), 2200m, Freitag 6745 (KAS). ***Cousinia raddeana* C. Winkl.**, (subg. *Cousinia*, sect. *Hoplophylla* Tschern.), Iran: NE, Khorassan, Mashad, Kalat-Naderi road, Sanganeh, Chahchaheh, 1600m, Ghahreman et al. 27315 (TUH). ***Cousinia radians* Bunge**, (subg. *Cousinia*, sect. *Coronophora* (Juz.) Rech. f.), Iran: NE, Khorassan, 66 km from Mashad to Kalat-Naderi, 1000m, Ghahreman & al 227 (JGM). ***Cousinia raphiocephala* Rech. f.**, (subg. *Cousinia*, sect. *Hausknechtianae* Rech. f.), Iran: C, Isfahan, 12 km NW Muteh, 2150m, Mehregan 88247 (JGM). ***Cousinia rechingerorum* Bornm.**, (subg. *Cousinia*, sect. *Platyacanthae* Rech. f.), Iran: E, Khorassan: 30 km W of Torbat-e Djam, E slopes of Bezd mnt., 2000m, Mehregan 163 (JGM). ***Cousinia recurvata* DC.**, (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: NE, Khorassan, 17 km from Esferaien to Bodjnourd, 1450m, Mehregan 149 (JGM). ***Cousinia refracta* (Bornm.) Juz.**, (subg. *Cynaroides* Tschern., sect. *Chrysis* Juz.), Tadjikistan: Kondara river canyon, Varzowski Rayon reservation, Susanna 2456 (BC). ***Cousinia rhabdodes* Bornm. & Rech. f.**, (subg. *Cousinia*, sect. *Sphaerocephalae* Bunge), Iran: NNE, Semnan, Ahovan pass, 35 km E of Semnan, 2100m, Mehregan 118 (JGM). ***Cousinia rigida* Kult.**, (subg. *Cousinia*, sect. *Lopholepis* Tschern.), Kyrgyzstan: Talasskaya reg., north mountainside of Talassky Alatau, Kur-Bokair canyon, south rocky slope, Popova (LE). ***Cousinia rigidissima* Rech. f.**, (subg. *Cousinia*, sect. *Rigidissimae* Rech. f.), Afghanistan: W, Herat, Ghorat, in summo jugo 5 km S Dahan-e Kaftarkhan ad viam inter Tulak et Farsi, 2350m, Podlech 19193 (M). ***Cousinia rufidula* Bornm.**, (subg. *Cousinia*, sect. *Lepidae* Bunge), Afghanistan: NW, Herat, 10km W, at road to Ziarat Khaje Mollah-e Kohi, 1150m, Freitag 5346 (KAS). ***Cousinia salangensis* Rech. f.**, (subg. *Cousinia*, sect. *Immitantes* Rech. f.), Afghanistan: E, Kabul, S Salang valley, marble area, 2500m, Freitag 3490 (KAS). ***Cousinia* sp. (103)**, (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Iran: NNE, Khorassan, SW Bodjnourd, Salouk mnt., 2400m, Mehregan 103 (JGM). ***Cousinia scariosa* Regel**, (subg. *Cousinia*, sect. *Scariosae* Rech. f.), Afghanistan: N, Sar-e Pol, Sangcharak, 40 km SSW mnts. Above Damdaran, 1900-2500m, Freitag 6594 (KAS). ***Cousinia seidlitzii* Bunge**, (subg. *Cousinia*, sect. *Cousinia*, Iran: Azebaijan, 7 km from Khalkhal to Asalem, 1900m, Mehregan 200 (JGM). ***Cousinia* sp. (Sepidan)**, (subg. *Cousinia*, sect. -), Iran: Fars, Pass inter Sepidan and Yassoudj, 15 km from Sepidan, 2300m, Attar s.n. (JGM). ***Cousinia sewerzowii* Regel**, (subg. *Cousinia*, sect. *Pulchellae* Rech. f.), Kazakhstan: AY373740, AY373707. ***Cousinia shahvarica* Rech. f.**, (subg. *Cousinia*, sect. *Sphaerocephalae* Bunge), Iran: NNE, Semnan, Shahroud, mnt. Shahvar, S Slopes, 3000m, Mehregan 117 (JGM). ***Cousinia shahvarica* Rech. f. x *C. decumbens* Rech. f.**, (subg. *Cousinia*; hybrid), Iran: NNE, Semnan, Shahroud, mnt. Shahvar, SW Slopes, 3600m, Mehregan 244 (JGM). ***Cousinia smirnowii* Trautv.**, (subg. *Cousinia*, sect. *Kopetdagia* Tschern.), Iran: NE, Khorassan, SW Bodjnourd, Salouk mnt., 2300m, Mehregan 152 (JGM). ***Cousinia* sp. (153)**, (subg. *Cousinia*, sect. -), Iran: NE, Khorassan, 80 km from Darreh Gaz to Ghoutchan, 2100m, Mehregan 153 (JGM). ***Cousinia* sp. (245)**, (subg. *Cousinia*, sect. *Hausknechtianae* Rech. f.), Iran: C, Arak, Komijan, Kuh-e Ghalanje, 2500m, Mehregan 245 (JGM). ***Cousinia* sp. (=Jurenia pungens Boiss.)**, (subg. *Cousinia*, sect. -), Iran: Khorassan, the pass inter Fariman ad Zharf, 2200m, Mehregan s.n. (JGM). ***Cousinia* sp. (=Tiarocarpus hymenostephanous Rech. f.)**, (subg. *Cousinia*, sect. -), Afghanistan: W, Herat, Band-e Farsi, 10 SW Farsi, 3200m, Freitag 6841 (KAS). ***Cousinia stahljana* Bornm. & Gauba**, (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: Khorassan, Shirvan, 10 km from Ziarat to Lojelli, 1215m, Mehregan 121 (JGM). ***Cousinia stechmaniopsis* Rech. f.**, (subg. *Cousinia*, sect. *Badghysia* Tschern.), Afghanistan: NW, Badghys, 20 km W of Gulran, 900m, Freitag 5626a (KAS). ***Cousinia stocksii* C.Winkl.**, (subg. *Cousinia*, sect. *Stocksianae*

Rech. f.), Afghanistan: W, Farah, Schucht, 1 km nördlich Hakumate Purchaman, 1880m, Podlech 21787 (M). ***Cousinia stocksii* C. Winkl.**, (subg. *Cousinia*, sect. *Stocksianae* Rech. f.), Iran: S, Baft, Rabor to Saruieh, before Geluchar, 2400 m, Ghahreman et al. 28618 (TUH). ***Cousinia syrdariensis* Kult.**, (subg. *Cousinia*, sect. *Cousinia*), Kazakhstan: AY373741, AY373708. ***Cousinia takhtajanii* Tamanyan**, (subg. *Cousinia*, sect. *Cynaroideae* Bunge), Armenia: Sjunik province, Kapan district, N Kapan, ca. 0.5 km E of Jeritzavank, 46° 29' 28" E, 39° 16' 53", 1650 m, Vitek et al. 04-0991 (JGM). ***Cousinia tashkurghanica* Rech. f.**, (subg. *Cousinia*, sect. *Actinia* Bunge), Afghanistan: N, Mazar Sharif, Tang-e Sayyad, S of Tashkurghan, 600m, Freitag 3905 (KAS). ***Cousinia tenella* Fisch. & C. A. Mey.**, (subg. *Cousinia*, sect. *Tenellae* Bunge), Iran: NNE, Golestan Nat. Park, between Sharlegh and Cheshmeh Khan, Akhani 243 (JGM). ***Cousinia tenuifolia* C. A. Mey.**, (subg. *Cousinia*, sect. *Cousinia*), Iran: NW, Azerbaijan, 10 km from Sarab to Ardebil, 1400m, Mehregan 186 (JGM). ***Cousinia tenuiramula* Rech. f.**, (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: C, Bakhtiari, Rokh pass, 2200m, Mehregan 206 (JGM). ***Cousinia tenuispina* Rech. f.**, (subg. *Cousinia*, sect. *Parvicipites* Rech. f.), Afghanistan: C, Bamian, Near Bande amir, 3000m, Japanese Mycologist 7045 (KAS). ***Cousinia thamnodes* Boiss. & Hausskn.**, (subg. *Cousinia*, sect. *Stenocephalae* Bunge), Iran: SW, Gachsaran, Khami mnt., above Tol Chegah, 3170m, Mehregan 237 (JGM). ***Cousinia thomsonii* Clarke**, (subg. *Cousinia*, sect. *Alpinae* Bunge), Pakistan: Chitral, Golen (Krui Uts), 36° 1' N, 72° 10' E, 13000 ft., Lyon 133 (W). ***Cousinia tianschanica* Kult.**, (subg. *Cousinia*, sect. *Carduncellus* (Juz.) Rech. f.), Kazakhstan: AY373743, AY373710. ***Cousinia tirinensis* Rech. f.**, (subg. *Cousinia*, sect. *Pugioniferae* Bunge), Afghanistan: C, Orozgan, 5 km NE Faramoz, in road from Orozgan to Malestan, 2150m, Podlech 31699 (M). ***Cousinia tomentella* C. Winkl.**, (subg. *Cynaroides* Tschern., sect. *Pseudarctium* Juz.), Tadjikistan: South mountainside of Guissar Range, left bank of Varzob river, Deamalik kishlak surroundings, 1800 m, Tschukavina 10512 (LE). ***Cousinia trachylepis* Bunge**, (subg. *Cousinia*, sect. *Badghysia* Tschern.), Iran: NNE, Semnan, 10 km from Shahroud to Semnan, 1000m, Mehregan 214 (JGM). ***Cousinia trachyphyllaria* Bornm. & Rech. f.**, (subg. *Cousinia*, sect. *Platyacanthae* Rech. f.), Iran: NE, Khorassan, Neishabour, Khorw, 2100m, Mehregan 217 (JGM). ***Cousinia triceps* Kult.**, (subg. *Cousinia*, sect. *Leiacanthos* Tschern.), Uzbekistan: Kughitang range, Tanghydevol canyon, rocky area, 870 m, Kamelin 870 (LE). ***Cousinia tricolor* Rech. f.**, (subg. *Cousinia*, sect. *Tricolores* Rech. f.), Afghanistan: W, Ghorat, Dolaini, Darreh Garmak, inter Qala Chahrak (Shahrak) et Naourak, 2540 m, Rechinger 18904-II (W). ***Cousinia triflora* Schrenk.**, (subg. *Cynaroides* Tschern., sect. *Oligantha* Juz.), Iran: NNE, Golestan Nat. Park, Yakhbala pass, Akhani 102 (JGM). ***Cousinia triflora* Schrenk.**, (subg. *Cynaroides* Tschern., sect. *Oligantha* Juz.), Kazakhstan: AY373744, AY373711. ***Cousinia turcomanica* C. Winkl.**, (subg. *Cousinia*, sect. *Leucocaulon* Tschern.), Iran: NNE, Khorassan, 110 km W. of Bojnourd, between Spakhou and Kastan, 2000m, Mehregan 105 (JGM). ***Cousinia turkmenorum* Bornm.**, (subg. *Cousinia*, sect. *Chrysoptera* Tschern.), Iran: NE, Khorassan, 20 km from Mashhad to Neishabour, 1150m, Mehregan 197 (JGM). ***Cousinia umbrosa* Bunge**, (subg. *Cynaroides* Tschern., sect. *Pseudarctium* Juz.), Kazakhstan: AY373745, AY373712. ***Cousinia urumiensis* Bornm.**, (subg. *Cousinia*, sect. *Cousinia*), Iran: Azerbaijan, Urmia, inter Silvana and Razhan, 1650m, Mehregan 201 (JGM). ***Cousinia vavilovii* M. Kult.**, (subg. *Hypacanthodes* Tschern., sect. *Serratulopsis* Tschern.), Kyrgyzstan: Prov. Syr-Darja, distr. Aulie-ate, ad declivia saxosa regionis subalpinae in montibus Alexandri prope Utsch-Bulak, Popov s. n. (W). ***Cousinia verticillaris* Bunge**, (subg. *Cousinia*, sect. *Alpinae* Bunge), Afghanistan: E, Paktia, Jaji, Logar, 10 km E of Dohmandi, 2750m, Freitag 3536 (KAS). ***Cousinia vvedenskyi* Tschern.**, (subg. *Cousinia*, sect. *Cousinia*), Uzbekistan: Surhandarya region, mountains Chul'-Bair, near village Cina, granite broken stony slopes, in "juniperus", Bochanzev 111 (LE). ***Cousinia xanthacantha* Regel**, (subg. *Cousinia*, sect. *Eriocousinia* Tschern.), Afghanistan: Kabul, in dec. orient. jugi Unai, Breckle 2286 (M). ***Cousinia xiphiolepis* Boiss.**, (subg. *Cousinia*, sect. *Sphaerocephalae* Bunge), Iran: Tehran, Inter Firouzkouh and Polur, 5 km W of Lasem, 2600m, Mehregan 179 (JGM). ***Cousinia zardkuhensis* Attar & Ghahreman**, (subg. *Cousinia*, sect. *Cynaroideae* Bunge), Iran: C, Bakhtiari, Farsan to Filabad, 2400m, Mehregan 205 (JGM). ***Hypacanthium echinopifolium* (Bornm.) Juz.**, Kyrgyzstan: AY373746, AY373713. ***Jurinea albicaulis* Bunge**, Greece: Makedonia, Halkidiki, between Arnea and Paleokastro, Susanna et al. 1957 (BC). ***Saussurea elegans* Ledeb.**, Kazakhstan: AY373750, AY373717. ***Schmalhausenia nidulans* (Regel) Petrak**, Kazakhstan: AY37352, AY373719.

CHAPTER 4**TAXONOMIC REVISION OF *COUSINIA* SECT. *CYNAROIDEAE*****IRAJ MEHREGAN & JOACHIM W. KADEREIT**

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4.1 ABSTRACT

Cousinia sect. *Cynaroideae*, the largest section of *Cousinia* with 110 published species, is characterized by a chromosome number of $2n = 24$ and by having \pm decurent to spiny-winged leaves and appendaged phyllaries. It is distributed in Iran, Iraq, the Caucasus, Turkey, Turkmenistan, Afghanistan, Pakistan, Lebanon and Anti-Lebanon, with centres of specific diversity mainly in W & NW Iran, N Iraq and SE Turkey. A comprehensive treatment of *C.* sect. *Cynaroideae*, mainly based on the study of ca. 2250 herbarium specimens, resulted in a reduction of species number to 31 species plus eight subspecies. All species are typified. Diagnostic keys, descriptions, illustrations and distribution maps for each species are given.

Keywords: *Cousinia*, *C.* sect. *Cynaroideae*, taxonomy, morphology

4.2 INTRODUCTION

According to current understanding, *Cousinia* sect. *Cynaroideae* Bunge is the largest section of the genus with 110 published species (Fig. 1); these are distributed in Iran (75 species; Rechinger, 1972, 1979; Attar & Ghahreman, 2006, 2007), Iraq (24 species; Huber-Morath in Townsend & Guest, unpublished), the Caucasus (10 species; Tamanian, 1999), Turkey (eight species; Huber-Morath in Davis, 1975), Turkmenistan (two species; Tscherneva, 1962), Afghanistan and Pakistan (one species; Rechinger, 1972; Stewart in Ali & Nasir, 1972) and Lebanon and Antilebanon (three species; Post, 1933). No monographic treatment of *C.* sect. *Cynaroideae* exists, and none of the above regional accounts has covered all species or the entire distribution area of the section. However, Flora Iranica (Rechinger 1972, 1979) covers most species and also the main centres of specific diversity of the section in W Iran and N Iraq.

Rechinger's (1972, 1979) treatment in Flora Iranica was mainly based on material deposited in European herbaria, his own collections from the area, and some material from two major Iranian herbaria, TARI and IRAN (Rechinger, 1972). Large numbers of new collections from Iran were made after 1979. At the same time, exchange between Iranian herbaria and herbaria elsewhere has been seriously limited since 1979. In consequence, the thousands of herbarium specimens collected by staff of TARI and IRAN were not available to scientists outside Iran, and newly described species of *C.* sect. *Cynaroideae* often were based mainly on this new material plus material from TUH without considering other collections.

4.2.1 Taxonomic history of *C.* sect. *Cynaroideae*

Before the end of the 18th century only little unnamed or misidentified material later included in *Cousinia* was available. The genus *Cousinia* was first described by Cassini (1827) based on *Carduus orientalis* Adams. In a first attempt to classify the genus, Bunge (1865) grouped its species into 23 sections based on characters such as habit, texture of receptacular bristles and capitulum and flower morphology. Section *Cynaroideae* as currently known contains three different sections originally introduced by Bunge. These are 1) the monotypic sect. *Macrocephalae* Bunge with smooth receptacular bristles and including only *C. macrocephala* C. A. Mey., 2) the monotypic sect. *Grandis* Bunge with rough receptacular bristles and including only *C. grandis* C. A. Mey., and 3) sect. *Cynaroideae* with rough receptacular bristles which was recognized to contain 18 species by Bunge (1865). These 18 species include *C. cynaroides* (M.B.) C. A. Mey., originally published as *Carthamus cynaroides* M. B. (Bieberstein, 1800), as type of the section. Bunge (1865), followed by Boissier (1875), placed *C. libanotica* DC. along with five more species in sect. *Alpinae* Bunge. Based on our results, *C. libanotica* should be transferred to sect. *Cynaroideae* and will be treated here.

Cousinia macrocephala was transferred to sect. *Cynaroideae* by Boissier in Flora Orientalis (1875) where 28 species were accepted in the section. Winkler (1892, 1897) did not accept Bunge's (1865) concept of the section. Instead, he distributed its known members among four sections based on the morphology of the phyllaries. These were 1) sect. *Constrictae* C. Winkl. including *C. kotschyi* Boiss. and *C. hermonis* Boiss. plus seven other species which today are classified outside sect. *Cynaroideae*, 2) sect. *Appendiculatae* C. Winkl. with 26 species, three of which do not belong to sect. *Cynaroideae*, 3) sect. *Foliaceae* C. Winkl.

with five species, one of which is now classified in sect. *Scariosae* Rech. f. and 4) sect. *Odontocarpae* C. Winkl. including *C. libanotica* and *C. dayi* Post plus 29 other species which have been classified in sections other than sect. *Cynaroideae*.

The most comprehensive treatment of *C.* sect. *Cynaroideae* is that by Rechinger in *Flora Iranica* (1972, 1979). He used characters such as habit and leaf and capitulum morphology to delimitate the section. Rechinger's (1972, 1979) concept of *C.* sect. *Cynaroideae* has been accepted by the major recent regional Floras and publications (Huber-Morath in Davis, 1975, Huber-Morath in Townsend & Guest, unpublished; Tamanian, 1999, Attar & Ghahreman 2006).

4.2.2 Monophyly of *C.* sect. *Cynaroideae*

Cousinia as part of the “*Arctium-Cousinia* complex” consists of three subgenera (Tscherneva 1988), i.e., subg. *Cousinia*, subg. *Cynaroides* Tscherneva and subg. *Hypacanthodes* Tscherneva. Section *Cynaroideae* belongs to *Cousinia* subg. *Cousinia* (*Cousinia* s.s.). Several recent studies (Susanna et al. 2003 & 2006; Ghaffari et al. 2006; López-Vinyallonga et al., in press) have shown a clear subdivision of the monophyletic “*Arctium-Cousinia* complex” into an Arctioid group with *Arctium* L., *Cousinia* subgg. *Cynaroides* and *Hypacanthodes*, *Hypacanthium* Juz., *Schmalhausenia* C. Winkl., and a Cousinioid group with only *Cousinia* subg. *Cousinia* supported by chromosome number, pollen and style morphology. *Cousinia* s.s. as currently understood consists of ca. 600 species with styles with sweeping hairs scattered on the stylar branches (instead of being arranged in a ring; Susanna et al. 2003), oblong and smooth pollen grains of the ‘*Cousinia* type’ (Susanna et al. 2003) and diverse diploid chromosome numbers ($2n = 2x = 18, 20, 22, 24, 26$; Ghaffari et al. 2006).

In a molecular phylogenetic analysis of 138 species of the “*Arctium-Cousinia* complex” using ITS and *rpS4-trnT-trnL* sequences, very little resolution was obtained for the species of subg. *Cousinia*. However, all three species of *C.* sect. *Cynaroideae* included in the analysis (*C. araneosa* DC., *C. macrocephala* & *C. purpurea* C. A. Mey. in DC.) formed a monophyletic clade with very high posterior probability in a Bayesian analysis of the ITS sequences (López-Vinyallonga et al., in press). In a Bayesian analysis of an enlarged ITS data set of 216 species, the nine species of sect. *Cynaroideae* included in the analysis still formed a monophyletic clade but with clearly lower posterior probability (*C. araneosa*, *C. canescens* DC., *C. hermonis*, *C. macrocephala*, *C. onopordioides* Ledeb. in Eichw., *C. pergamacea* Boiss. & Hausskn. in Boiss., *C. purpurea*, *C. takhtajanii* Tamanian, *C. zardkuhensis* Attar & Ghahreman; Mehregan & Kadereit, submitted).

Cousinia sect. *Cynaroideae* has capitula with very characteristic phyllaries; phyllaries are usually enlarged from an adpressed, constricted base into a \pm large appendage (appendiculate). The species of sect. *Cynaroideae* also are relatively uniform by having herbaceous to leathery, usually spiny lobed leaves which are \pm decurent and thus form spiny-winged stems. Also, the species of sect. *Cynaroideae* are distributed continuously in a relatively large area from Lebanon to Afganistan and Pakistan with centres of specific diversity in NE Turkey, N Iraq and W and NW Iran.

We here regard the combination of molecular, morphological and distributional data as evidence for the monophyly of the group. Considering the size of *Cousinia*, however, the possibility of future inclusion or exclusion of species can not be ruled out.

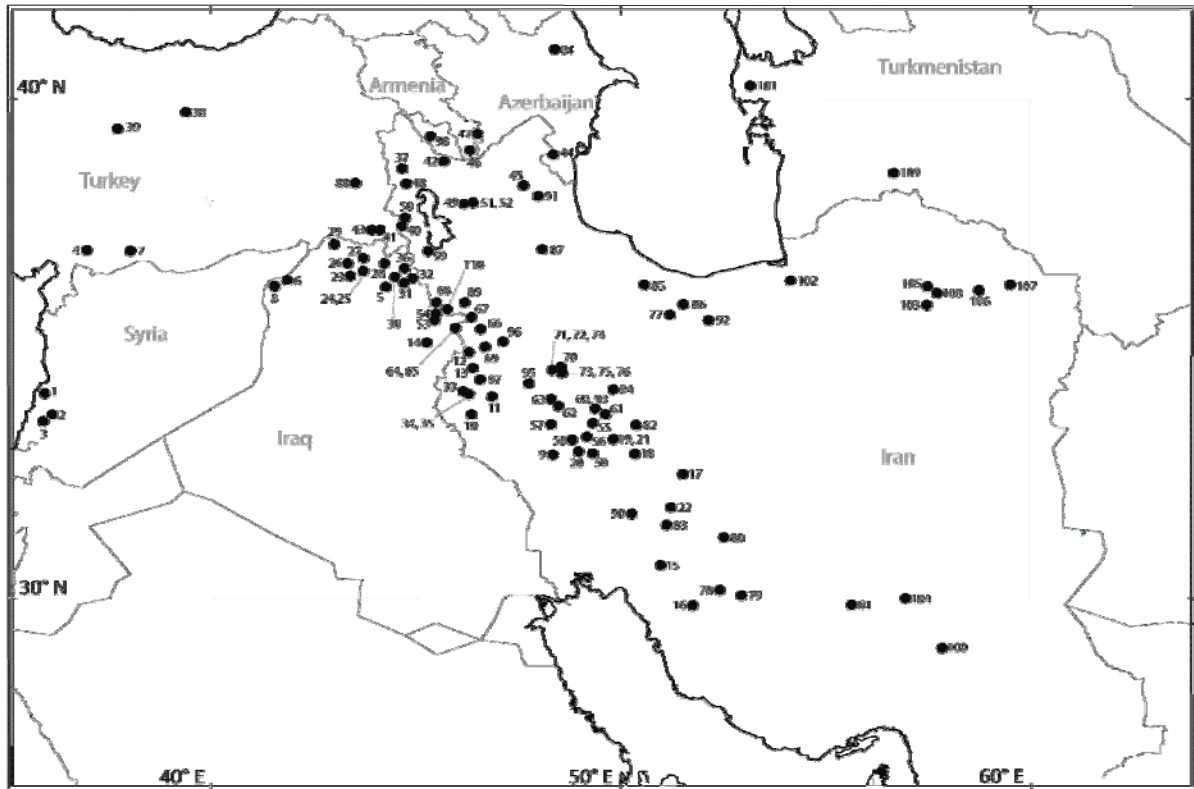


Fig. 1. – Type localities of published species of *C.* sect. *Cynaroideae* (each number indicates one species); 1. *C. libanotica*; 2. *C. hermonis*; 3. *C. dayi*; 4. *C. aintabensis*; 5. *C. arbelensis*; 6. *C. handelii*; 7. *C. birecikensis*; 8. *C. sinjarensis*; 9. *C. disfulensis*; 10. *C. jacobsii*; 11. *C. kermanshahensis*; 12. *C. inflata*; 13. *C. anoplophylla*; 14. *C. kopi-karadaghensis*; 15. *C. barbeyi*; 16. *C. mozaffariani*; 17. *C. silyboides*; 18. *C. lactiflora*; 19. *C. kivar*; 20. *C. shulabadensis*; 21. *C. aligudarzensis*; 22. *C. zardkuhensis*; 23. *C. odontolepis*; 24. *C. cymbolepis*; 25. *C. schultzi*; 26. *C. baueri*; 27. *C. leatherdalei*; 28. *C. mazu-shirinensis*; 29. *C. acanthophysa*; 30. *C. kurdica*; 31. *C. carduchorum*; 32. *C. qandilica*; 33. *C. noeana*; 34. *C. kirrindica*; 35. *C. mobayenii*; 36. *C. algurdina*; 37. *C. canescens*; 38. *C. onopordon*; 39. *C. eriocephala*; 40. *C. zagrica*; 41. *C. satdaghensis*; 42. *C. qaradaghensis*; 43. *C. hakkarica*; 44. *C. macrocephala*; 45. *C. gigantolepis*; 46. *C. gabrieljanae*; 47. *C. takhtajanii*; 48. *C. grandis*; 49. *C. wettsteiniana*; 50. *C. grantii*; 51. *C. gilliatii*; 52. *C. shebliensis*; 53. *C. macrolepis*; 54. *C. gigantosphaera*; 55. *C. sagittata*; 56. *C. rhombiformis*; 57. *C. phyllocephala*; 58. *C. köieana*; 59. *C. khorramabadensis*; 60. *C. iranica*; 61. *C. straussii*; 62. *C. chlorosphaera*; 63. *C. hamadanensis*; 64. *C. pergamacea*; 65. *C. wheeler-hainesii*; 66. *C. fursei*; 67. *C. millefontana*; 68. *C. sardashtensis*; 69. *C. concinna*; 70. *C. araneosa*; 71. *C. kornhuberi*; 72. *C. elwendensis*; 73. *C. ecbatanensis*; 74. *C. medorum*; 75. *C. pichleriana*; 76. *C. parsana*; 77. *C. keredjensis*; 78. *C. kotschy*; 79. *C. farsistanica*; 80. *C. persopolitanus*; 81. *C. pariziana*; 82. *C. khansaricus*; 83. *C. lordeganensis*; 84. *C. cynaroides*; 85. *C. calocephala*; 86. *C. squarrosa*; 87. *C. adnata*; 88. *C. vanensis*; 89. *C. stroterolepis*; 90. *C. sefidiana*; 91. *C. sabalanica*; 92. *C. behboudiana*; 93. *C. astrocephala*; 94. *C. nana*; 95. *C. lurorum*; 96. *C. sanandajensis*; 97. *C. dalahuensis*; 98. *C. purpurea*; 99. *C. bobekii*; 100. *C. sarzehensis*; 101. *C. onopordioides*; 102. *C. albicaulis*; 103. *C. grandiceps*; 104. *C. bornmülleri*; 105. *C. sabzevarensis*; 106. *C. verbascifolia*; 107. *C. monocephala*; 108. *C. lyrata*; 109. *C. caesia*; 110. *C. caroli-henrici*.

4.2.3 Geographical distribution, biology, chromosome numbers

Section *Cynaroideae* is distributed in SW Asia (Lebanon, Syria, Turkey, Iraq, Caucasus, Iran, Turkmenistan, Afganistan and Pakistan), and most of its species are centred in W Iran and N Iraq. The vegetation of this area, which is part of the Zagros-Makran Mt. arch ranging from the Diyala river near the Iraqi-Turkish border to Makran in SE Iran, is "Kurdo-Zagrosian steppe-forest" according to the classification by Zohary (1973). It consists mainly of deciduous, broad-leaved trees or shrubs with a dense ground cover - dominant species are *Quercus* spp. and *Pistacia* spp. - or of steppe vegetation. The area has a semi-arid and temperate climate. Annual precipitation ranges from 400 – 800 mm and mostly falls in winter and spring. Winters are severe and temperatures often fall to -25°C, and summers are extremely arid (Frey & Probst 1986).

In the northern parts of the Zagros-Makran Mt. range, lower altitudes (400 – 500 m) host communities dominated by, e.g., *Astragalus* spp. and *Salvia* spp., while higher up (700 – 800 m) forests or forest remnants of *Quercus brantii* and/or *Q. boissieri* occur up to an altitude of about 1700 m. Above the timberline (1900 – 2000 m) a relatively broad zone of sub-alpine vegetation is found. Further south in the mountain range, the forest floor vegetation becomes impoverished and a rich steppe flora develops among the trees. Forest remnants consist primarily of *Quercus persica* and, up to an elevation of 2400 m, xerophilous forest of *Quercus* spp., *Crataegus* spp., *Amygdalus* spp., *Celtis* sp. and *Pyrus* spp. predominates. Below 1400 m, the vegetation is steppic, with shrubs predominating (Zohary 1973).

Little is known about pollination in the section. We observed different beetles, including species of the genus *Larinus* (Coleoptera, Curculionidae), feed and lay eggs on most species of *C.* sect. *Cynaroideae*. It is unknown whether they also act as pollinators. As regards fruit dispersal, capitula remain closed and attached to the plants after maturity, and the entire plants are dispersed by wind as tumbleweeds or by exozoochory, a phenomenon which is common in part of *Cousinia* (Susanna et al. 2003).

Only seven of the species recognized here have been reported to be involved in hybridization (Rechinger 1972). These are: *C. chlorosphaera* Bornm., *C. araneosa* Bornm., *C. inflata* Boiss. & Hausskn., *C. algurdina* Rech. f., *C. odontolepis* DC., *C. macrolepis* Boiss. & Hausskn. and *C. sagittata* C. Winkl. & Strauss. This number may well not be accurate at all because of the difficulties of deciding whether intermediate forms indeed are hybrids or part of the variation of taxonomically poorly understood groups.

In the 14 species of the section examined for chromosome number, invariably $2n = 24$ chromosomes were found (Ghaffari et al. 2000).

We here present a revision of all species of sect. *Cynaroideae* known to us.

4.3 MATERIAL AND METHODS

This revision is based on the study of ca. 2250 herbarium sheets from ANK, B, BM, E, G, GAZI, IRAN, JE, K, LD, M, P, TARI, TUH, W and WU (acronyms according to Holmgren et al., 1990). In addition, 50 specimens from W Iran collected by the first author and deposited in MJG were examined. Measurements were made on the herbarium material. In some areas of W, NW, N, NE and C Iran, field work was carried out.

4.4 RESULTS AND DISCUSSION

4.4.1 *Cousinia*

Cousinia Cass., Dict. Sci. Nat. 47: 503 (1827).

Type: *Cousinia orientalis* (Adams) C. Koch, Linnaea 24: 386 (1851). ≡ *Carduus orientalis* Adams in Weber f. & Mohr., Beitr. Naturkd. 1: 63 (1805), nom. illeg. ≡ *Cousinia carduiiformis* Cass., Dict. Sci. Nat. 47: 503 (1827). ≡ *Arctium carduiforme* Kuntze, Revis. Gen. 1: 307 (1891).

Note. – Cassini (1827) established the generic name *Cousinia* along with the illegitimate name *Cousinia carduiiformis*. He doubtfully cited the previously published name *Carduus orientalis* as synonym for this new taxon. The type species of the genus, *Cousinia carduiiformis* Cass., was later replaced by *Cousinia orientalis* (Adams) C. Koch by Koch (1851).

= *Auchera* DC., Prodr. 6: 557 (1838).

= *Lipskyella* Juzz., Tr. Bot. Inst. AN SSSR ser. 1, 3: 323 (1936).

= *Tiarocarpus* Rech. f., Anz. Math.-Nat. Kl. Österr. Akad. Wiss. 108: 3 (1971).

Suffruticose or suffrutescent, monocarpic, perennial, biennial or rarely annual, spiny or rarely non-spiny herbs. Leaves often leathery and spiny, rarely herbaceous and/or non-spiny, dentate, lobed, pinnatifid to pinnatipartite or rarely entire, decurrent or not decurrent. Capitula homogamous, discoid. Involucre infundibuliform, cylindrical to globose; phyllaries pluriseriate, rigid, imbricate, with or without an appendage; appendage usually ending in a prickle or spine. Receptacle densely covered with rough and/or smooth bristles. Flowers hermaphrodite, white, yellow or pink to purple; anther appendages fringed. Stigma and upper part of style covered with scattered short hairs. Achenes glabrous, very variable in form and size, compressed or winged, round or truncate at apex. Bristles of pappus scabrous, free, caducous.

4.4.2 *Cousinia* sect. *Cynaroideae*

Cousinia sect. *Cynaroideae* Bunge, Mém. Acad. Imp. Sciences St.-Petersbourg, VII^E Sér., 9: 47 (1865). – Type: *C. cynaroides* (M.B.) C. A. Mey.

Note. – Although the ending “-oideae” today is used for names at the rank of subfamily (ICBN, Vienna Code, 2006), the sectional name “*Cynaroideae*” as used by Bunge (1865) not be corrected (ICBN, Art. 35). Therefore, correction of “*Cynaroideae*” to “*Cynaroides*” as pointed out by Attar & Ghahreman (2006) is incorrect.

= *C. sect. Macrocephalae* Bunge, Mém. Acad. Imp. Sciences St.-Petersbourg, VII^E Sér., 9: 41 (1865). – Type: *C. macrocephala* C. A. Mey.

= *C. sect. Grandis* Bunge, Mém. Acad. Imp. Sciences St.-Petersbourg, VII^E Sér., 9: 47 (1865). – Type: *C. grandis* C. A. Mey.

= *C. sect. Alpinae* Bunge, Mém. Acad. Imp. Sciences St.-Petersbourg, VII^E Sér., 9: 45 (1865), p.p. – Type: *C. alpina* Bunge

= *C. sect. Constrictae* C. Winkl., Acta Horti Petropolitani 12: 264 (1892), p.p.

= *C. sect. Appendiculatae* C. Winkl., Acta Horti Petropolitani 12: 268 (1892).

= *C. sect. Foliaceae* C. Winkl., Acta Horti Petropolitani 12: 279 (1892).

= *C. sect. Odontocarpae* C. Winkl., Acta Horti Petropolitani 12: 253 (1892), p.p.

Biennials or perennials, monocarpic. Leaves herbaceous to leathery, spiny lobed to deeply pinnatisect, ±decurent to form spiny-winged stems. Capitula terminal, 1.5 – 12 cm (including appendages), usually with 50 to more than 200 flowers. Phyllaries numerous, usually ±abruptly enlarged from an adpressed, constricted base into a ±large appendage. Anthers glabrous. Achenes obovate to obpyramidal, 4 – 8 mm long, often longitudinally ribbed or wrinkled, truncate, emarginate and denticulate or rounded at apex.

4.4.3 Identification of species

Species belonging to *C. sect. Cynaroideae* often are very variable morphologically. Accordingly, it sometimes is difficult to identify specimens on the basis of morphological characters alone. Therefore, our key in many cases includes geographical distribution to allow the accurate identification of specimens. In order to facilitate the use of the key, we here define and illustrate some of the morphological characters used.

Leaves. – Basal leaves vary from entire to deeply pinnatifid or lyrate (Fig. 2, A-D). Basal leaves usually differ from rosette leaves formed in the first year of growth. These usually are dentate to lobate. Leaves are smaller and less divided towards the apex. Stem leaves vary from dentate to pinnate. In some species upper leaves enclose the involucre at least in its lower part (Fig. 2, F).

Capitulum. – Capitulum morphology is most important in identifying species of sect. *Cynaroideae*. Involucral bracts are multiseriate. The outer sessile or shortly stalked phyllaries usually are gradually transformed into the stalked and appendiculate middle and linear inner phyllaries. Our descriptions and the key are based on the morphology of middle phyllaries (Fig. 2, E). The free part of the middle phyllaries is constricted at the base and thus forms a recurved or spreading to upright or imbricate appendage (Fig. 2, E-I). Appendages usually are broader than the base of the phyllary and possess or lack spines or prickles on

both sides and terminally (Fig. 2, J-S). Receptacular bristles are smooth or rough or a mixture of rough and smooth bristles is present. Our descriptions are based on the texture of the longer bristles (Fig. 2, T).

Fig. 2. (next page) – Variation of characters in *Cousinia* sect. *Cynaroideae*; A - D: leaves; A. entire (*C. sagittata* p.p.), B. sinuate-lobate (*C. onopordioides*), C. lyrate (*C. verbascifolia*), D. Pinnatisect (*C. aintabensis* p.p.); E - I: capitulum; E. inflated imbricate phyllaries (*C. inflata*), F. adpressed and imbricate phyllaries with uppermost leaves enclosing the involucre (*C. sagittata* p.p.), G. spreading-recurved phyllaries (*C. cynaroides*), H. spreading-erect phyllaries (*C. grandis*), I. adpressed-imbricate phyllaries (*C. pergamacea*); J - S: middle phyllaries; J. boat-shaped, lanceolate appendage (*C. odontolepis* subsp. *kurdica*), K. boat-shaped, rhomboid- or sagittate-lanceolate appendage (*C. macrolepis*), L. lanceolate appendage without spines on sides (*C. canescens*), M. lanceolate appendage with spines on sides (*C. sarzehensis*), N. rhomboid-lanceolate appendage, recurved at apex (*C. sagittata*), O. deltoid-lanceolate appendage, straight at apex (*C. kotschyi* subsp. *khansaricus*), P. flabellate appendage (*C. kotschyi* subsp. *khansaricus*), Q. deltoid appendage, at least twice as broad as base (*C. pergamacea*), R. deltoid appendage, as broad as base (*C. concinna*), S. boat-shaped, keeled, deltoid appendages (*C. aintabensis*); T. rough receptacular bristles (*C. aintabensis*). Abbr. **m. ph.**: middle phyllaries; **app.**: appendage. (All illustrations exp. Fig. 2-D by I. Mehregan; Fig. 2-D simplified from C. Winkl. & Bornm., Bull. Herb. Boissier 3 (11), pl. 14).

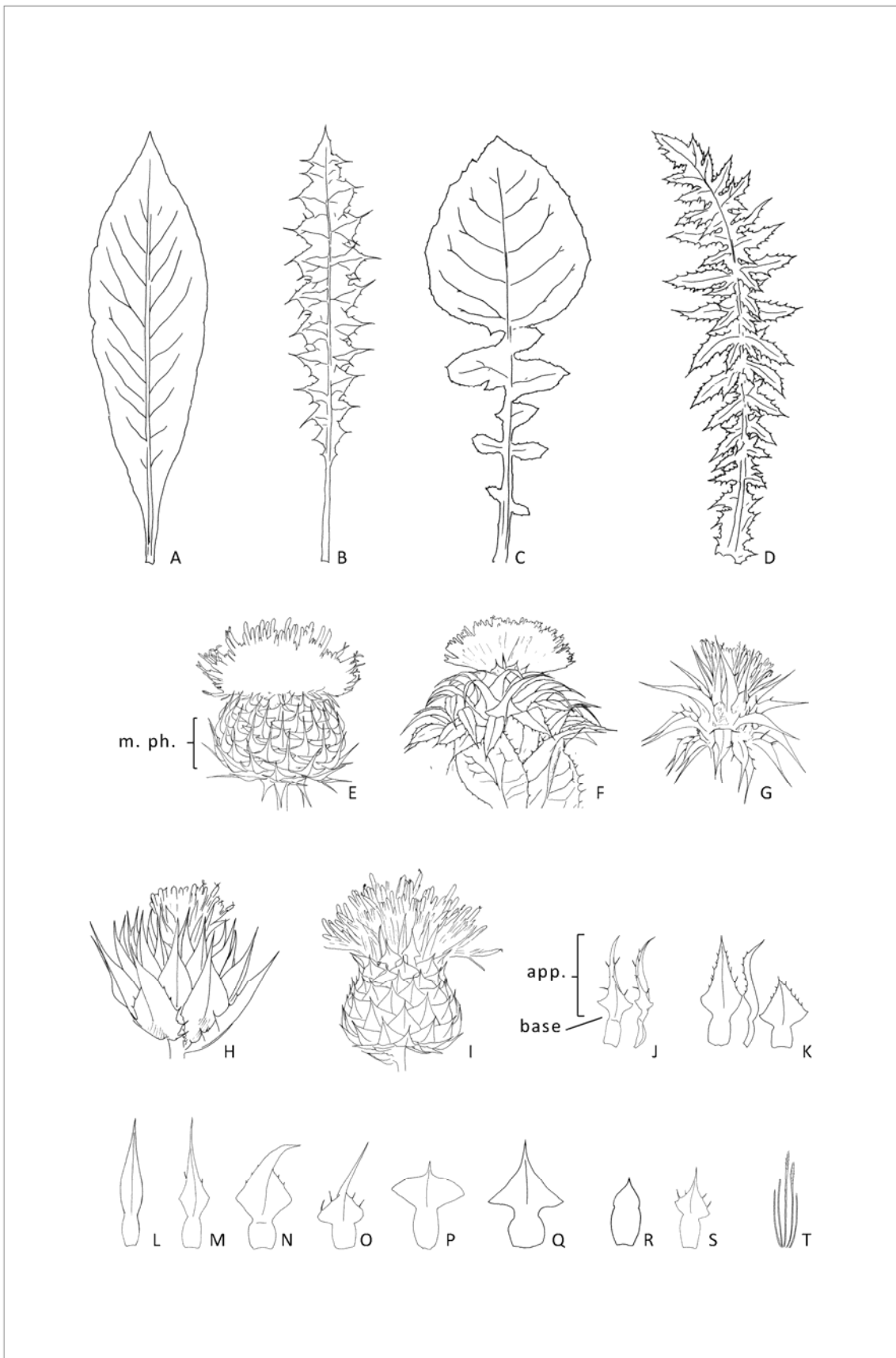


Fig. 2. (caption in previous page)

4.4.4 Key to species of *C. sect. Cynaroideae*

1. Phyllaries with adpressed and imbricate appendages (Fig. 2, F & I). 2
 – Phyllaries with straight, spreading to recurved or inflated-spreading appendages (Fig. 2, E, G & H). 13
2. Uppermost leaves usually enclosing the involucre (at least its lower part), appendages recurved at apex (except slightly recurved phyllaries in *C. sagittata* subsp. *iranica* p.p.; Fig. 2, F). 3
 – Uppermost leaves not enclosing the involucre, appendages straight to slightly recurved at apex. 5
3. Appendages entire or with appressed tiny spines on sides (Fig. 2, N; CW Iran, provinces Luristan & Markazi). **16a. *C. sagittata***
 – Not as above (N Iraq and neighbouring areas). 4
4. Appendages deltoid, rhomboid- or sagittate-lanceolate, more than 8 mm broad (Fig. 2, K). **15. *C. macrolepis***
 – Appendages narrowly lanceolate, less than 8 mm broad (Fig. 2, J).
 **7b. *C. odontolepis* subsp. *kurdica***
5. Appendages deltoid- or sagittate-lanceolate, incurved, carinate, spiny on sides (N Iraq/Turkey border area). **7a. *C. odontolepis***
 – Not as above (Iran and neighbouring areas in Iraq, province Sulaimaniya). 6
6. Phyllaries glabrous, regularly arranged, usually without spines on sides (exp. *C. pergamacea* subsp. *sardashtensis* with spines on both sides; provinces S Azerbaijan, Kurdistan, Hamedan and Luristan in Iran and province Sulaimaniya in Iraq; Fig. 2, I, Q & R). 7
 – Not as above. 9
7. Appendages as broad as to less than twice as broad as their base (Fig. 2, R), 3 – 6 mm broad. Corolla rose or purple. **19. *C. concinna***
 – Appendages at least twice as broad as their base, usually 6 – 15 mm broad. Corolla yellow, rose or purple. 8
8. Appendages deltoid or deltoid-sagittate (Fig. 2, Q). Corolla yellow. . . **18a. *C. Pergamacea***
 – Appendages broadly rhomboid-deltoid or rhomboid-flabellate. Corolla rose or purple.
 **17. *C. chlorosphaera***
9. Appendages 12 – 20 mm, lateral spines 3 mm or more long (endemic to N Iran, C Elburz, province Tehran, W of Tehran). **21. *C. keredjensis***
 – Not as above (W to S Iran). 10

10. Appendages 8 mm broad or broader. 11
 – Appendages less than 7 mm broad. **26. C. lurorum** p.p.
11. Appendages of middle and upper phyllaries usually covered by arachnoid indumentum. Involucre usually horizontally elliptic in outline (endemic to W Iran, province Hamedan (Alvand Mts. and neighbouring areas)) **20. C. araneosa**
 – Not as above (CW to S Iran, provinces Markazi, Esfahan, Bakhtiari & Fars). 12
12. Appendages lanceolate. **6c. C. silyboides** subsp. *zardkuhensis* p.p.
 – Appendages rhomboid-, sagittate-lanceolate or flabellate.
 **22b. C. kotschyi** subsp. *khansaricus*
13. Appendages deltoid-lanceolate to linear-lanceolate, gradually attenuate into a long spine at apex, without spines on the sides (Lebanon and anti-Lebanon). . . **1. C. libanotica**
 – Not as above (Turkey and further east). 14
14. Involucre cylindrical to conical; phyllaries with ±spreading, concave, keeled, ovate to deltoid-lanceolate appendages (S Turkey, N Iraq, western part of Zagros Mts. from W to SW Iran; Fig. 2, S). 15
 – Not as above. 20
15. Appendages horizontally spreading in lower part, straight to incurved in upper part, deltoid, usually glabrous or glabrescent (Shahu and Oraman Mts. in Iran and province Sulaymaniyah in Iraq; Fig. 2, E). **3. C. inflata**
 – Not as above. 16
16. Appendages usually arachnoid-tomentose on outside, glabrous on inside, sagittate-lanceolate (SW Iran, provinces Kuhgiluyeh & Boirahmad and Fars). **5. C. barbeyi**
 – Not as above. 17
17. Plants densely canescent-tomentose (S Turkey & N Iraq). **2. C. aintabensis**
 – Plants ±sparsely arachnoid-tomentose or virescent, ±glabrescent or glabrous (N Iraq, W and CW Iran). 18
18. Appendages strongly incurved, forming a semicircle (N Iraq). . . **7. C. odontolepis** p.p.
 – Appendage only slightly incurved (Iran). 19
19. Plants from western slopes of Zagros Mts. **6c. C. silyboides** subsp. *disfulensis*
 – Plants from eastern slopes of Zagros Mts. **6a. C. silyboides** p.p.
20. Corolla purple to purplish-lilac, longer than 35 mm (NNE, NE to SE Iran, Turkmenistan, Afghanistan & Pakistan). **30. C. onopordioides**
 – Not as above. 21

21. Appendages flat, \pm horizontal, \pm straight, 7 – 12 mm long, 4 – 9 mm broad, attenuated into a usually long spine at apex, glabrous or \pm glabrescent. **4. *C. kopi-karadaghensis***
– Not as above. 22
22. Leaves white arachnoid-tomentose beneath, glabrous or glabrescent above. Corolla white. Anthers rose or purple (SE Turkey, NW Iran). **11. *C. hakkarica***
– Not as above. 23
23. Appendages keeled, spreading or slightly recurved, rhomboid-lanceolate, 20 – 38 mm long, 5 – 12 mm broad. Corolla pale purple (SE Iran, province Kerman, Jebal Barez, Sarzeh Mts.) **29. *C. sarzehensis***
– Not as above. 24
24. Basal leaves lyrate. Appendages cordate, ovate to lanceolate, 10 – 40 mm long, 7 – 15 mm broad. Corolla pink, rose or purple (NE Iran and SW Turkmenistan) **31. *C. verbascifolia***
– Not as above. 25
25. Plants white arachnoid-tomentose. Corolla usually yellow, 28 – 38 mm long (S Caucasus, NW Iran, province Azerbaijan s.l.) **12. *C. macrocephala***
– Not as above. 26
26. Lowermost phyllaries leaf-like, similar to uppermost leaves, glandulose-punctate or glabrous, rarely tomentose; middle ones spreading to erect, with cordate, ovate, cordate-lanceolate to lanceolate appendage (Fig. 2, H). **13. *C. grandis***
– Not as above. 27
27. Plants completely arachnoid-tomentose, usually yellowish, especially in upper parts. Phyllaries \pm spreading. Corolla creamy-white or flavescent (alpine regions of the Qnadil range between provinces Erbil and Sulaymaniyah/Iraq and Iran). **9. *C. alگردina***
– Not as above. 28
28. Plants completely white arachnoid-tomentose. Upper stem leaves sessile, usually oblong or ovate, round to cuneate at base (Turkey & NW Iran). **10. *C. canescens***
– Not as above. 29
29. Upper phyllaries usually red-tinted; appendages of middle phyllaries usually truncate at base. Basal leaves lyrate or deeply pinnatisect (Fig. 2, C & D; N Iraq).
. **7a. *C. odontolepis* p.p.**
– Not as above (Turkey, Caucasus and Iran). 30
30. Phyllaries with erect appendages; appendages without spines on sides. Plants completely white arachnoid-tomentose (plants from Iran, Bakhtiari). **23. *C. lordeganensis***
– Not as above. 31

31. Phyllaries usually keeled, slightly recurved or horizontally spreading at apex, appendages ovate to lanceolate, 5 – 12 mm long, 3 – 5 mm broad, usually with 2 spines on both sides. Corolla purple (Caucasus). **27. *C. purpurea***
– Not as above. 32
32. Appendages usually with 2 – 3 irregular spines in their lower quarter; spines yellow, 4 mm or more. Anthers usually milky white (S and SE Iran, provinces Fars, Yazd and Kerman). **22a. *C. kotschyi*** p.p.
– Not as above (C, W, NW and N Iran and SE Turkey). 33
33. Phyllaries spreading to recurved; appendages keeled, straight to recurved, lanceolate to linear-lanceolate, 20 – 40 mm long, 5 – 12 mm broad, with 1- 4 spines on both sides. Corolla rose (endemic to a small area E of Tabriz, “Shebli pass”) **14. *C. gilliati***
– Not as above. 34
34. Plants completely white arachnoid-tomentose. Phyllaries spreading to recurved. Corolla and anthers yellow (Caucasus, Iranian Azerbaijan, province Ardebil). . . **24. *C. cynaroides***
– Not as above. 35
35. Involucre 2 cm or more in diameter (without appendages), short-conical; base of appendages visible from the side (appendages interrupted, not covering each other); appendages usually abruptly expanded just above base, ovate to rhomboid or linear-lanceolate, 4 – 15 mm broad (Iran, provinces Luristan, E of Esfahan, Bakhtiari).
. **6a. *C. silyboides*** p.p.
– Not as above. 36
36. Middle phyllaries recurved or ±spreading; appendages usually as long as or longer than diameter of involucre, keeled or flat, lanceolate to linear, 12 – 30 mm long, 3 – 6 mm broad. Corolla and anthers purple or rose (Iran, provinces Ilam and Kermanshah). . . . **8. *C. noeana***
– Not as above. 37
37. Corolla yellow. Anthers purple or pale. Stems usually divaricately branched (Iran, C and S of province Azarbaijan-e Gharbi, W and S of lake Urmia). **28. *C. bobekii***
– Not as above. 38
38. Appendages keeled, usually ±erect, deltoid to lanceolate, without or with one (-2) tiny spine on both sides (Iran, provinces Kermanshah, Kurdistan & Hamedan)
. **26. *C. lurorum*** p.p.
– Not as above. **25. *C. calocephala*** s.l.

4.4.5 Description of taxa

4.4.5.1 *Cousinia libanotica* DC., Prodr. 6: 556 (1838). ≡ *Arctium libanoticum* (DC.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Lebanon, “in monte Libano”, *Aucher-Eloy* 3489 (K!; isotypes: G, P!), syntype: “Syria”, 1790, Labillardiere (G).

= *C. hermonis* Boiss., Diagn. Pl. Orient. Ser. 1, 10: 102 (1849). ≡ *Arctium hermonis* (Boiss.) O. Kuntze, Revis. Gen. 1: 307 (1891). – Lectotype (designated here): Syria, “inter Ainete et Deir el Achmar, Mai-Jul. 1846”, *Boissier* (G00152018, G-BOIS!; syntypes G-BOIS! [marked with “var. *cana*”], JE!, K!, W!), **syn. nov.**

Note. – Material of *C. hermonis* collected by Boissier in Syria deposited in G-BOIS as G00152018 is mounted on two sheets. The first sheet with a label including the phrase “inter Ainete et Deir el Achmar, Jul. 1846” matches the locality given in the original publication (Boissier, l.c.) and therefore was designated as lectotype. The herbarium sheet in G-BOIS marked with “var. *cana*”, this name was never published by Boissier, as well as other material in JE, K and W collected by Boissier in Syria but without exact locality (only “Syria”) is regarded as syntype material here.

= *C. dayi* Post, Pl. Postianae, II: 13 (1891). – Type: Syria, Antilebanon, “Asal-ul-Ward, Halimat-ul-Kabu, *Post* (G; isotype W!, “fragment”), **syn. nov.**

= *C. hermonis* Boiss. var. *cana* (Boiss. ex) C. Winkl., Acta Horti Petropolitani 12: 268 (1892). – Holotype: Syria, *Boissier* (G-BOIS!; sub “var. *cana*”).

= *C. hermonis* Boiss. f. *cana* Bornm., Öst. Bot. Zeitschr. 62: 423 (1912). – Lectotype (designated here): Syria, in montis “Hermon” regione subalpina ad alpinam, 1950 m, 25. VI. 1897, *Bornmüller* 943 (B100157170, B!; isotypes JE!, K!, W!, WU!).

= *C. hermonis* Boiss. f. *patens* Bornm., Öst. Bot. Zeitschr. 62: 423 (1912). – Holotype: Syria, in montis “Hermon” regione subalpina ad alpinam, 1950 m, 25. VI. 1897, *Bornmüller* 943c (B100157167, B!).

= *C. hermonis* Boiss. f. *glabrescens* Bornm., Öst. Bot. Zeitschr. 62: 423 (1912). – Holotype: Syria, in montis “Hermon” regione subalpina ad alpinam, 1950 m, 25. VI. 1897, *Bornmüller* 943b (B1000884, B!).

Illustration. – Fig. 3, A.

Plant up to 60 cm high, tomentose. Stems branched from the base or higher. Leaves leathery, tomentose on both sides; basal leaves up to 15 × 5 cm, lanceolate to linear-lanceolate, pinnatifid to pinnatisect, with spiny-dentate lobes; stem leaves gradually smaller and less divided towards the apex, ovate-lanceolate to lanceolate, spiny-lobed, round to cuneate at base, decurrent for up to 2.5 cm. Capitula 2.5 – 7.5 cm broad with phyllaries,

arachnoid-tomentose to glabrescent. Phyllaries 25 – 70; middle ones spreading to spreading-recurved; free part of middle phyllaries gradually or sometimes abruptly expanded above into a \pm erect, keeled or flat, deltoid-lanceolate to linear-lanceolate appendage; appendage 10 – 30 mm long, 2.5 – 7 mm broad, attenuated into a long spine at apex, without spines on the sides. Receptacular bristles rough. Flowers 40 – 60; corolla pink or purple, 20 – 30 mm long; anthers concolorous. Achenes 4 - 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – The "Mount Lebanon" in Lebanon and the "Anti-Lebanon" (including Mt. Hermon) in E Lebanon and a small part of W Syria are two parallel mountain ranges in a relatively small area. They are connected in southern Lebanon. Study of all herbarium specimens of *C. libanotica*, *C. hermonis* (incl. all varieties and forms) and *C. dayi* revealed continuous variation in plant size, density of indumentum and shape and size of phyllaries. Plants from "Mount Lebanon" and southern and lower parts of the "Anti-Lebanon" have a relatively dense indumentum, more divided leaves and phyllaries with longer appendages, while material collected from high alpine areas of the "Anti-Lebanon" have a less dense indumentum, less divided leaves and phyllaries with shorter appendages. However, we could not detect any discontinuity in these characters which had been used to distinguish species. Therefore, we consider *C. hermonis* and *C. dayi* as part of *C. libanotica*.

Distribution and habitat. – Endemic to Lebanon, W Syria and N Israel (Fig. 6, A), on stony slopes.

Specimens seen. – Lebanon: In rupestribus calcareis supra Eden, July 1846, Boissier (P); In Libano as Bscherre et circa Cedretum, 5800 ft., 25. VI. 1855, Kotschy 321 (P, W); Between Bakaфра and Cedrus forest, above Bscherre, 1500 - 1800 m, 21. VII. 1931, Zohary 3854 (W); In Libani alpini declivitatibus occidentalibus, in monte Dschebel Keneise, 1600 - 1700 m, 21. VI. 1910, Bornmüller 12033 (W); In reg. subalpina jugi Sanin, 1500 - 1900 m, 21. VII. 1897, Bornmüller 945 (B, W); Mnt Hermon, Shib'ah to Ain Zbib, 11. VIII. 1929, Gabrielith 3853 (W).

– Syria: In territorio montis Hermon, 5000 ft., 28. VI. 1855, Kotschy 198 (P, K, W); Hermon, Geröllhalde, 2350 m, 26. VI. 1936, Bertschinger 1343 (B); Hermon, 1700 m, 16. IX. 1924, Meyers & Dinsmore 1998 (K); Hermon, 12. VII. 1890, Post (K); Anti-Libani, inter Rschidani et Damascus, 1400 m, 27. VI. 1897, Bornmüller 944 (B).

4.4.5.2 *Cousinia aintabensis* Boiss. & Hausskn. in Boiss., Fl. Orient. 3: 503 (1875). \equiv *Arctium aintabense* (Boiss. & Hausskn.) O. Kuntze, Revis. Gen. Pl. 1: 307 (1891). – Lectotype (designated here): Turkey, "in monte Tullupbaba Syriae borealis prope Aintab, in apric. calc.", 22. VI. 1868, Haussknecht 962 (G00152015, G-BOIS!; isotype JE!).

Note. – The type specimen in G collected by Haussknecht was inappropriately referred to as the holotype of *C. aintabensis* by Huber-Morath (1975). During our search for original material in Herbarium Haussknecht in Jena (JE) we found another specimen of type material. As no designation of a holotype was made by the original authors (Boissier & Haussknecht in Boissier l.c.), we here select the sheet in G as lectotype.

= *C. arbelensis* C. Winkl. & Bornm., Bull. Herb. Boissier 3: 566 et 567, pl. 14 (1895). – Lectotype (designated here): Iraq, "habitat in Kurdistaniae terra Arbela, ad radices montis Kuh-Sefin prope pagum Shaklava, 1200 m, s. m. 4. VI. 1893, Bornmüller 1403b" (B100088397, B!; isotypes B!, G!), **syn. nov.**

= *C. arbelensis* var. *pinnata* C. Winkl. & Bornm. Bull. Herb. Boissier 3: 568, pl. 14 (1895). – Lectotype (designated here): Iraq, "Habitat in Kurdistaniae terra Arbela, ad radices montis Kuh-Sefin prope pagum Shaklava, 1000 m, 30. V. 1893, Bornmüller 1403" (B100088396, B!; isotypes K!, P!, W!, JE!, WU!).

Note. – *Cousinia arbelensis* and *C. arbelensis* var. *pinnata* were originally published with detailed illustrations (Winkler & Bornmüller l.c., pl. 14). Material in B which completely matches the original illustrations of *C. arbelensis* and *C. arbelensis* var. *pinnata* were selected as lectotypes of these names.

= *C. handelii* Bornm., Öst. Bot. Zeitschr. 62: 187 (1912). – Holotype: Iraq, "Mesopotamia, in lapidosis (substrato calcareo) montium Dschebel Sindschar supra oppidum Sindschar, ca. 600 – 700 m, 8. VI. 1910" *Handel-Mazzetti* 1359 (W!; isotypes B!, WU!), **syn. nov.**

= *C. birecikensis* Hub.-Mor., Notes Roy. Bot. Gard. Edinburgh 32: 53 (1972). – Holotype: Turkey, Urfa, "Mesopotamia, Biredjik, in declivibus ad Euphratem, 8. V. 1888, Sintenis 1528" (LD!), **syn. nov.**

= *C. sinjarensis* Rech. f., in Publ. Cairo Univ. Herb. 78: 289 (1977). – Holotype: Iraq, west side of Jabal Sinjar, 800 m, rocky slope, ravine, 30. V. 1968, *Anders* 2172 (W!); Syntype: Iraq, west side of Jabal Sinjar, 600 – 1200 m, 12. V. 1969, *Anders* 2689 (W!), **syn. nov.**

Illustration. – Fig. 3, B.

Plant up to 60 cm high, archnoid- or canescent-tomentose to glabrous. Stems branched from the base. Leaves herbaceous or leathery, archnoid- or canescent-tomentose on both surfaces, ±glabrescent above or rarely glabrescent on both sides; basal leaves up to 25 × 10 cm, lyrate, pinnatisect or pinnately oblong-lanceolate, spiny-lobed or with spiny-dentate margin; stem leaves gradually smaller and less divided towards the apex, ovate, ovate-lanceolate to linear-lanceolate, spiny-lobed to –dentate, usually long decurrent to form winged stems. Capitula 3 – 7 cm broad with appendages, archnoid-tomentose, ±glabrescent or glabrous. Phyllaries 40 – 100; middle ones ±spreading to spreading-incurved or rarely bent downward; free part of middle phyllaries abruptly expanded above into usually concave, keeled, ovate, long-deltoid, deltoid- or rhomboid-lanceolate appendage; appendage 15 – 30 mm long, 7 – 15 mm broad, usually attenuated into a long or short spine at apex, with 2 – 5 or rarely more tiny spines or prickles on both sides. Receptacular bristles rough or smooth. Flowers (30-) 50 – 100; corolla rose, pink, purple or straw-coloured, 18 – 30 mm long; anthers rose, pink, purple or pale. Achenes 4 – 5 mm long.

Flowering period. – May to July.

Taxonomic remarks. – *Cousinia aintabensis*, *C. arbelensis*, *C. handelii*, *C. birecikensis* and *C. sinjarensis* from the transitional area between the Anatolian plateau and adjacent Iraqi and Syrian lowlands with a Saharo-Sindian climate all have usually lyrate basal leaves, cylindrical to conical involucre with \pm spreading, concave, keeled and ovate to deltoid-lanceolate appendages. We observed continuous variation among all material of these taxa in all qualitative and quantitative characters and were not able to circumscribe them as separate species. *Cousinia handelii* and *C. sinjarensis* were introduced based on the material from the same locality (Jabal Sinjar or Dschebel Sindschar). *Cousinia birecikensis* was described based on material with unopened capitula from a locality inside the normal distribution range of *C. aintabensis*.

Distribution and habitat. – *C. aintabensis* is discontinuously distributed in the mountainous area between the southern Anatolian plateau and the neighbouring lowlands of southern Turkey and northern Iraq (and north Syria?; Fig. 6, B) on stony slopes and in oak forests.

Specimens seen. – Turkey: Mardin: In declivibus montinum, 1.VII. 1888, *Sintenis* 1276 (B, E, JE, K, M, P, WU); 19 km N of Mardin, 930 m, 23. V. 1956, *Birand* 86 (ANK); Mardin kalesi, 24. VII. 1974, *Baytop* 18224 (E); Siirt: Mirga mira, über Scharanak (Siranak), 24. VII. 1910, *Nabelek* s. n. (B); Bitlis: Baykan-Bitlis, arid Quercus slope, 1300 m, 25. VI. 1954, *Davis* 22163 (ANK, E, K).

– Iraq: Mosul: Atrush - Rabetki, 1400 m, 28. V. 1947, *Chapman* 9338 (K); Between Atrush village and Pine woodland, 850 m, 9. VI. 1978, *Hossain* 4268 (E, K, P); 30 km from Mosul to Aqra, 320 m, 4. VI. 1978, *Keisi* 49718 (K); Arbil (Erbil): Shaqlawa, 18. VI. 1961, *Haines* 2049 (E), 18. VI. 1961, *Agnew et al.*, W2049 (K); Jabal Saffen, 6. VII. 1971, *Sakira* 38252 (K); Safin Dagh (Jabal Saffen), 1300 m, 19. VI. 1947, *Rawi* 9078 (K); Shaikh Adi prope Ayn Sifni, 13. VI. 1934, *Field & Lazar* 712 (B, G, K, W); Pirmum Dagh, 900 m, 8. V. 1947, *Gillet* 8024 (K).

4.4.5.3 *Cousinia inflata* Boiss. & Hausskn. in Boiss., Fl. Or. 3: 512 (1875). \equiv *Arctium inflatum* (Boiss. & Hausskn.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Iran, “in montium Avroman et Schahu Kurdistaniae Persicae”, 5 – 8000', VI. – VII. 1867, Haussknecht 568 (G00152013, G-BOIS!; isotypes G-BOIS!, JE!, K!, P!, W!).

Note. – Type material deposited in G-BOIS is mounted on three sheets. The sheet no. G00152013 with a handwritten label by Boissier (“*Cousinia inflata* Boiss. et Hausskn.”) was selected as lectotype.

= *C. anoplophylla* Rech. f., Fl. Iranica 139a: 140 (1979). – Holotype: Iran, Kermanshah, Shalane to Dalahu, 1020 - 1800 m, 25. VII. 1967, *Iranshahr & Terme* 34012-E (W!; isotype IRAN!), **syn. nov.**

Illustration(s). – Fig. 4, A.

Plant up to 50 cm high, arachnoid-tomentose, \pm glabrescent. Stems branched from the base or higher. Leaves leathery or \pm herbaceous, arachnoid-tomentose on both surfaces or \pm glabrescent above; basal leaves up to 25 \times 10 cm including spines, broadly oblanceolate, oblong, lanceolate or lyrate, dentate to deeply pinnatisect; stem leaves sessile, abruptly or gradually smaller and less divided towards the apex, obovate, ovate to lanceolate,

pinnatifid or spiny-lobed to spiny-dentate, usually long decurrent to form interrupted winged stems. Capitula 2 – 4 cm broad with appendages, glabrous. Phyllaries 60 – 160, ± inflated what does this mean? imbricate; outer ones usually bent downwards; middle ones inflated, spreading-erect; free part of middle phyllaries abruptly expanded above into a usually keeled, concave appendage, appendage horizontal in lower part, straight to incurved upper part, deltoid; appendage 8 – 15 mm long, 8 – 17 mm broad, attenuate into a spine at apex, usually with black glands, glabrous, ±glabrescent or arachnoid-tomentose, without or rarely with 1 – 2 tiny prickles on both sides. Receptacular bristles rough. Flowers 60 – 140; corolla purple, rose, white or yellow, 20 – 30 mm long; anthers purple. Achenes 4 – 6 mm long.

Flowering period. – June to July.

Taxonomic remarks. – *Cousinia inflata* is a narrow endemic characteristic in having phyllaries with distinctly inflated imbricate phyllaries. The species is very variable in the morphology of its leaves. Even within a single population plants with almost entire to dentate leaves can be found together with plants with deeply pinnatisect leaves. *Cousinia anoplophylla* also has phyllaries with distinctly inflated imbricate phyllaries similar to those of *C. inflata* and almost entire basal leaves. It clearly is part of the morphological variation of *C. inflata* and could not be delimited as a separate species.

Distribution and habitat. – Endemic to NE Iraq and W Iran (Fig. 6, D). On rocky slopes or in the upper zone of oak forests.

Specimens seen. – Iraq: Sulaimaniya (Kurdistan): Montes Avroman ad confines persiae, in ditione pagi Tawilla, 1300 m, 15. - 18. VI. 1957, *Rechinger* 10215 (E, K, M, W); In ditione pagi Tawilla, in saxosis calc., 2100 m, 15. VI. 1957, *Rechinger* 12358 (B, W); Tawela, 1360 m, 16. VI. 1957, *Al Rawi* 21947 (K). Pir Omar Gudrun, 4000 ft., Jun. 1867, *Hausknecht* s.n. (P); Hawara Baya Mt., 1800 m, 24. VI. 1960, *Al Rawi et al.* 29507 (K); Kamarspa (on road between Halabja & Tawela), 1840 - 2000 m, 18. VI. 1957, *Al Rawi* 22179 (K); Mollah Khort Mt., 1700 m, 22. VI. 1960, *Al Rawi et al.* 29467 (K).

– Iran: Kermanshah: In monte Schahü, 28. V. 1905, *Strauss* s. n. (B, JE); Mt. Shahu, NE of Mansour-Aghayee village, [34° 57.894'N, 46° 27.876'E], 2170 m, 4. VII. 2005, *Mehregan & Assadi* 29 (JGM); Shahu, W of Shamshir village, [34° 58.454' N, 46° 27.986' E], 2540 m, 4. VII. 2005, *Mehregan & Assadi* 31 (JGM); 14 km from Paveh to Bayangan, 1800 m, 11. VII. 1997, *Ghahreman et al.* 20561 (TUH); 14 km N of Kerend, 1800 - 2000 m, 21. VI. 1987, *Assadi* 60889 (TARI); 44 km N of Kerend Gharb, Dalahu, Kuh-e Ghalelan, 1940 - 2100 m, 21. VI. 1987, *Hamzehee & Hatami* 1383 (TARI); 45 km [from Marivan to Sanandaj], after Dezli, 2400 m, 17. VI. 1997, *Ghahreman & Attar* 22480 (TUH); 5 km after Paveh to Nosud, 1500 m, 3. VI. 1999, *Ghahreman & Attar* 22375 (TUH); 6 km after Paveh to Ravansar, 1600 - 1700 m, 7. VII. 1994, *Chehregani & Zarre* 17829 (IRAN, TUH); 60 km from Paveh on the road to Kermanshah, 1390 m, 11. VII. 1997, *Ghahreman, Attar & Ghahremaninezhad* 20573 (TUH); Paveh, mnts. above Paveh, 1700 m, 18. VI. 1987, *Assadi* 60705 (TARI); Paveh, mnts. above the village Shemshir, base of Kuh-e Shahu, 1700 - 1900 m, 18. VI. 1987, *Assadi* 60744 (TARI); Paveh, the hill above Sarab Houli, 1500 - 1800 m, 18. VI. 1987, *Hamzehee* 1221 (TARI); Road of Paveh, Palanganeh, 1510 m, 3. VII. 1996, *Attar & Mirtajadini* 19872 (TUH); Rijab, 19. VI. 1968, *Iranshahr* 13163E (IRAN, W). Kurdistan: 45 km after Dezli, 2400 m, 17. VI. 1999, *Attar & Mehdigholi* 22483 (TUH); ca. 30 km S Marivan, after Dezli, on the road from Hezbolah, [32° 10' N, 46° 08' E], 1800 m, 24. VI. 2003, *Assadi* 84977 (TARI); Marivan to Paveh, Gardaneh Tate, between Dezli and Hanigarmaleh, 1800 - 2600 m, 9. VII. 1995,

Mozaffarian 74698 (TARI), *Ghahreman & Mozaffarian* 18331 (TUH); Nosoud to Marivan, between Nosoud and Gardaneh Tateh, around Dezaveh and Hanigarmaleh, 2000 m, 27. VII. 1995, *Mozaffarian* 74816(TARI).



Fig. 3. – A. *C. libanotica* [Bornmüller 944 (B100157217, B)]; B. *C. aintabensis* [Bornmüller 1403b (B100157263, B)]. Photographs provided by BGBM.

4.4.5.4 *Cousinia kopi-karadaghensis* Rech. f., Fl. Iranica 90: 249 (1972). – Holotype: Iraq, Sulaymaniyeh, Kopi Qaradagh, rocky slope, 1500 m, 17. VI. 1959, Wheeler-Haines 1545 (E!; isotypes W!, K!).

Illustration. – Fig. 4, B.

Biennial or perennial, monocarpic, up to 60 cm high, finely adpressed tomentose, soon glabrescent. Stems divaricately branched from the base or higher. Leaves \pm herbaceous, tomentose beneath and \pm glabrescent above; basal leaves up to 10 \times 5 cm including spines, lyrate or deeply pinnatisect with large terminal lobe; lower leaves attenuated at base, stem leaves sessile, leaves usually abruptly smaller and less divided towards the apex, ovate to lanceolate, pinnatifid or spiny-lobed to spiny-dentate, long decurrent to form interrupted winged stems. Capitula 2 – 4 cm broad with appendages, arachnoid, \pm glabrescent. Phyllaries 120 – 130; middle ones \pm horizontally spreading; free part of middle phyllaries constricted at base, abruptly expanded above into a usually flat, \pm horizontal, \pm straight appendage, appendage 7 – 12 mm long, 4 – 9 mm broad, attenuated into a usually long spine at apex, glabrous or \pm glabrescent, without or rarely with 1 tiny prickle on both sides. Receptacular bristles rough. Flowers 50 – 90; corolla purple, 20 – 22 mm long; anthers concolorous. Achenes ca. 4 mm long.

Flowering period. – May to June.

Taxonomic remarks. – *Cousinia kopi-karadaghensis* is a distinct species in having horizontally spreading appendages. It probably is related to *C. inflata*.

Distribution and habitat. – Endemic to NE Iraq, Mt. Qara-Dagh (Fig. 6, E), in oak forests.

Specimens seen. – Iraq: Sulaymaniyeh: 16 km NW of Darbandikhan, 700 m, 21. VI. 1960, *Al Rawi et al.* 29443 (K); Darbandikhan, 2000 ft, 21. III. 1960, *Wheeler Haines* 1635 (E, K); Kopi Qaradagh, 5 km SW of Kanitacht, 1440 m, 12. IX. 1933, *Kig & Feinbrun* 507 (W); Kopi Qaradagh, rocky slope, 14. VII. 1961, *Wheeler Haines* s.n. (E, K, W); Qaradagh Mt., 18. VII. 1964, *Makki* 525 (W).

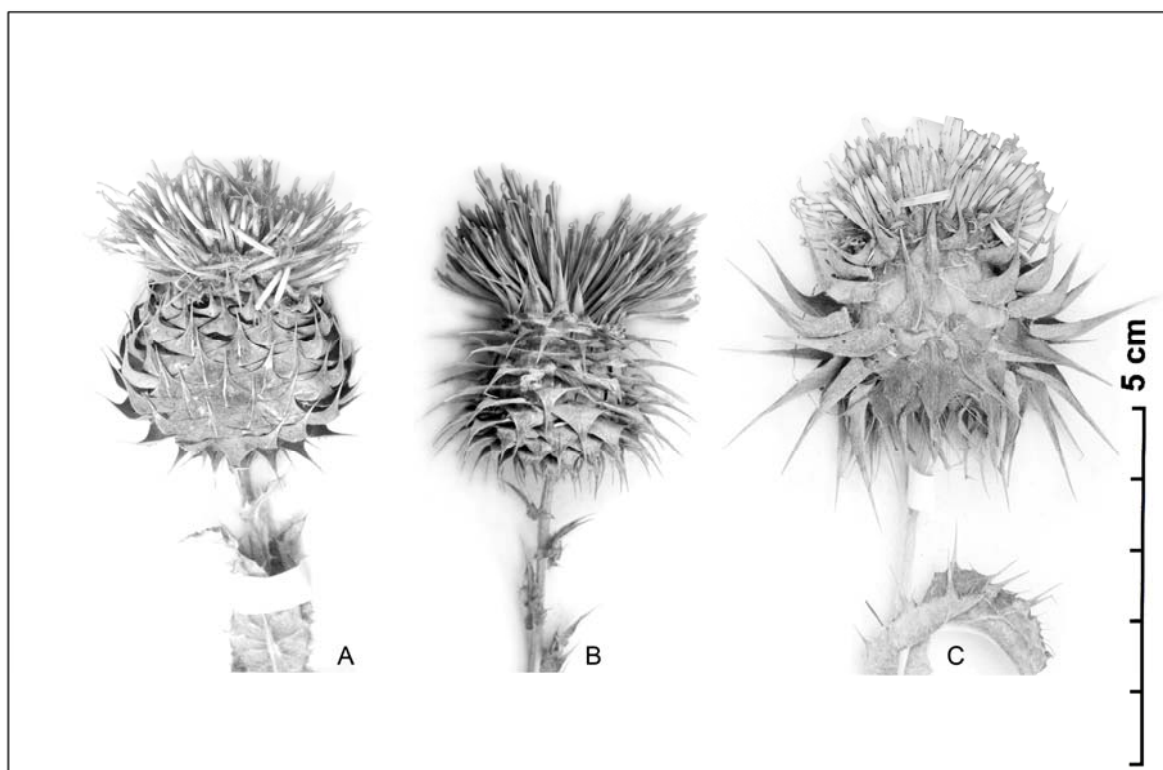


Fig. 4. – A. *C. inflata* [Assadi 84977 (TARI)]; B. *C. kopi-karadaghensis* [Makki 525 (W)]; C. *C. barbeyi* [Terme 13435E (W)]. Photographs by I. Mehregan.

4.4.5.5 *Cousinia barbeyi* C. Winkl., *Acta Horti Petropolitani* 12: 274 (1892). – Lectotype (designated here): Iran, "Persia austro-occidentalis, in monte Kuh-Gelu, monte Savers, 8000', Julio 1868", Haussknecht, s. n.", (G00034922, G-BOIS!; isotypes B!, G-BOIS!, JE!, K!, W!).

Note. – Type material of *C. barbeyi* is mounted on two sheets. The sheet labelled "G00034922" is selected as lectotype.

= *C. mozaffariani* Attar, Ghahreman & Assadi, *Pakistan J. Bot.* 32: 293 (2000). – Holotype: Iran; Fars, Nurabad, between Nurabad and Karkan, 1600m, 10.6.1992, Mozaffarian 71266 (TARI), **syn. nov.**

Note. – The original publication of *C. mozaffariani* provided contradictory data for all three diagnostic characters given to distinguish the new species from *C. barbeyi*. These are no. of flowers (± 85 in Latin diagnosis, ± 140 in English description), no. of phyllaries (± 70 in Latin diagnosis, ± 100 in English description) and corolla length (± 15 mm in Latin diagnosis, ± 24 mm in English description). Our search for material of *C. mozaffariani* deposited in TARI did not succeed in finding the holotype of this species (Mozaffarian 71266). Instead, we found a specimen collected by the same collector from an area not far from the type locality (Mozaffarian 71392 TARI) that matches the original illustration of *C. mozaffariani*.

Illustration(s). – Fig. 4, C.

Biennial or perennial, monocarpic, up to 60 cm high, arachnoid-tomentose or \pm glabrescent. Stems branched from the base or higher. Leaves leathery, tomentose on both sides or \pm glabrescent; basal leaves up to 20 \times 6 cm including spines, oblong - lanceolate to lyrate, coarsely dentate to completely pinnatisect, with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate to lanceolate, spiny-lobed, cordate to broadly cuneate at base, decurrent or sometimes long decurrent to form winged stems. Capitula 4 – 7 cm broad with appendages, arachnoid-tomentose, glabrescence or glabrous. Phyllaries 50 – 80; middle ones incurved or spreading-incurved; free part of middle phyllaries constricted at base, expanded above into a usually keeled, concave, deltoid to deltoid-lanceolate appendage; appendage 14 – 27 mm long, 7 – 16 mm broad, attenuate into a long spine at apex, usually tomentose on outside, glabrous on inside, with 0 – 2 (– 4) usually fine spines on both sides. Receptacular bristles rough or smooth. Flowers 60 – 110; corolla purple or rose, 17 – 28 mm long; anthers concolorous. Achenes 3 – 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – *C. barbeyi* is a distinct species endemic to SW Iran. The original illustration of *C. mozaffariani* as well as material collected near its type locality along with material belonging to *C. barbeyi* show that *C. mozaffariani* forms part of the morphological variation of *C. barbeyi* and can not be segregated as a separate species.

Distribution and habitat. – Endemic to SW Iran (Fig. 6, C), on stony slopes and mainly in oak forests.

Specimens seen. – Iran: Kuhgiluyeh & Boirahmad: Sisakht to Kuh Daena, Gardaneh Bizhan, 20. VI. 1969, Terme 13435E (W); Gardaneh Bizhan, 2400 - 2600 m, 4. VIII. 1978, Assadi & Mozaffarian 31300 (TARI); Tut-Nadeh to Pataveh, 3. VI. 1973, Iranshahr & Moussavi 33925E (W); 10 - 30 km from Yasouj to Sisakht, 2000 m, 24. VI. 1998, Mozaffarian & Massoumi 77990 (TARI); 30 km from Yasouj to Sisakht, 1550 m, 1. VII. 1999, Ghahreman & Attar 22494 (TUH); Between Yasouj and Dehdasht, Dilegoon, Kuh-e Saverz, 2200 - 3200 m, 19. VII. 1983, Assadi & Abouhamzeh 46423 (TARI); Between Yasouj and Dehdasht, near Sadat, 2300 m, 20. VII. 1983, Assadi & Abouhamzeh 46457 (TARI); Yasouj to Dehdasht, mt. Saverz, 2000 m, 16. VII. 2000, Ghahreman, Attar & Mehdigholi 26304 (TUH); Yasouj, near Abshar, 2200 - 2500 m, 17. VII. 1983, Assadi & Abouhamzeh 46249 (TARI); Fars: Fahlian to Hossein-Abad, 1100 - 2100 m, 1. VI. 1973, Iranshahr & Moussavi 33921E (W); Nurabad, Doshman Ziary region, Darreh Gorg

to Korekan, 2400 m, 11. VI. 1992, *Mozaffarian* 71392 (TARI); Pass between Yasuj and Babamaydan, 2300 m, 18. VI. 1977, *Edmondson & Bokhari* 2060 (E).

4.4.5.6 *Cousinia silyboides* Jaub. & Spach, Ill. Pl. Or. 2: 94, tab. 176 (1846). ≡ *Arctium silyboides* (Jaub. & Spach) O. Kuntze, Revis. Gen. 1: 308 (1891).– Holotype: Iran, “prope Ispahan”, Aucher-Eloy 4804 (P!).

Plant up to 40 cm high, canescent- or arachnoid-tomentose or glabrescent. Stems usually branched from the base or higher. Leaves leathery or leathery-herbaceous, ±arachnoid-tomentose on both surfaces, ±glabrescent or glabrous; basal leaves up to 20 × 5 cm including spines, oblong to lanceolate or oblanceolate, dentate, sinuate-lobate to deeply pinnatisect, with spiny-dentate lobes; stem leaves sessile, usually abruptly smaller and less divided towards the apex, ovate to lanceolate, spiny-lobed or -dentate, long decurrent to form winged stems. Capitula 5 – 8 cm broad with appendages, arachnoid-tomentose, glabrescent or glabrous. Phyllaries 70 – 100; middle ones ±spreading to spreading-incurved or spreading-erect, rarely imbricate, with a prominent midrib; free part of middle phyllaries usually abruptly expanded above into a keeled, ovate to rhomboid- or linear-lanceolate, ±straight appendage, appendage sometimes bent inwards or slightly backwards, 15 – 28 mm long, 4 – 15 mm broad, gradually attenuate into a long spine at apex, canescent- or arachnoid-tomentose, glabrescent or glabrous, usually with 2 – 3 spines on both sides. Receptacular bristles smooth or rough. Flowers 40 – 150; corolla pink, purple, straw-coloured or milky white, 16 – 30 mm long; anthers pink, purple or white. Achenes c. 5 mm long.

Key to the subspecies of *C. silyboides*

1. Basal leaves lyrate (western part of Zagros Mts.). subsp. *disfulensis*
– Basal leaves not lyrate (eastern part of Zagros mountains and C Iran). 2
2. Leaves and phyllaries usually densely canescent-tomentose. Involucre hidden by spreading-erect to erect appendages subsp. *zardkuhensis*
– Leaves and phyllaries usually sparsely arachnoid-tomentose, ±glabrescent or glabrous. Involucre ± visible from side; appendages usually ± spreading subsp. *silyboides*

4.4.5.6.1 *Cousinia silyboides* subsp. *silyboides*

= *C. lactiflora* Rech. f., Fl. Iranica 139a: 143 (1979). – Holotype: Iran, Esfahan, prope Daran, 2350 m, 7. VI. 1974, *Iranshahr* 34024-E (W!; isotype IRAN!), **syn. nov.**

= *C. kivar* Parsa, Fl. de l’Iran 10: 124 (1980). – Lectotype (designated here): Iran, Luristan, Aligoudarz, Ovdodareh, 17. VIII. 1957, *Houshang Pey* 10032 (K!; holo hb. Mus. Tehran, destroyed), **syn. nov.**

Note. – The holotype of *C. kivar* was deposited in the former “hb. Mus. Tehran”. According to a personal communication dated 30. April 1994 between A. Parsa and A. Ghahreman (Tehran University), all type material by A. Parsa in “hb. Mus. Tehran” was destroyed

during transfer between institutes. We found an isotype of this name in K. This specimen is selected as lectotype.

= *C. shulabadensis* Attar & Ghahreman, Iran. Journ. Bot. 9: 162 (2002). – Holotype: Iran, Luristan, Darreh Takht to Shulabad, 20 km to Shulabad, 2600 m, 29. VI. 1998, Ghahreman & Attar 21874 (TUH!; isotype TUH!); paratype: Lorestan: Khorram-Abad, Shulabad to Aligoudarz, after Sarab-e Firuz Abad, 2500 m, 24. VII. 2001, Ghahreman, Attar & Mehdigholi 27593 (TUH!), **syn. nov.**

= *C. aligudarzensis* Attar & Ghahreman, Novon 17: 145 (2007). – Holotype: Iran. Luristan: [Aligoudarz], 10 km on rd. to Khomeyn City from 3-way intersection at Aligoudarz, ca. 1500 m, 21. July 2001, Attar & A. Ghahreman 27613 (TUH; isotype TUH), paratype: same locality, 16 June 2002, Attar & Ghahreman 25000A (TUH), **syn. nov.**

Illustration. – Fig. 5, A.

Leaves and phyllaries usually sparsely arachnoid-tomentose, \pm glabrescent or glabrous. Involucre \pm visible from side; appendages usually \pm spreading.

Flowering period. – June to August.

Taxonomic remarks. – Because of some morphological similarity, *C. silyboides* was regarded as a synonym of *C. kotschyi* by Boissier (1875). The holotype of *C. silyboides* was collected by Aucher-Eloy near Esfahan (prope “Ispahan”) ca. 350 km N of the type locality of *C. kotschyi*. We studied material from both areas and found that it is different morphologically. Aucher-Eloy’s material represents part of the continuous variation of a taxon widely distributed in C Iran and matches the description and material of *C. lactiflora*, *C. kivar*, *C. shulabadensis* and *C. aligudarzensis*. None of these species can be maintained as separate.

Distribution and habitat. – Endemic to C and CW Iran (Fig. 6, F), on stony slopes and in open areas.

Specimens seen. – Iran: Luristan: Aligoudarz, Shulabad, Ghali-Kuh, 2200 - 3500 m, 20. VIII. 1982, Mozaffarian & Sardabi 42514 (TARI); Lorestan: 58 km on road from Aligoudarz to Shoulabad, the pass N of Ghali Kuh, 2900 m, 29. VI. 1977, Runemark & Lazari 26181 (TARI); Veisian, Chaleh-Ahmad mts, Tang-e Tir, 1600 m, Veiskarami 22599 (TUH); Shulabad to Aligoudarz, after Sarab-e Firuz Abad, 2500 m, 24. VII. 2001, Ghahreman, Attar & Mehdigholi 27589 (TUH); Between Aligoudarz and Khomian, 1950 m, 31. V. - 4. June. 2000, Djavadi & Ghanbari, 29546 (IRAN); Bei Gülpaigan (Golpayegan), VIII. 1899, Strauss s.n. (B); Golpayegan, Golpayegan Dam, 31. V. - 4. June. 2000, Djavadi & Ghanbari 29544 (IRAN); Golpayegan, Hendeh village, 2100 - 2250 m, 5. VII. 1983, Mowrouzi & Ashtari 3055 (TARI); Khansar, 2400 m, 27. VI. 1997, Ghahreman & Attar 20037 (TUH); Boin, Tang-Doozan, Kuh-e Hashtad, S slopes, 2700 - 3000 m, 13. VII. 1981, Etemadi 1270 (TARI); Ghaleh Musa, 75 km W Esfahan, Steinwüste, 2100 m, 10. VII. 1953, Aellen 19 (W); Ghameshloo protected area, 2400 - 2600 m, 19. VI. 1996, Assadi & Khatamsaz 76457 (TARI); Ghameshloo, 2200 m, 4. VI. 1996, Youssefi 1366 (TARI); Hazarmani versus Hossein Abad, 2000 m, 26. VI. 1996, Youssefi 1822 (TARI); Esfahan, 1600 m, 22. VII. 1971, Asefi 24407 (TARI, W); Shahreza to Semirom, 35 km to Semirom, Alijough (Dasht), 2500 m, 10.

VII. 1990, *Delghani & Tehrani* 15182 (IRAN); Kuh-e Alijough, 2600 - 3250 m, 11. VII. 1990, *Delghani & Tehrani* 15183 (IRAN); In jugo 10 km a Kohruyeh meridiem versus, Inter Shahreza et Semirom, 2600 m, 5. VI. 1974, *Rechinger* 47291 (W), *Iranshahr* 34034E (IRAN).

4.4.5.6.2 *Cousinia silyboides* subsp. *zardkuhensis* (Attar & Ghahreman) Mehregan, **comb. et stat. nov.** \equiv *C. zardkuhensis* Attar & Ghahreman, Iran. Journ. Bot. 9: 164 (2002). – Holotype: Iran, Bakhtiari, Gandoman to Boroujen, 2250 m, Attar 21887 (TUH!), paratype: Esfahan: ca. 5 km from Tiran to Shahr-e Kord, 1800 m, Ghahreman & Attar 20038 (TUH).

Illustration. – Fig. 5, B.

Leaves and phyllaries usually densely canescent-tomentose. Involucre hidden by spreading-erect to erect appendages.

Flowering period. – June to August.

Taxonomic remarks. – In comparison with *C. silyboides* subsp. *silyboides*, material of subsp. *zardkuhensis* collected mainly from Bakhtiari province has leaves and phyllaries which usually are densely canescent-tomentose (not sparsely arachnoid-tomentose as in subsp. *silyboides*) and an involucre which usually is hidden by spreading-erect to erect appendages. The involucre of subsp. *silyboides* has \pm spreading appendages that leave the base of the phyllaries visible. Although to some extent distinct, the two species are connected by intermediate forms.

Distribution and habitat. – Endemic to C Iran (Fig. 6, H), on stony slopes.

Specimens seen. – Iran: Bakhtiari: Borujen, Wastagan, 2480 m, 27. VII. 1973, *Riazi* 10276 (W); Gandoman to Boroujen, 2250 m, *Attar & Ghahreman* 21887 (TUH); In jugo inter Shahreza et Borujen, in pascuis, 2300 m, 2. VI. 1974, *Rechinger* 47038 (W); Inter Shahr-e Kord et Surashdjan, 2020 m, 1. VII. 1977, *Afzal-Rafii & Zehzad* 427 (W); Shahr-e Kord, neck Mt. between Arjenak and Margh-e Malek, Kuh-e Ghater Lang, 2450 m, 7. VIII. 1986, *Mozaffarian* 57956 (TARI); Shahr-e Kord, Shamsabad, E slope of Kuh-e Jahanbin from Kharaji, 2100 - 2400 m, 9. VII. 1986, *Mozaffarian* 57635 (TARI); Shahr-e Kord, Shamsabad, Kuh-e Zangian, E of Kharaji, 2120 - 2800 m, 17. VII. 1986, *Mozaffarian* 57872 (TARI); Shahr-e Kord, Tange Sayyad protected area, 2400 m, 19. VII. 1986, *Mozaffarian* 57914 (TARI); Tange Sayyad protected area, Pir Kuh, 2400 m, 14. VI. 1987, *Mozaffarian* 62126 (TARI); Shahr-e Kord, Top mnts. of Saldaron from Deh-e Cheshmeh, W slope, 2200 m, 16. VII. 1986, *Mozaffarian* 57844 (TARI); Esfahan: Between Tiran and Saman, ca. 15 km from Tiran, 2000 m, 23. VI. 1998, *Mozaffarian & Massoumi* 77958 (TARI); 12 km E of Borujen, prope Faradoneh, 31. V. 1974, *Iranshahr* 34022E (IRAN, W); In declivibus montium 12 km a Borujen versus Sefid Dasht, substr. calc., 2300 - 2700 m, 2. VII. 1974, *Rechinger* 47082 (B, M, W); In jugo inter Shahreza et Borujen, in pascuis, 2300 m, 2. VII. 1974, *Rechinger* 47041 (B, W).

4.4.5.6.3 *Cousinia silyboides* subsp. *disfulensis* (Bornm.) Mehregan, **comb. et stat. nov.** \equiv *C. disfulensis* Bornm. in *Köie*, Beitr. Fl. Südwest-Irans 1 (Danish Sci. Invest. Iran Pt. 4): 23 (1945). – Lectotype (designated here): Iran, "Luristan, Chah-Bazan, 60 km nördl. von Dizful, 1200 m, 28. IV. 1937", *Köie* 793 (B!; isotype C).

Note. – Type material of *C. disfulensis* is deposited in B and C. Since no holotype was designated by the original author, material deposited in B was selected as lectotype.

= *C. jacobsii* Rech. f., *Fl. Iranica* 90: 237 (1972). – Holotype: Iran, Ilam, open forest dominated by *Quercus persica*, on slopes of rocky limestone, 46° 26' E, 33° 42' N, 1700 - 1900 (-2400) m, 9. VI. 1963, Jacob 6834 (W!; isotype K!), **syn. nov.**

= *C. kermanshahensis* Attar, Ghahreman & Assadi, *Iran. Journ. Bot.* 9: 56 (2001). – Holotype: Iran, Kermanshah, Eslam-Abad-Gharb, Mahi Dasht, Gardaneh Bouzhan, 1300 m, 2. VII. 1996, Attar & Mirtajadini 19810 (TUH!; isotype TUH!), **syn. nov.**

Illustration. – Fig. 5, C.

Leaves lyrate. Leaves and phyllaries usually sparsely arachnoid-tomentose, ±glabrescent or glabrous. Involucre ± visible from side; appendages usually ± spreading.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia silyboides* subsp. *disfulensis* was first published as a species by Bornmüller (l.c.) based on two young specimens collected by Köie. Köie's specimens are characteristic in having lyrate basal leaves and distinct phyllaries with spreading and ±deltoid-lanceolate appendages, characters also found in combination in widely distributed populations in oak forests in W Iran. Our study of new and mature material recently collected in neighbouring areas but published as *C. jacobsii* and *C. kermanshahensis* revealed that these species have the diagnostic characters of subsp. *disfulensis* and grow in essentially the same habitat, i.e., in *Quercus brantii* forests. *Cousinia silyboides* subsp. *disfulensis*, distributed on western slopes of the Zagros mountains, differs from subsp. *silyboides* mainly in having lyrate basal leaves.

Material of *C. shulabadensis* represents an extreme part of the variation and has more xeromorphic features such as less divided and more leathery leaves.

Distribution and habitat. – *Cousinia silyboides* subsp. *disfulensis* is distributed in the mountainous transitional area of the western part of the Zagros Mts. (Fig. 6, G) on stony slopes and mainly in oak forests.

Specimens seen. – Iran: Ilam: Between Eyvan-e Gharb and Ilam, 1500 m, 5. VII. 1999, Ghahreman, Attar & Mehdigholi 22370 (TUH); 10 due N of Ilam, NE side of Kuh-i Sharazul, 4650 ft., 3. VI. 1960, Wright & Bent 603-106 (K, W); Kermanshah: Near Kermanshah, [34° 25' N, 46° 15' E], 5500 ft., 18. VIII. 1963, Corley 58 (K); Krend, 1600 m, 25. VI. 1991, Shahsavari 69804 (TARI); Luristan: ca. 30 km S of Kuh-e-Dasht, [33° 21' N, 47° 30' E], 1300 m, 16. VI. 1959, Wendelbo 2010 (W).

Materials of *Veiskarami* 22600 (Iran, NW of Khorram-Abad, 1400 m, TUH) shows a morphologically intermedicity between *C. aintabensis* subsp. *disfulensis* & *C. sagittata*.

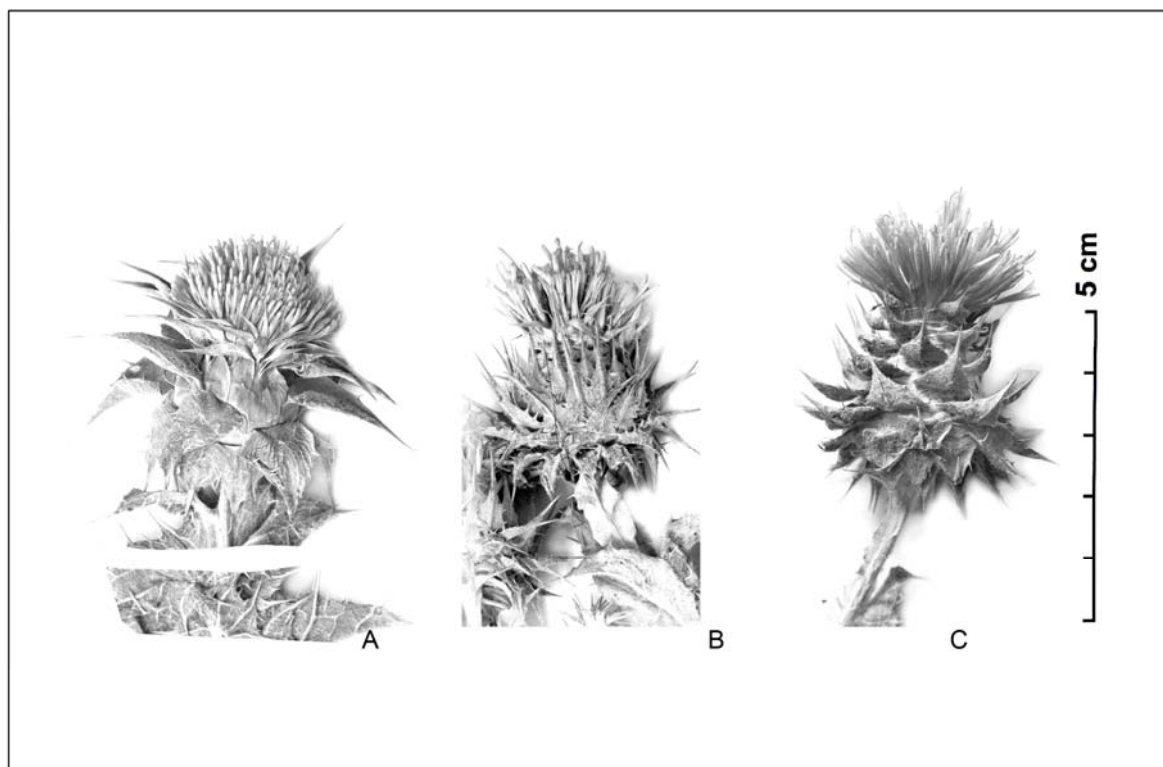


Fig. 5. – A. *C. silyboides* subsp. *silyboides* [Djavadi & Ghanbari 29546/3 (IRAN)]; B. *C. silyboides* subsp. *zardkuhensis* [Mozaffarian 62126 (TARI)]; C. *C. silyboides* subsp. *disfulensis* [Ghahreman et al. 22370 (TARI)]. Photographs by I. Mehregan.

4.4.5.7 *Cousinia odontolepis* DC., Prodr. 6: 556 (1838). ≡ *Arctium odontolepis* (DC.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Iraq, "in deserto Assyriae", 1837, Aucher-Eloy 3496 (G!; isotypes P!, K!).

Note. – We found three herbarium sheets with no. 3496 collected by Aucher-Eloy deposited in G, K and P. As no lectotype has been designated before, the sheet deposited in G is selected as lectotype of *C. odontolepis*. As noted before by Rechinger (1972), the origin of the Aucher-Eloy's material clearly can not have been "In deserto Assyriae" because the species grows in mountainous regions of N and NE Iraq and not in deserts.

Plant up to 50 cm high, densely arachnoid-tomentose, tomentose or ±glabrescent. Stems branched from the base or higher. Leaves leathery to herbaceous, tomentose on both sides, or tomentose beneath and glabrescent above; basal leaves up to 25 × 10 cm including spines, usually lyrate, sometimes lanceolate or oblanceolate, dentate to deeply pinnatisect or pinnatipartite, with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate to oblong-lanceolate, spiny-lobed, cuneate at base, decurrent to form winged stems. Capitula 2.5 – 7 cm broad with appendages, usually arachnoid-tomentose or ±glabrescence. Phyllaries 50 – 120; middle ones recurved, ±spreading, spreading-incurved, appressed-incurved or –erect or imbricated; free part of middle phyllaries usually abruptly expanded above into a usually keeled, concave or flat, rhomboid, deltoid, rhomboid- or deltoid-lanceolate or lanceolate appendage; appendage 10 – 30 mm long, 4 – 10 mm broad, attenuate into a long spine at apex, arachnoid-tomentose, tomentose or glabrescent, with 2 – 4 (– 6) spines on both sides. Receptacular bristles usually

rough. Flowers (20-) 40 – 120; corolla purple, rose or flavescent, 18 – 30 mm long; anthers concolorous. Achenes 4 – 5 mm long.

Key to the subspecies of *C. odontolepis*

1. Uppermost leaves enclosing the involucre. Phyllaries usually densely arachnoid-tomentose, with recurved appendages (Iraq, Erbil, Mts. Qandil and E of Rawanduz) subsp. *kurdica*
 – Uppermost leaves not enclosing the involucre. Phyllaries usually sparsely arachnoid-tomentose or glabrescent, with ±spreading, recurved or inflated-incurved appendages (Iraq, provinces Mosul and Sulaymaniyah). subsp. *odontolepis*

4.4.5.7.1 *Cousinia odontolepis* subsp. *odontolepis*

= *C. cymbolepis* Boiss., Diagn. Pl. Orient. Ser. 1, 6: 119 (1846). "Jul. 1846" ≡ *C. schultziiana* Jaub. & Spach, Ill. Pl. Or. 2: 95, tab. 177 (1846). "Jul. 1846". ≡ *Arctium cymbolepis* (DC.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Iraq, "in regionibus superioribus montis Gara Kuristaniae", 6. VIII. 1841, Kotschy 380 (G!; isotypes B!, E!, G!, JE!, K!, M!, P! "also lectotype of *C. schultziiana*", W!), **syn. nov.**

Note. – *Cousinia cymbolepis* and *C. schultziiana* are based on the same material collected by Kotschy from N Iraq. There are several herbarium sheets with no. 380 collected by Kotschy now deposited in B, E, G, JE, K, M, P and W.

= *C. baueri* Bornm. & Nab. In Bornm., Öst. Bot. Zeitschr. 63: 61 (1913). – Type: Iraq, "Assyria, in derelictis horti coenobii Mâr-Jakub prope Mossul", ca. 1000 m, 7. VI. 1910. Nábělek 3903 (BRA, photo!).

= *C. odontolepis* DC., var. *leiolepis* Bornm., Feddes. Rep. 46: 282 (1939). – Lectotype (designated here): Iraq, "Jebel Baykhair near Zakho", 15. – 18. VI. 1934, Field & Lazar 798 (W!; isotypes P!, K!, G!).

= *C. leatherdalei* Rech. f., Österr. Bot. Zeitschr. 100: 462 (1953). – Holotype: Iraq, Mosul, Sursang, 8 km W of Amadia, 3200 ft., 4. VI. 1947, Leatherdale 101 (holo BM000927947, BM!; isotype W!, "fragment"), **syn. nov.**

= *C. mazu-shirinensis* Rech. f., Fl. Iranica 90: 226 (1972). – Holotype: Iraq, Kurdistan, Arbil, Kani Mazu Shirin, 5000 ft., 20. VI. 1961, Wheeler-Haines 2046 (E!; isotypes W!, K!).

= *C. acanthophysa* Rech. f., Fl. Iranica 90: 227 (1972). – Holotype: Iraq, Kurdistan, Mosul, ad confines Turciae prov. Hakkari, in ditione pagi Sharanish, in montibus calc. a Zakho septentrionem versus, in declivibus saxosis (Tonschiefer) montis Zawita, 1400 m, 4. - 9. VII. 1957, Rechinger 10922 (W!; isotypes B!, E!, K!, M!), **syn. nov.**

Illustration(s). – Fig. 7, A-C.

Very variable. Uppermost leaves not enclosing the involucre. Phyllaries usually sparsely arachnoid-tomentose or glabrescent, with tightly imbricate, appressed-incurved, \pm spreading, spreading-erect, recurved or inflated-incurved appendages.

Flowering period. – (May-) June to August.

Taxonomic remarks. – Study of material of *C. odontolepis* subsp. *odontolepis*, *C. cymbolepis* (= *C. schultzi*), *C. baueri*, *C. leatherdalei*, *C. mazu-shirinensis* and *C. acanthophysa* revealed that all these are very variable but connected by intermediate forms. None of them can be circumscribed as separate species. Appendages vary from \pm tightly imbricate and appressed in material of *C. mazu-shirinensis* and *C. acanthophysa* to \pm spreading in some populations of *C. odontolepis* and *C. baueri* or strongly recurved in *C. leatherdalei*. Even the type material of *C. cymbolepis* mounted on several sheets has phyllaries with recurved, \pm spreading or incurved appendages. The phyllaries of *C. acanthophysa* are imbricated, appressed-incurved or –erect as in *C. mazu-shirinensis*, but larger.

Distribution and habitat. – Endemic to the mountains of N & NE Iraq, provinces Mosul and Sulaymaniyah (Fig. 11, A), on stony slopes and in oak forests.

Specimens seen. – Iraq: Mosul: Galli Zawita, NE of Zakho nr. Turkish border, 1400 m, 8. VII. 1957, *Al Rawi* 23563 (K); Zawita Gorge, Aqra-Dinart, 8. VI. 1958, *Ghafran* 26137 (K); Berd Agha Gin Village, c. 18 km NW of Rania, 1115 m, 12. V. 1959, *Al Rawi et al.* 28691 (K); Ad confines Turciae prov. Hakari, in ditione oppidi Zakho, in jugo inter Dagh al Radzjiem et Sharanish, in saxosis calc., ca. 900 m, 2. - 4. VII. 1957, *Rechinger* 10796 (E, W); Inter Dohuk et Amadiya, in apertis quercetorum supra Suwara Tuka, 1500 m, 10. - 12. VII. 1957, *Rechinger* 11552 (B, E, K, M, W); Inter Dohuk et Amadiya, in pinetis (*P. brutia*) saxosis ad Zawita, 21 km a Dohuk orientum versus, substr. dolomit, ca. 800 m, 10 - 12. VII. 1957, *Rechinger* 11549 (E, W); Inter Dohuk et Amadiya, in Quercetim infra Sirsank, ca. 800 m, 10 - 12. VII. 1957, *Rechinger* 11952 (M, W); Inter Dohuk et Amadiya, ca. 12 km a Dohuk orientum versus, ca. 800 m, 10 - 12. VII. 1957, *Rechinger* 11979 (W); Inter Mosul et Zakho. In saxosis calc. 103 km a Mosul septentr. versus, 2. VII. 1957, *Rechinger* 10652 (B, E, K, M, W); Sarsang, 1100 m, *Anders* 2289 (W); Sarsang, 1200 m, 20. VI. 1968, *Anders* 2334 (W); Inter Dohuk et Amadiya, in saxosis calc. supra Sirsank, 1200 m, 10. - 12. VII. 1957, *Rechinger* 11643 (E, W); Jabal Khantur prope Sharanish, 1100 - 1400 m, 4. - 9. VII. 1957, *Rechinger* 12049 (B, E, G, K, M, W); Ispindari, above Suwaratuka, 1250 m, 11. VI. 1958, *Chapman* 26328 (K); Sersang, 3500 ft, 18. VII. 1955, *Wheeler Haines* 581 (E, K); Sersang, 3500 ft, 5. VIII. 1957, *Wheeler Haines* 1333 (E, K); Sersang, 3500 ft, 18. VII. 1955, *Wheeler Haines* s.n. (E); Sersang, 15. V. 1957, *Wheeler Haines* s.n. (E); 23 km NE of Zakho, 25 km S of Sharanish, 990 m, 4. VII. 1957, *Al Rawi* 23189 (K); 5 km S of Zakho, 700 m, 3. VII. 1957, *Al Rawi* 23092 (K); Bikher Mt. near Zakho, 700 - 800 m, 2. VII. 1957, *Al Rawi* 23049 & 22984 (K); Sirsang, 9. VIII. 1961, *Wheeler Haines* s.n. (E); Amadia-Sirsang road, gentle smooth slope with cut oak and scrub, 9. VIII. 1961, *Wheeler Haines* s.n. (W); Badi, 860 m, 2. VI. 1978, *Omar et al.* 49639 (K); Dori Village, 5 km E Kani Masi, 1320 m, 6. VII. 1976, *Omar & Kaisi* 45432 (K); Kergedraija, 1800 m, 21. VI. 1947, *Al Rawi* 9140 (K); Khantur Mt., NE of Zakho, 1770 m, 6. VII. 1957, *Al Rawi* 23478 & 23403 (K); Seramadia, 5900 ft., 3. VIII. 1933, *Guest* 4981 (K); Seramadia, 13. VIII. 1961, *Agnew & Haines* W2107 (K, W); Sulaf, hillside with cut oak shrub, 9. VIII. 1961, *Wheeler Haines* 2062 (E, K, W); Sundur, near Dohuk, 19. VIII. 1959, *Wheeler Haines* 1570 (E, K, W); Zawitah Gorge, 2800 ft., 26. IX. 1933, *Guest* 3715 (K, W); M. Potine (Botin) 10 km NNW Shirwan Mazin (Mazu Shirin), 21. VI. 1961, *Wheeler Haines* (E); Zewita pr. Shirwan Mazin (Mazu Shirin), 19. VI. 1961, *Wheeler Haines* 2147 (E, K); On the Mt. NNW of Seri Hasan Beg, 6500 ft., 24. VII. 1932, *Guest*

2907 (K); Sulaymaniyah: Asme, 13. VII. 1961, *Wheeler Haines* 2107 (E, W); 10 Km from Sulaimaniyah to Choart, 26. VII. 1973, *Noori & Khamidi* 41254 (K); Azmir, 860 m, 15. V. 1971, *Omar et al.* 38041 (K); Gweija Dagh above Sulaimaniyah, 1400 m, 4. VI. 1948, *Al Rawi & Gillett* 11715 (K).

4.4.5.7.2 *Cousinia odontolepis* subsp. *kurdica* (C. Winkl. & Bornm.) Mehregan, **comb. et stat. nov.** \equiv *C. kurdica* C. Winkl. & Bornm., Bull. Herb. Boissier 3: 564 et 567 (1895). – Lectotype (designated here): Iraq, Arbil (Erbil), "In terrae Riwandous monte Sakri-Sakran altitudine 13 - 1700 m, Junio mense anni 1893, Bornmüller 1404", (B100093376, B!; isotypes B!, G!).

= *C. carduchorum* C. Winkl. & Bornm., Bull. Herb. Boissier 3: 566 et 568 (1895). "as α minor" – Lectotype (designated here): Iraq, "in Kurdistaniae terra Riwandous, in monte Händarin", 12 - 1300 m, 28. VI. 1893, Bornmüller 1406 (B100088384, B!; isotypes B! „1406b“, G!, JE!). **syn. nov.**

= *C. carduchorum* var. *major* C. Winkl. & Bornm., Bull. Herb. Boissier 3: 569 (1895). "as β major" – Holotype: Iraq, "in monte Sakri-Sakran ditionis Riwandous", 1700 m, 23. VI. 1893, Bornmüller 1405 (B100088383, B!; fragment in JE!).

Note. – According to Bornmüller (l.c.), *C. carduchorum* var. *carduchorum* (autonym, originally as " α minor") and *C. carduchorum* var. *major* were described based on material collected by Bornmüller from Mt. "Händarin" near "Riwandous" (no. 1406 "with duplicates"; stems 15 – 25 cm long) and Mt. "Sakri-Sakran" (syntypes including no. 1405 "unicum"; 1406b "unicum"; stems 30 – 40 cm long), respectively. We found several herbarium sheets in B, G and JE which match the description of *C. carduchorum* var. *carduchorum* under no. 1405, 1406 and 1406b, plus a single sheet in B under no. 1405 which matches the description of *C. carduchorum* var. *major*. Examination of the type material, its labels and the original publication revealed some contradictions. We designated sheet B100088384 as lectotype of *C. carduchorum* var. *carduchorum*. Sheet B100088384 clearly matches the original illustration of *C. carduchorum* (α minor), but is mistakenly labeled as no. 1405 (not 1406 as cited by Bornmüller). The label can not be correct because the type material of *C. carduchorum* var. *major* (no. 1405) in B and JE (fragment) is from a single sheet (B100088383) designated by Bornmüller as "unicum". Therefore, the label of sheet B100088384 must be corrected to no. 1406.

Citing no. 1406b as material for *C. carduchorum* var. *major* in the original publication seems to be a mistake by Bornmüller himself. Sheet B100088382, collected by Bornmüller as no. 1406b clearly matches the description of *C. carduchorum* var. *carduchorum* (α minor), was mistakenly named var. *major* in the original publication. Its label seems to have been later corrected by Bornmüller himself to var. *minor* (designated by Bornmüller's handwriting as "unicum").

On this background, some clarification and correction is necessary: 1) type material of *C. carduchorum* var. *carduchorum* (α minor) includes sheets no. 1406 (multiple) and 1406b (single), 2) The type material of *C. carduchorum* var. *major* is a single sheet under no. 1405 and does not include sheet no. 1406b.

= *C. qandilica* Rech. f., Fl. Iranica 90: 223 (1972). – Holotype: Iraq, Arbil, Montes Qandil, ad

confines Persiae, in quercetis saxosis inter Shahidan et Pushtashan, substr. Calc., 1200 m, 28. VII. 1957, Rechinger 11003 (W!; isotype M!), **syn. nov.**

Illustration. – Fig. 7, D.

Uppermost leaves enclosing the involucre. Phyllaries usually densely arachnoid-tomentose, with recurved appendages.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia odontolepis* subsp. *kurdica*, *C. carduchorum* and *C. qandilica*, all distributed in NE Iraq (Qandil mountain range and neighbouring area), are connected by intermediate forms. Subspecies *kurdica* is similar to subsp. *odontolepis* and differs mainly in having a densely arachnoid-tomentose indumentum.

Distribution and habitat. – Endemic to N Iraq (province Erbil; Fig. 11, B), on stony slopes and in oak forests.

Specimens seen. – Iraq: Erbil: Kermasur lake, Qandil range, 2210 - 2610 m, 1. VIII. 1957, *Al-Rawi & Serhang* 24137 (K); Mons Helgurd ad confines Persiae, in valle supra pagum Nowanda, [36° 40' N, 44° 50' E], 2600 m, 10. - 14. VIII. 1957, *Rechinger* 11348 (E, K, M, W); Montes Qandil ad confines Persiae, in decliv. orient. supra Pushtashan, in Astragaletis, [36° 30' N, 45° E], 2000 - 2200 m, 28. VII. - 1. VIII. 1957, *Rechinger* 11748 (E, W); Montes Qandil, in quercetis infra Pushtashan versus Shahidan, 1000 m, 8. - 9. VIII. 1957, *Rechinger* 11022 (E, G, K, W); Baaki Hawaran Mt., roadside, 1500 - 1820 m, 29. VII. 1957, *Al-Rawi* 23960 (K); Koorak Mt., N of Shahidan Project, ca. 1000 m, 28. VII. 1957, *Al-Rawi & Serhang* 23800 (K).

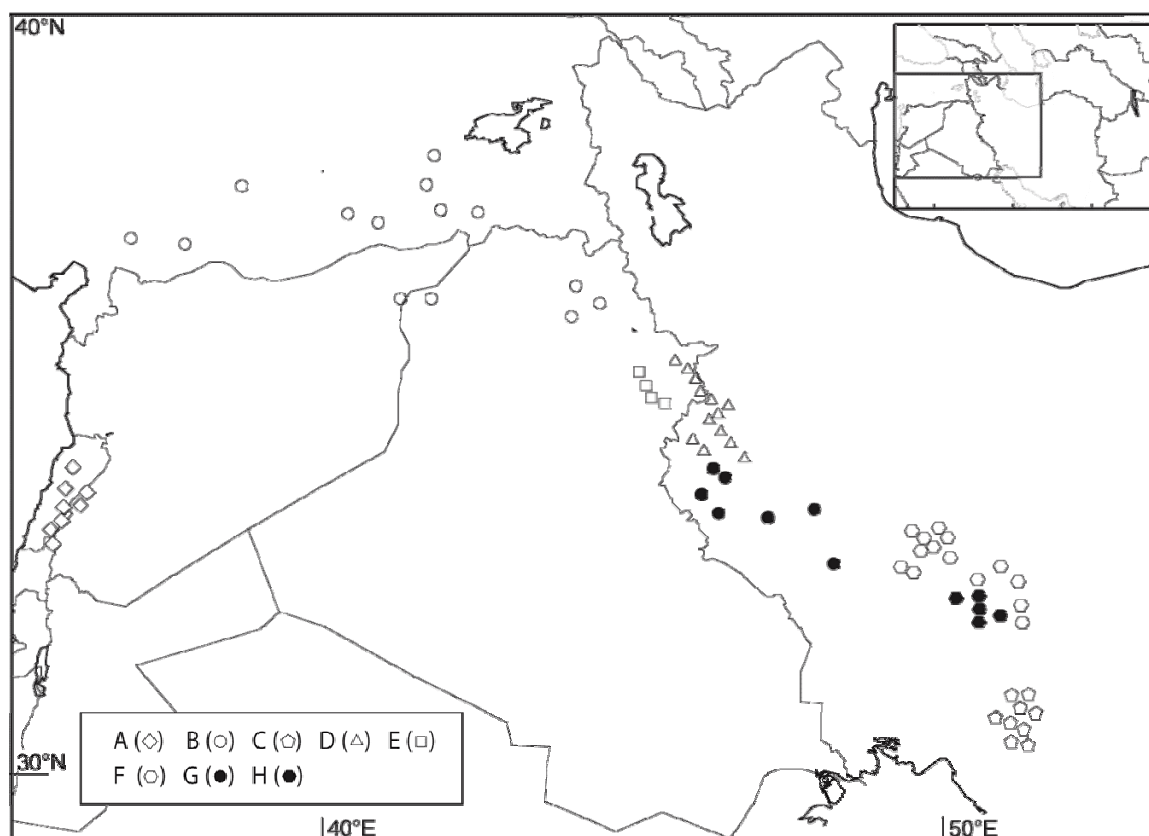


Fig. 6. – Distribution of A. *C. libanotica*; B. *C. aintabensis*; C. *C. Barbeyi*; D. *C. Inflata*; E. *C. kopi-karadaghensis*; F. *C. silyboides* subsp. *silyboides*; G. *C. silyboides* subsp. *disfulensis*; H. *C. silyboides* subsp. *zardkuhensis*. Each symbol indicates the locality of a single collection or several collections made from the same or nearby localities.

4.4.5.8 *Cousinia noeana* Boiss., *Diagn. Pl. Orient. Ser. 2, 3: 57* (1856). = *Arctium noeanum* (Boiss.) O. Kuntze, *Revis. Gen. 1: 308* (1891). – Lectotype (designated here): Iran, “Kirrind in Persia in montibus ibidem”, VIII. 1851, Nöe 1028 (G-BOIS!; isotypes P!).

= *C. kirrindica* Bornm. & Rech. f., *Bornm. & Rech. f., Feddes Repert. 48: 141* (1940). – Holotype: Iran, Kermanshah, inter Kermanshah et Kirrind, substrato calcareo, 17. VIII. 1937, Rechinger 2136 (W!; isotype B! “fragment”), **syn. nov.**

= *C. mobayenii* Ghahreman & Attar, *Iran. Journ. Bot. 8: 260* (2000). – Type: Iran, Kermanshah, between Eslamabad-e Gharb and Kerend-e Gharb, 3 km after Firouzabad village, 1490 m, 16. VII. 1997, Ghahreman & Attar 20569 (holo TUH!); Paratypes: Kermanshah, between Eslamabad-e Gharb and Kermanshah, 1500 m, Ghahreman & Attar 22378 (TUH); Hamz’ee & Hatami 1425 (TARI); Assadi 60789 (TARI), **syn. nov.**

Illustration. – Fig. 7, E.

Plant up to 40 cm high, arachnoid-tomentose or ±glabrescent. Stems branched from the base or higher. Leaves leathery or herbaceous, tomentose on both sides, or ±glabrescent

above; basal leaves up to 20 × 6 cm including spines, oblong-lanceolate, pinnatifid to deeply pinnatisect, with spiny-dentate lobes; stem leaves sessile, abruptly or gradually smaller and less divided towards the apex, ovate to lanceolate, spiny-lobed, usually long-decurrent to form winged stems. Capitula 2 – 7.5 cm broad with appendages, arachnoid-tomentose or ±glabrescence. Phyllaries 70 – 120; middle ones recurved or ±spreading; free part of middle phyllaries slightly expanded above into a usually keeled or flat, lanceolate to linear appendage; appendage 12 – 30 mm long, 3 – 6 mm broad, attenuate into a long spine at apex, tomentose or glabrous, with 2 – 3 spines on both sides. Receptacular bristles usually rough. Flowers 20 – 120, corolla purple or rose, 15 – 23 mm long; anthers concolorous. Achenes 3 – 5 mm long.

Flowering period. – Juni to August.

Taxonomic remarks. – The type material of *C. noeana* deposited in G-BOIS and P was not seen by Rechinger when he published his treatment of *C. sect. Cynaroideae* (Rechinger 1972). The type material of *C. noeana*, *C. kirrindica* and *C. mobayenii* was collected in a relatively small area near Kerend (Iran, province Kermanshah). Examination of this type material and other specimens collected around Kerend shows that all material belongs to a single species with limited morphological variation.

Distribution and habitat. – Endemic to W Iran (provinces Kermanshah; Fig. 11, C), in oak forests.

Specimens seen. – Iran: Ilam: Quercus forest, 1800 m, 10. VII. 1997, *Ghahreman & Attar* 19711 & 19705 (TUH); 100 km W of Kermanshah, Beig-Rezaee village, 1560 m, 24. VIII. 1987, *Hamzehee & Hatami* 1683 (TARI); 18 km N of Kerend-e Gharb, Lotfeh village, 1760 m, 21. VI. 1987, *Hamzehee & Hatami* 1425 (TARI); 43 km SW of Kermanshah, 1680 m, 14. VI. 1959, *Pabot* 1873 (TARI); Kermanshah, Resarch Inst. of Forests & rangelands, 1450 m, 24. VI. 1987, *Hamzehee & Hatami* 1514 (TARI); Mnts. above Kerend, beginning of the road Dalahu, 1700 - 2000 m, 18. VI. 1987, *Assadi* 60789 (TARI); Road of Eslamabad-Zavar-e Kuh, 1600 m, 4. VII. 1997, *Ghahreman & Attar* 19962 (TUH); Road of Ilam, Kalleh-Joub, 1350 m, 16. VII. 1997, *Ghahreman & Attar* 20563 (TUH); Sarabe Kerend, 2030 m, 29. VI. 1967, *Iranshahr & Terme* 12200E (IRAN, W); Inter Qasr Shirin et Kermanshah, inter Shahabad et Kermanshah, substr. calc., 28. VIII. 1957, *Rechinger* 14618 & 14621 (B, E, K, M, TARI, W); Kirrind (Karand) in Persia in montibus ibidem, VIII. 1851, *Noe* 629 (P).

4.4.5.9 *Cousinia algurdina* Rech. f., Anz. Österr. Akad. Wiss., Mat.-Naturwiss. 101: 344 (1964). – Lectotype (designated here): Iraq, Erbil, Mons Helgurd (Algurd) ad confines Persiae, in valle supra pagum Nowanda, 2600 – 3000 m, 36° 40' N, 44° 50' E, 10. - 14. VIII. 1957, *Rechinger* 11465 („11465-II“, W!; iso B!, E!, K!, M!, „14465-I“ W!).

Note. – Type material of *C. algurdina* at W is mounted on two sheets, both of them with a “Typus” stamp. Sheet no. 11465-II is here selected as lectotype.

= *C. cynaroides* (M.B.) C. A. Mey. var. *arlgirdensis* Blakelock, Kew Bull. 1949: 50 (1949). – Lectotype (designated here): Iraq, Sulaymaniyah, Arl Gird Dagħ, 2700 m, 24. VII. 1932, *Guest* 2951 (K!; isotype K!).

Note. – The specimen with five capitula is here selected as lectotype.

Illustration. – Fig. 12, A.

Plant up to 50 cm high, densely arachnoid-tomentose or tomentose, usually yellowish especially in upper part. Stems erect, branched above. Leaves leathery, tomentose on both sides; basal leaves up to 15 × 4 cm including spines, linear-lanceolate to oblanceolate, pinnatilobed to pinnatisect, with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate to lanceolate, spiny-lobed, round to cuneate at base, up to 2 cm decurrent. Capitula 4.5 – 7 cm broad with appendages, usually yellowish arachnoid-tomentose. Phyllaries 40 – 60; middle ones ± spreading; free part of middle phyllaries more or less expanded above into a usually keeled, lanceolate appendage, appendage 20 – 25 mm long, 5 – 8 mm broad, attenuate into a long spine at apex, arachnoid-tomentose, usually with 2 – 3 spines on both sides. Receptacular bristles usually rough. Flowers 120 – 150; corolla creamy white or flavescent, 22 – 27 mm long; anthers concolorous. Achenes 4 - 6 mm long.

Flowering period. – July to August.

Taxonomic remarks. – Although *C. algurdina* along with *C. odontolepis* subsp. *kurdica* are distributed in the Qnadil range in N Iraq, they are not sympatric. *Cousinia algurdina* grows mainly at alpine altitudes, and *C. odontolepis* subsp. *kurdica* grow at subalpine altitudes or lower. *Cousinia algurdina* is more similar to *C. canescens* but differs by having appendages with spines on their sides and by having a yellowish indumentum especially in its upper part.

Distribution and habitat. – Endemic to the alpine regions of Qnadil range (mountainous area between provinces Erbil (Iraq), Sulaymaniyah (Iraq) and Iran; Fig. 13, F), on rocky alpine summits and east- and south-facing mountain slopes.

Specimens seen. – Iraq: Erbil: Montes Qandil ad confines Persiae, [36° 30' N, 45° E], 2000 - 2600 m, 28. VII. - 1. VIII. 1957, *Rechinger* 11116 (E, W); Sulaymanieh: Malikh Mt. (Goomasur), Qnadil range, 2400 - 2600 m, 30. VII. 1957, *Al Rawi* 24042 (K).

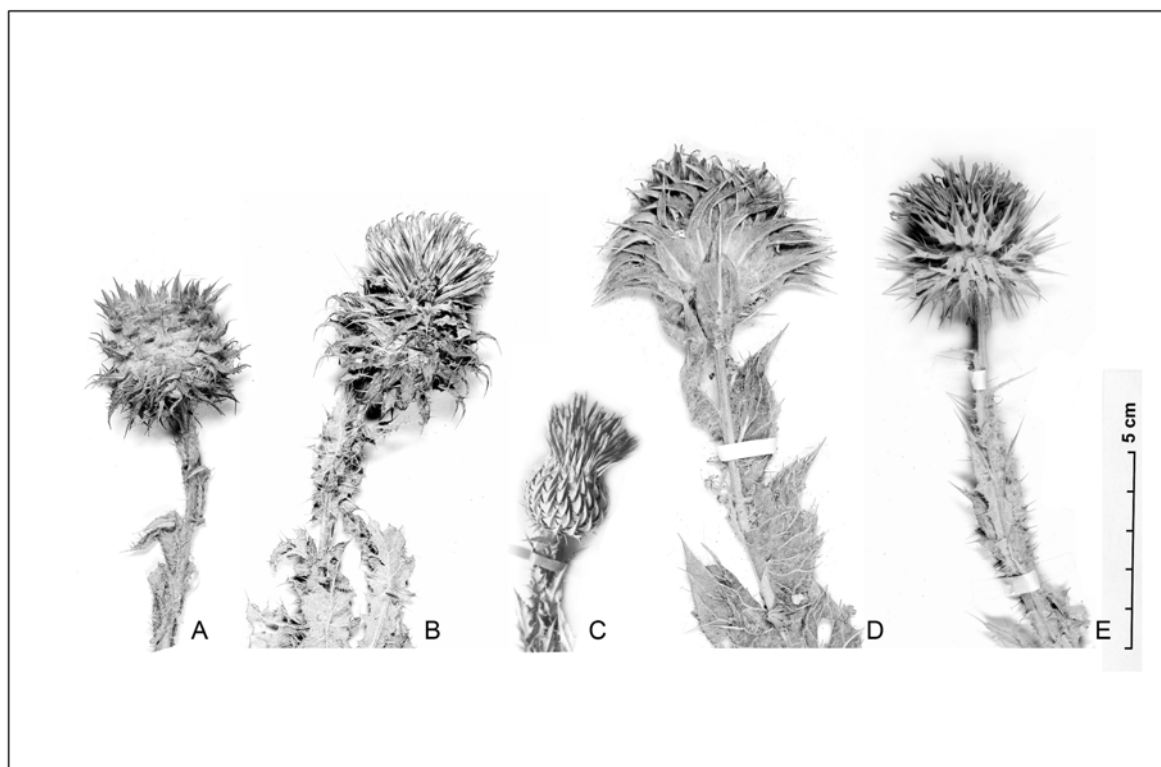


Fig. 7. – A. *C. odontolepis* subsp. *odontolepis* [Kotschy 380 (B100158867, B)]; B. *C. odontolepis* subsp. *odontolepis* [Rechinger 12049 (B100157224, B)]; C. *C. odontolepis* subsp. *odontolepis* [Agnew et al. 2147 (E)]; D. *C. odontolepis* subsp. *kurdica* [Bornmüller 1404 (B100093377, B)]; E. *C. noeana* [Rechinger 14618 (B100158891, B)]. Photographs A, B, D & E provided by BGBM. Photograph C by I. Mehregan.

4.4.5.10 *Cousinia canescens* DC., Prodr. 6: 556 (1838). – Lectotype (designated here): Iran, “Persia”, 1837, Aucher-Eloy 3494 (G!; isotypes K!, P!).

= *C. onopordon* Freyn. & Sint., Öst. Bot. Zeitschr. 42: 207 (1892). – Lectotype (designated here): Turkey, Erzincan, Sipikordagh, In declivib. supra pag. Sipikor., 25. VII. 1890, Sintenis 3285 (W!; isotypes P!, JE!, WU!).

= *C. onopordon* β *lancea* Bornm., Feddes. Rep. 46: 284 (1939). – Holotype: Turkey, ad Euphratem superiorem, 1834, Montbert 2397 (W!; isotypes B!, E!, P!).

Note. – Sheet no. 1889-171723 is the holotype.

= *C. onopordon* f. *anodonta* Bornm., Feddes. Rep. 46: 285 (1939). – Lectotype (designated here): Turkey, Euphrat, 1834, Montbert 2397 (W!; isotype W!).

Note. – Sheet no. 1889-170989 is the lectotype.

= *C. onopordon* α *genuina* Bornm., Feddes. Rep. 46: 284 (1939). – Lectotype (designated here): Turkey, Chama ad Euphratem inter Altbuschik Surek, 30. VI. 1889, Sintenis 1062 (W!; isotypes K!).

= *C. eriocephala* Boiss. & Hausskn. in Boiss., Fl. Or. 3: 504 (1875). ≡ *Arctium eriocephalum* (Boiss. & Hausskn.) O. Kuntze, Rev. Gen. Pl. 1: 307 (1891). – Lectotype (designated here): Turkey, Taurus Cataonicus, “in lapidosus pr. Berytdagh”, 8000', 6. VIII. 1865, Haussknecht 1002 (G00152016, G-BOIS!; isotypes E!, G-BOIS!, JE!, P!, W!); Syntype (supplement): Armenia, In valle Goshkar warto, 5600 ped., 20. VIII. 1859, Kotschy Suppl. 630 (G!, W!), **syn. nov.**

= *C. zagrica* Attar, Ghahreman & Assadi, Sendtnera 8: 5 (2002). – Holotype: Iran, Azarbaijan, West of Urmieh, Mavana, Hakki Mts., West of Darreh Rash village, 2100 – 2700 m, 31. VII. 1995, Mozaffarian 74871 (TARI!; isotypes TARI!), **syn. nov.**

= *C. satdaghensis* Hub.-Mor., Notes R. B. G. Edinb. 32: 55 (1972). – Holotype: Turkey, Hakkari, 21 km from Bajirge to Yüksekova, meadow on shaley hillside, 2230 m, 18. VI. 1966, Davis 45230 (E!), **syn. nov.**

C. qaradaghensis Rech. f., Fl. Iranica 90: 258 (1972). – Lectotype: Iran, Azarbaijan, Qara Dagh, in monte Kiamaki Dagh (Kamcheh) prope Daran, SE Jolfa, 1400 – 2400 m, 26. VII. 1971, Terme in Rechinger 43662 = Terme 5062-IRAN (43662-II W!; isotypes IRAN!, K!, IRAN!), **syn. nov.**

Illustration. – Fig. 12, B.

Plant up to 60 cm high, white arachnoid-tomentose, rarely glabrous or glandular. Stems usually branched from the middle or higher. Leaves leathery, white arachnoid-tomentose on both surfaces, rarely glabrous or glandular; basal leaves up to 27 × 10 cm including spines, lanceolate to oblong-lanceolate, undulate, sinuate-lobate with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, oblong, ovate to lanceolate, spiny-lobed, rounded to cuneate at base, up to 5 cm decurrent. Capitula 3 – 9 cm broad with appendages, arachnoid or ±glabrescent. Phyllaries 40 – 100; upper ones often tinted red-brown; middle ones spreading-erect, spreading to recurved, rarely erect-incurved; free part of middle phyllaries expanded above into a keeled, (ovate-) lanceolate to linear-lanceolate appendage, 6 – 30 mm long, 3 – 8 mm broad, gradually attenuate into a spine at apex, usually arachnoid-tomentose, without or rarely with 1 – 2 tiny spines on both sides. Receptacular bristles rough or smooth. Flowers 70 – 150; corolla rose or purple, 22 – 30 mm long; anthers concolorous. Achenes 5 – 7 mm long.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia canescens* s.l. consists of variable populations widely distributed in Turkey and NW Iran, and is relatively uniform in vegetative morphology and corolla colour, but very variable in involucre morphology. Appendages vary from small to large, recurved to incurved, (ovate-) lanceolate to linear-lanceolate. As an extreme, the indumentum may be absent (Davis 22708b). The type material of *C. eriocephala* has relatively shorter appendages but falls within the variation of *C. canescens*. Therefore, we are unable to maintain *C. eriocephala* as a distinct species.

Type material of *C. zagrica* is very similar to *C. eriocephala* but differs in having straight lanceolate appendages, a character common in *C. canescens*.

Type material of *C. satdaghensis* at E is an immature plant with closed flowers and recurved lanceolate phyllaries. Stems and leaves are similar to *C. canescens*. *Cousinia satdaghensis* has been incorrectly classified under *C. sect. Sphaerocephalae*, a small group of species endemic to N Iran. Flowering material in E and K (Davis 24130) matches the description of *C. satdaghensis* and shows the diagnostic characters of *C. canescens* including the arachnoid-tomentose involucre and rose or purple flowers.

Type material of *C. qaradaghensis* described from NW Iran (Terme in Rechinger 43662 = Terme 5062) clearly was collected in the late flowering and fruiting period. It has the typical characters of *C. canescens* including arachnoid-tomentose leaves, stems and involucre, lanceolate phyllaries and rose or purple flowers and can not be regarded as a distinct species.

Distribution and habitat. – C to E Turkey and NW Iran (Fig. 13, A), on stony slopes.

Specimens seen. – Turkey: Sivas: 5km W Susehri, 950 m, 8. VII. 1969, *Sorger* 69-32-3 (W); Artvin: 29 km E Demirkent (S Saliöy), 2300 - 2650 m, 16. VIII. 1981, *Sorger* 81-83-14 (W); Kars: distr. Olty pr. pg. Erjük, 2. VII. 1911, *Gosnowsky* s. n. (B); Akcay-Cumacay, 20 km S Akcay, 2200 m, 30. VII. 1984, *Nydegger* 19503 (G); Near Kötek, dry shaley yellow hills, 1450 m, 16. VII. 1966, *Davis* 46679 (E, K); Bayburt, 5000 ft., 10. VIII. 1962, *Furse* 3850 (K); Agri: 15 km from Eleskirt to Horasan, E of Tahir pass, sloping meadow, 2200 m, 24. VII. 1966, *Davis* 47117 (E, K); E side of Tahir pass, 19 km from Eleskirt to Horasan, 2400 m, 24. VII. 1966, *Davis* 47115 (E); Agri to Horasan, E of pass, Roadsides and fieldsides, ca 2150 m, 3. VIII. 1965, *Lamond* 2568 (E); W side of Tahir pass (Horasan-Eleskirt), dry slopes on sandy soil, 2350 m, 21. VII. 1966, *Davis* 47308 (E, K); In jugo inter Agri (Karaköse) et Horasan, 2000 - 2500 m, 3. VIII. 1965, *Rechinger* 32865 (B, G, M, W); C9 Hakkari: Zwischen Uludere und Hakkari, 14 Km E Uludere, felsiger Abhang, 2080 m, 20. VII. 1983, *Nydegger* 18348 (B, M); Bingöl/Erzurum, Karlioiva - Cat, 31 km N Karlioiva, 2440 m, 21. VII. 1982, *Nydegger* 18432 (G); Kayseri: Binboga Daghi, Yalak Mevkii, hareketli Yamaclar, 1620 - 2100 m, 4. VIII. 1988, *Aitac* 2502 (GAZI); Yalak muk, Tekke kayasi, 1800 - 2200 m, 4. VIII. 1991, *Aitac & Duman* 4292 (GAZI); Sarkisla - Ortakay yolu, 1250 - 1350 m, 27. VIII. 1995, *Aytoa & Dönmez* 6719 (GAZI); Sivas: Gürün, Sivas, 36 km N Gürün bei Bögrüdelik, 1700 m, 11. VII. 1981, *Nydegger* 16864 (G); Erzincan: Kemah - Erzincan, bei Sürek, 1300 m, 25. VI. 1992, *Nydegger* 46445 (G, GAZI); Kemah, bei Sürek, 1200 m, 16. VII. 1988, *Nydegger* 43802 (G); Grands ravins pris Ispir, 1862, *Beurgeo* s.n. (P); Pasinler - Hınıs, 62 km N Hınıs, 1680 m, 1. VIII. 1984, *Nydegger* 19550 (G, GAZI, M); 66 km from Hınıs to Erzurum, in Aras gorge, 1650 m, 12. VII. 1966, *Davis* 46436 (E, K, W); Van: Mt. 10 km SE of Pelli, E side of summit ridge, 9600 ft, 8. VII. 1957, *Davis* 22585 (E, K); Hasap - Güzeldere, 2200 m, 30. VI. 1989, *Güner* 7350 (GAZI); Hasap - Güzeldere, 2800 m, 18. VIII. 1993, *Altan* s. n. (GAZI); Artos dagh, above Cevas, rocky slopes, 6500 ft, 14. VII. 1954, *Davis* 22708b (ANK, E, K, W); Artos Dagh, north ridge, 8000 - 9000 ft, 3. VIII. 1966, *Tong* 313 (E); Baskale: Ispiriz Dagh, dry rocky slope, 2700 m, 31. VII. 1954, *Davis* 23722 (E, K, ANK); Güzeldere Gecidi, 2790 m, 7. VII. 1981, *Sorger* 81-36-2, (W); Gürpınar Samran Anakanali, Baset Daghi eteckleri Nemli yerler stepte, 2000 m, 4. VII. 1993, *Actan* 5298 (GAZI); In faucibus 25 km NW Baskale, 2400 m, 23. VII. 1974, *Rechinger* 49901 (G, W); In summo jugo inter Baskale et Hosap, 2700 m, 31. VI. 1975, *Rechinger* 53880 (G, W); 26 km from Baskale to Hosap, calc. rocky slopes of ravine, 2400 m, 3. VII. 1966, *Davis* 45886 (E, K); Hakkari: Cilo Dagh, 10 km W of Cilo Tepe, dry rocky slope, 10000 ft, 9. VIII. 1954, *Davis* 24130 (ANK, E, K); Kara Dagh, Eroded S slope, 9000 ft, 15. VIII. 1954, *Davis* 24377 (ANK, E, K); Sat Daghi, NW of Sat Gölü, rocky igneous slopes, 2850 m, 28. VI. 1966, *Davis* 45488 (E, K); Esendere, Yüksekova, 23 km W Esendere, beim Tunnel, 2230 m, 24. VII.

1983, *Nydegger* 18432 (G); Pass between Hakkari and Kaval (Piyannis), shaley N slopes, 2500 m, 23. VI. 1966, *Davis* 45422 (E, K); Bitlis: Kotum, Karz Dag above Kamer, 2600 m, 24. VIII. 1954, *Davis* 24568 (K); Kambos Dag above Hurmuz, rocky slops, 6000 feet, 31. VII. 1954, *Davis*, 23415 (ANK, E, K); Southern slopes of Kambos Dagh above Tutu, Rocky slopes, 2000 m, 17. VIII. 1956, *Mc Neill* 617 (E, K); In monte Meleto (Meretug) Dagh district Bitlis, in lapidosis usque in vallem Sassim descendens, 1400 - 2700 m, 10. - 12. VIII. 1910, *Handel-Mazzetti* 2866 (B, W, WU); Maras: Distr. Goksun, Binboga dag above Yalak, in gravel at edge of ravine bed, 2000, 17. VII. 1952, *Davis* 20163a & 20163b (ANK, E, W); Distr. Cardak, Berit dagh, above Ericek, 2100 m, 27. VII. 1952, *Davis* 20397 (ANK, E); Tunceli: Munzur dagh, above Ovacik, rocky limestone slopes, 2400 m, 16. VII. 1957, *Davis & Hedge* 31150 (ANK, E, K); Euphrati Superior, *Montbret* s.n. (P); Eqin: Kainartschar, in lapidosis, 13. VII. 1890, *Sintenis* 2907 (B).

– Iran: Azarbaijan: Khoy, Ghotur, 1600 m, 23. VI. 1999, *Ghahreman & Attar* 22442 (IRAN, M, TUH); Maku, 2000 m, 20. VI. 1995, *Siami* 79101 (TARI); Siahcheshmeh, 2600 m, *Siami* 79102 (TARI); In valle flavii Qotur W Khvoy versus fines Turcicas, 1800 - 2000 m, 10. VI. 1971, *Rechinger* 41627 (W); Inter Ashgharabad et Kolavana NNW Khvoy, 2100 m, 16. VII. 1974, *Rechinger* 49437 (B, E, G, K, M,); Maku, Khan Goli, Kalissa-Kandi, 2500 m, 1. VII. 1973, *Siami* 01793 = 7634 (W); ca. 70 km W of Khoy, Mt. above the village Razi, 2000 - 2250 m, 26. VII. 1990, *Assadi & Olfat* 68887 (TARI); Khoy, Ghotur, 1600 m, 23. VI. 1999, *Ghahreman & Attar* 22442 (IRAN, M, TUH); Khoy, Razi station, 1950 m, 20. VII. 2000, *Attar & Mehdigholi* 21981 (TUH).

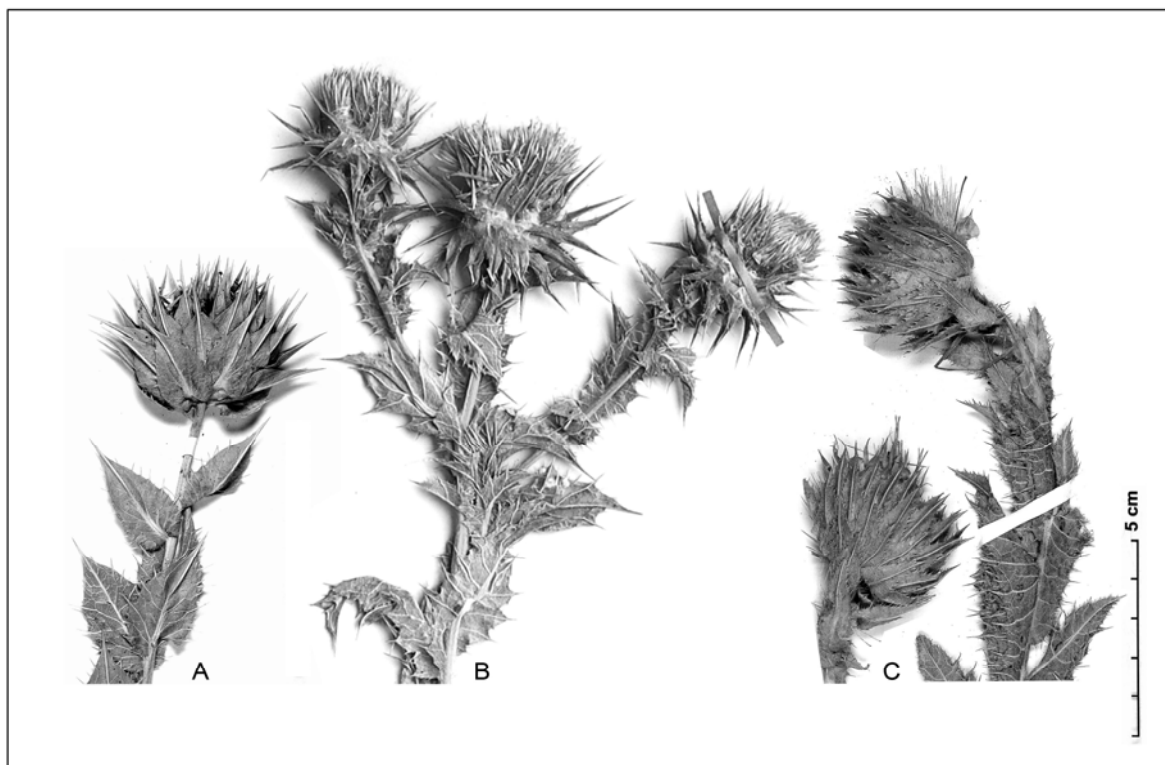


Fig. 8. – A. *C. grandis* [*Rechinger* 57020 (B100157173, B)]; B. *C. gilliatii* [*Rechinger* in Lamond 5104 (E)]; C. *C. macrolepis* [*Hausknecht* 570 (B100093390, B)]. Photographs A & C provided by BGBM. Photograph B by I. Mehregan.

4.4.5.11 *Cousinia hakkarica* Hub.-Mor., Notes R. B. G. Edinb. 32: 54 (1972). – Holotype: Turkey, Hakkari, Zap gorge beneath (2 - 3 km from) Cölemerik, stony S slopes, 1400 m, 24. VI. 1966, Davis 45467 (E; isotypes K!, W!).

Illustration. – Fig. 12, C.

Plant up to 60 cm high, glabrous or glabrescent. Stems usually branched from the base or higher. Leaves leathery or ±herbaceous, white arachnoid-tomentose beneath, glabrous or glabrescent above; basal leaves up to 25 × 10 cm including spines, lanceolate, sinuate-lobate with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate to lanceolate, spiny-lobed, round to cuneate at base, up to 6 cm decurrent. Capitula 3 – 5 cm broad with appendages, arachnoid, ±glabrescent. Phyllaries 90 – 120; middle ones ±spreading or spreading-incurved; free part of middle phyllaries expanded above into a keeled, lanceolate to narrowly lanceolate-mucronate appendage, appendage 7 – 17 mm long, 3 – 9 mm broad, gradually attenuate into a spine at apex, usually glabrous, with 1 – 2 (-4) tiny spines on both sides. Receptacular bristles rough. Flowers 110 – 150; corolla white, 23 – 25 mm long; anthers rose or purple. Achenes ca. 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – Similar to *C. canescens* but differing mainly by lacking an arachnoid-tomentose indumentum on the vegetative parts and by having dicolorous leaves and white flowers.

Distribution and habitat. – Endemic to SE Turkey and NW Iran (Fig. 13, B), on rocky slopes.

Specimens seen. – Turkey: Hakkari: Kara Dag, Eroded S slopes, 8000 ft, 15. VIII. 1954, Davis 24376 (ANK, E, K).

– Iran: Azerbaijan: Between Agh-Bolagh and Silvana, before Dizej, Darabad, 2200 m, 27. VI. 2003, Assadi 85176 (TARI).

4.4.5.12 *Cousinia macrocephala* C. A. Mey., Verz. Pfl. Cauc. 231 (1831). ≡ *Onobroma macrocephalum* C. A. Mey., Verz. Pfl. Cauc. 67 (1831). ≡ *Arctium macrocephalum* (C. A. Mey.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Azerbaijan, in montibus Talüsç prope pagum Drych et versus rupem Kis-Kale, locis lapidosis, 500 – 800 hexap., Junio 1830, Meyer s. n. (G!; isotypes LE, P!).

= *C. macrocephala* C. A. Mey. β *spinulosa* (Lomak, ex.) Lipsky, Fl. Kavk.: 355 (1899). – Type: Azerbaijan, Talysch, in m. Mapajünt, 7000', Lomakin s. n. (LE; isotype B!).

= *C. gigantolepis* Rech. f., Fl. Iranica 90: 257 (1972). – Holotype: Iran, Azarbaijan, versant nord de la Kuh-i Savelan (Sabalan), au-dessus de Mishgin Sar (Meshgin Shahr), 1600 – 3550 m, 22. – 26. VIII. 1956, Schmid 6539 (W!; isotype G!), **syn. nov.**

= *C. gabrieljanae* Takht. & Tamnaian, Bot. Zurn. (Leningrad) 73: 1612 (1988). – Holotype: Armenia, Kafan district, in the suburbs of Town Kafan, shiblik on the territory of forestry company, 31. VII. 1986, Gabrielian, Tamanian & Fajivush 132334 (ERE; isotypes B!, LE, WU!), **syn. nov.**

= *C. takhtajanii* Tamanian, Flora, vegetation and plants resources of Armenia 13: 16 (1991). – Holotype: Armenia, Goris district, vicinity of Galidzor village, 04. VII. 1987, Tamanian 132335 (ERE), **syn. nov.**

Note. – We did not see the type material of *C. takhtajanii*. Instead, we saw a specimen collected from near the type locality of *C. takhtajanii* which was identified by Tamanian as *C. takhtajanii* (Vitek et al. 04-0991, JGM).

Illustration. – Fig. 12, D.

Plant up to 60 cm high, white arachnoid-tomentose. Stems usually branched from the base or higher. Leaves leathery, white arachnoid-tomentose on both surfaces; basal leaves usually petiolate, up to 30 × 8 cm including spines, lanceolate to oblong-lanceolate, undulate, sinuate-lobate to pinnatisect, with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, oblong, ovate to lanceolate or linear-lanceolate, spiny-lobed, rounded to cuneate at base, up to 4.5 cm decurrent, sometimes forming winged stems especially in lower part. Capitula 4 – 12 cm broad with appendages, arachnoid-tomentose or ±glabrescent. Phyllaries 40 – 80; middle ones usually ±spreading; free part of middle phyllaries expanded above into a keeled, ovate, broadly lanceolate to linear-lanceolate appendage, appendage 15 – 30 mm long, 5 – 25 mm broad, gradually attenuate into a spine at apex, usually arachnoid-tomentose, rarely ±glabrescent, smooth at margin, rarely with 2 – 3 spines at both sides. Receptacular bristles rough or smooth. Flowers 70 – 200; corolla usually yellow, rarely purple or white (in dried material), 28 – 38 mm long; anthers concolorous. Achenes 3 – 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – According to Rechinger (1972), *C. gigantolepis* is endemic to NW Iran and differs from Caucasian *C. macrocephala* in having phyllaries with broader appendages. *Cousinia gabrieljanae* has phyllaries with deltoid-cordate appendages similar to those of *C. gigantolepis*. Tamanian (1999) reported *C. gigantolepis* from the Caucasus and Talysh. Comparison of *C. gigantolepis* with *C. macrocephala* revealed continuous variation in size and morphology of the phyllaries and we were unable to distinguish these two taxa. Material of *C. gabrieljanae* and of *C. takhtajanii* is connected with material of *C. macrocephala* by intermediate forms.

Distribution and habitat. – Endemic to the Caucasus (and Talysh) and NW Iran (Fig. 13, C), on dry stony slopes.

Specimens seen. – Armenia: Goris: inter opp. Goris et pag. Latschin, in siccis lapidosis, 27. VI. 1962, Gabrielian s. n. (E, G, W); Gegharkunik: Chambarak distr., area NE of lake Seven, along road between

Tzovagyugh and Shordzha, c. 4 km WNW Shardzha; rocks and cliffs, [40° 31' E, 45° 14' N], 1920 m, 15. VI. 2002, *Oberprieler* 10072 (B, M, W); Sjunik province, Kapan district, N Kapan, ca. 0.5 km E of Jeritzavank, [46° 29' 28" E, 39° 16' 53"], 1650 m, Vitek et al. 04-0991 (JGM).

– Azerbaijan: In collibus aprisi Surnabad, Prov. Elisabethpol., *Hohenacker* s. n. (JE, P, WU); In saxosis montanis prope blanem Sura ditionis Elisabethpol Gaorg., VI. 1838, *Hohenacker* s. n. (E, K, P, W); Distr. Schuscha. in collibus prope locum Chan-Kendy, VII. 1900, *Fedossejew* s. n. (B); Iberia caucasica, *Hohenacker* s. n. (P); Iberia, *Besser* s. n. (K).

– Iran: Azarbaijan: Ahar, Yarmadouz, 1. VIII. 1968, *Terme* 9012 (IRAN); 10 km from Kaleybar to Ahar, 1600 m, 22. VII. 1971, *Terme*, 9011 & 9013 (IRAN); 13 km after Peigham village, on the road to Ahar, 1700 m, 13. VII. 1991, *Zehzad et al.* 70677 (TARI); 14 km from Namin to Chulandarreh Sofla to Germi, after Anbaran, 1600 m, 20. VI. 1980, *Mozaffarian & Nowrouzi* 34486 (TARI); 20 km from Kaleybar on road to Ahar, 1600 m, 22. VII. 1971, *Lamond* 4940 = *Lamond in Rechinger* 44207 (E, G, M, W); 40 km from Razi to Germi, 1700 m, 22. VI. 1980, *Mozaffarian & Nowrouzi* 34780 (TARI); Ahar, 1400 m, 21. VI. 1988, *Assadi & Shahsavari* 65915 (TARI); Ahar, Marzrud vers Peyghan, 6 km E de Barzin, 1650 m, 29. VI. 1978, *Terme, Moussavi & Habibi* 9010 (IRAN); Arasbaran protected area, between Tolua-Ali and Veinagh, 900 m, 26. V. 1977, *Assadi & Vosoughi* 24574 (TARI); Arasbaran protected area, Doghroon mt., 2000 m, 23. VIII. 1976, *Runemark & Assadi* 20942 (TARI); Arasbaran protected area, Ghaghalu, 650 m, 25. V. 1977, *Assadi & Vosoughi* 24528 (TARI); Arasbaran protected area, Veinagh to Dasharasi, 1000 m, 26. VI. 1997, *Hamzehee & Asri* 81343 (TARI); Veinagh to Ghaghalu, 1000 m, 11. VI. 1976, *Assadi & Massoumi* 20513 (TARI); Arasbaran, Asheghlou road, Toup Khaneh mnts., 2000 m, 22. VI. 1997, *Hamzehee* 21344 (TUH); Ardebil, Kuh-e Sabalan, 2650 m, 24. VII. 1974, *Foroughi & Assadi* 13871 (TARI); Between Meshkin-Shahr and Ahar, Now-Duz, 1000 m, 30. V. 1978, *Wendelbo & Assadi* 27886 (TARI); ca. 40 km N of Meshkinshahr, near Moradlu, 1500 m, 7. VII. 1995, *Assadi* 73804 (TARI); Ghotour-Sou, 1900 m, 16. VII. 1993, *Attar & Dadjou* 17240 (TUH); Kaleybar, just before Gahleh Babak, 1500 m, 17. V. 1993, *Ghahreman et al.* 17507 (TUH); Mashkin-Shahr, 4. VI. 1998, *Pour-Mohammadi* 21808 (TUH); Pres de Tabriz, 22. VIII. 1968, *Abai & Mojib* 9014 (IRAN); Salavat, Goli Daragh village, Goli Daragh mnts., 1500 - 1850 m, 24. VI. 1980, *Mozaffarian & Nowrouzi* 35001 (TARI); 20 km N of Ahar on road to Kaleibar, [38° 36' 30" N, 47° 13' E], 1770 m, 20. VI. 2001, *Podlech & Zarre* 55338 (M, TUH); Ahar, Iarmadouz, 1. VIII. 1968, *Terme* 13197 (W).

4.4.5.13 Cousinia grandis C. A. Mey. in DC., Prod. 6: 557 (1837). ≡ *Arctium grande* (C. A. Mey.) O. Kuntze, Rev. Gen. Pl. 1: 307 (1891). – Holotype: Iran, Azarbaijan, „in montibus Seidchadschi, distr. Khoi“, 1832, Szovits s. n. (P!; isotypes G!, K!).

= *C. grandis* var. *minor* Bornm., Verh. Zool.-Bot. Ges. Wien 60: 139 (1910). – Lectotype (designated here): Iran, Urumia, in lapidosis ad Sameschli, 7. VII. 1884, Knapp s. n. (WU!; isotypes B!, JE!, WU!).

Note: The sheet with a long root is the lectotype.

= *C. wettsteiniana* Bornm. Verh. Zool.-Bot. Ges. Wien 60: 137 (1910). – Lectotype (designated here): Iran, Azerbaijan, Tabriz, „Güldize“ (Gülisähr), in aridis declivitatibus, 21. IX. 1884, Knapp s. n. (WU!; isotypes JE!, B!), **syn. nov.**

= *C. grantii* Rech. f., Fl. Iranica 90: 245 (1972). – Holotype: Iran, Azerbaijan, 23 km W Rezaiyeh, 1700 m, 12. VII. 1964, Grant 16123 (holo W!), **syn. nov.**

Illustration. – Fig. 8, A.

Plant up to 60 cm high, either completely glandulose-punctate or glabrous, rarely arachnoid-tomentose or ±glabrescent. Stems branched from the base or higher. Leaves herbaceous-leathery, glandulose-punctate, rarely arachnoid-tomentose on both surfaces; basal leaves up to 30 × 9 cm including spines, oblong to linear-lanceolate, sinuate-lobate to pinnatisect; stem leaves sessile, gradually smaller and less divided towards the apex, ovate to lanceolate, spiny-lobed to spiny-dentate, rounded to cuneate at base, usually long decurrent to form interrupted wings in lower part of stems. Capitula 2.5 – 12 cm broad with appendages, glabrous, ±glabrescent or arachnoid. Phyllaries 40 – 110; outer ones usually similar to uppermost leaves; middle ones spreading to erect; free part of middle phyllaries expanded above into a usually keeled, often leaf-like, straight to incurved, cordate, ovate, cordate-lanceolate to lanceolate appendage, appendage 10 – 40 mm long, 5 – 20 mm broad, attenuate into a spine at apex, usually with black glands, glabrous, ±glabrescent or arachnoid-tomentose, without or with up to 3 tiny spines on both sides. Receptacular bristles smooth or ±rough. Flowers 45 – 160; corolla dirty cream, dirty white or rose, 20 – 30 mm long; anthers concolorous. Achenes 4 - 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia grantii* was compared with *C. gilliatii* by Rechinger (1979) but differs from it in having phyllaries with entire appendages (as opposed to middle phyllaries with obviously spiny appendages in *C. gilliatii*). *Cousinia grantii* is more similar to *C. grandis* but differs from it mainly in having phyllaries with narrower appendages. However, intermediate forms exist. Our study showed that plants with narrower appendages are distributed throughout the range of *C. grandis* but can not be delimited either geographically or morphologically. Appendages vary from cordate, ovate, cordate-lanceolate to lanceolate and are 10 – 40 mm long and 5 – 20 mm broad.

The type material of *C. wettsteiniana* with relatively broad, leaf-like, dentate outer appendages is more similar to *C. grandis* than to *C. canescens* with usually entire, lanceolate outer phyllaries but differs from *C. grandis* in having an exceptionally dense indumentum. *Cousinia wettsteiniana* has phyllaries similar to those of *C. grandis* p.p. For example, glabrous material (Ghahreman & Attar, no. 21343; TUH) is clearly similar to the arachnoid-tomentose type of *C. wettsteiniana*. Also, some material of *C. grandis* with an arachnoid-tomentose indumentum was seen by us (e.g., *Siami* 3708 (TARI), *Mozaffarian* 69907 (TARI)).

Distribution and habitat. – Endemic to SE Turkey and NW Iran (Fig. 13, D), on rocky slopes.

Specimens seen. – Iran: Azarbaijan: Maku, Khak-e Sorkh Pass, 5. VIII. 1973, *Siami* 7632 (TARI); Khoy, Seyyed Hajin, 1490 m, 1. VIII. 1998, *Ghahreman* 21803 (TUH); 16 km S Rezaiyeh, roadside, 1350 m, 15. VI. 1971, *Lamond* 4168 (E); Between Khoy and Salmas, Gharetappe, 1600 m, 10. VIII. 1996, *Mozaffarian* 77146 (TARI); Between Oroumieh and Salmas, 1900 m, 19. VII. 1998, *Assadi* 78929 (TARI); Inter Oshnoviyeh et Dizaj, Mahal-e Dasht-Bel, 2050 m, 14. VII. 1974, *Zehzad & Siami* 3625 (W); Rezaiyeh to Balansh, 15. VI. 1971, *Iranshahr* 9027 (IRAN); Rezaiyeh, Ghasemlu valley, 1650 m, 26. VII. 1972, *Sabeti* 6791 (TARI); S of Urumieh, 1500 m, 3. VIII. 1997, *Ghahreman & Attar* 21805 (TUH); Seluk, Margavar, 28. VIII. 1972, *Siami* 1245 (W); Silvana, Bardeh-Su, 10. VII. 1973, *Siami* 01975 (W); Bardeh-Su, 6. VII. 1973, *Zehzad & Siami* 1173 (W); Bardeh-Su, 2000 - 2200 m, 1. VII. 1974, *Cesad* 2890 (W); Urumieh, 1350 m, 15. VI. 1999, *Attar* 22490 (TUH), 1400 m, 15. VI. 1999, *Attar* 22567 (TUH); Urumieh, Gardaneh

Ghoushchi, 1750 - 2000 m, 16. VII. 1991, *Mozaffarian* 70086 (TARI); Urumieh, Khoshakuh to Jermi, 2500 m, 7. VII. 1991, *Mozaffarian* 69907 (TARI); Urumieh, Mavana, Makki, mnts. W of the village Kuh-e Dare Rash, 2100 - 2700 m, 31. VII. 1995, *Mozaffarian* 74886 & 74870 (TARI); Targevar region, 3 km from Movana toward Sero, 1400 - 1450 m, 26. VII. 1990, *Mozaffarian* 68265 (TARI); Urumieh, Targevar region, Kay villag, Germe, 2000 - 2100 m, 5. VII. 1991, *Zarre* 12778 (TUH); Targevar, before Mavana, 30. VII. 1997, *Ghahreman & Attar* 20578 (TUH); Rezaiyeh (Urmia), in valle Targavar-Benar, 28. IX. 1972, *Siami* 1327 (TARI, W); Prope Sero, 21. VII. 1974, *Siami* 3517 (TARI, W); Ad versuras 16 km S Rezaiyeh, 1350 m, 15. VI. 1971, *Rechinger* 42100 (B, G, K, M, TARI, W); Ad versuras N Sero, 62 - 69 km WNW Rezaiyeh, 1600 - 1800 m, 21. VII. 1974, *Rechinger* 49769 (B, E, G, K, M, W); Chalil Kuh, In faucibus NW Selvana, 1750 - 2000 m, 4. VII. 1974, *Rechinger* 48931 (B, G, M, W); In colle argilloso SW Rezaiyeh, 1500 m, 12. - 13. VII. 1974, *Rechinger* 49321 (B, W, WU); Marand to Evoghli, Kashk-Saray to Erelan, 1250 m, 5. VI. 1990, *Ghahreman & Mozaffarian* 9767 (TUH); Between Zonouz and Zonouzagh, 1750 m, 29. VII. 1997, *Ghahreman & Attar* 21343 (TUH); Marand, Kuh-e Mishoudagh, 2000 m, 4. VII. 1998, *Assadi* 78971 (TARI); 20 km W of Marand, Mts. above the village Orlan, Mishoudagh, 2000 - 2500 m, 15. VI. 1988, *Assadi & Shahsavari* 65470 (TARI); 30 km from Tabriz to Ahar, 1600 m, *Ghahreman & Attar* 20577 (TUH); 35 km NW Bonab to Azadshahr, 1550 m, 8. VII. 1971, *Terme* 9029 (IRAN); Between Marand and Sufian, Payam, Mishoudagh, 2400 - 2700 m, 29. VI. 2003, *Assadi* 85329 (TARI); ca. 18 km NW of Marand, between Kashk-Saraj and Orlan, 1500 m, 15. VI. 1988, *Assadi & Shahsavari* 65432 (TARI); ca. 35 km N of Marand, above the village Miab, slopes of Kiamaki Dagh, 1790 - 1800 m, 24. VII. 1990, *Assadi & Olfat* 68558 (TARI); Tabriz, Osko, Kandavan, Ains, Kuh-e No'ur, 2200 - 2350 m, 8. VIII. 1984, *Terme & Moussavi* 15188 (IRAN); Tabriz to Marand, after Sufian, 1500 m, 26. VI. 1978, *Assadi & Mozaffarian* 29816 (TARI); Tabriz to Sahand, between Basmanj and Vaighan, 2100 m, 10. VII. 1995, *Assadi* 73988 (TARI); Tabriz, Sperkhan (Sefideh Khan), Sahand Mt., 2650 m, 30. VIII. 1987, *Mozaffarian* 64324 (TARI), 2400 m, 23. VI. 1994, *Attar & Dadjou* 18038 (TUH); Tabris (Atropatana), 1350 - 1500m, 25. VI. 1924, *Grossheim* s. n (B); 38 km N of Bonab on road to Tabriz, 1550 m, 8. VII. 1971, *Rechinger* 43163 (B, G, K, W), *Lamond* 4650 (E); Ad versuras lapidosas inter Miab et Babre ad radices montium Kiyamaki Dagh, 1600 m, 18. VI. 1977, *Rechinger* 57020 (B, G); In valle fluvii Talkkeh Rud (Atschi Tschai), 20 - 30 km NE Tabriz, 1600 m, 2. VII. 1971, *Rechinger* 43567 (G, W); Near Tabriz, 28. VIII. 1927, *Gillet-Smith* 2103 & 2367 (K); Achi Chay valley, 20 - 30 km NE Tabriz, limestone hills with salt and gypsum, 1600 m, 20. VI. 1971, *Rechinger* 5191 (E, IRAN).
 – Turkey: Van: Catak, Dalbasti köyö-seytanderesi, mese acikligi, 1350 - 1600 m, 20. VII. 2002, *Bani* 1283 (GAZI); Zab valey 25 miles S of Baskale, edge of fallow fields, 2. VIII. 1954, *Davis* 23808 (ANK, E, K, W); 39 km S Gürpınar, 2200 m, 22. VIII. 1984, *Sorger* 84-73-2 (W); 65 km S Gürpınar, 2500 m, 22. VIII. 1984, *Sorger* 84-76-9 (W).

4.4.5.14 *Cousinia gilliatii* Rech. f., Fl. Iranica 90: 244 (1972). – Holotype: Iran, Azerbaijan, near Tabriz, 25. VI. 1927, *Gilliat-Smith* 1955 (K!; iso K!).

= *C. shebliensis* Ghahreman, *Iranshahr & F. Attar Iran. Journ. Bot.* 8: 19 (1999). – Holotype: Iran, Azerbaijan, Tabriz, Shebli pass, 1830 m, 30. VII. 1997, Ghahreman, Attar & Ghahremani-Nezhad 20580 (TUH!; isotype TUH!), **syn. nov.**

Illustration. – Fig. 8, B.

Plant up to 50 cm high, arachnoid-tomentose or \pm glabrescent. Stems branched from the base or higher. Leaves leathery, arachnoid-tomentose on both surfaces or \pm glabrescent above or on both surfaces; basal leaves up to 15 \times 5 cm including spines, oblong to lanceolate, pinnatipartite to pinnatisect; stem leaves sessile, gradually smaller and less

divided towards the apex, ovate to lanceolate, spiny-lobed to spiny-dentate, rounded to cuneate at base, usually long decurrent to form interrupted wings in the lower part of the stems. Capitula 2.5 – 9.5 cm broad with appendages, arachnoid, or \pm glabrescent. Phyllaries 70 – 110; middle ones spreading to recurved; free part of middle phyllaries expanded above into a usually keeled, straight to recurved, lanceolate to linear-lanceolate appendage, 20 – 40 mm long, 5 – 12 mm broad, attenuate into a spine at apex, arachnoid-tomentose or \pm glabrescent, with 1- 4 spines on both sides. Receptacular bristles \pm rough. Flowers 60 – 115; corolla rose (dirty cream in dried material), 20 – 24 mm long; anthers concolorous. Achenes 4 - 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – The type material of *C. gilliatii* and *C. shebliensis* collected around Tabriz is very similar and characterised by having middle phyllaries with obviously spiny appendages. This is the main difference from *C. grandis* with middle phyllaries with usually entire appendages. We can not find any character justifying the recognition of *C. shebliensis* as a separate species.

Distribution and habitat. – Endemic to NW Iran (Fig. 13, E), on rocky slopes E of Tabriz.

Specimens seen. – Iran: Azerbaijan: In declivibus siccis 8 km E Tabriz, 1650 m, 14. VII. 1971, Rechinger 43189 & 43190 = 5104 (B, E, M, W); Tabriz, 21. VII. 1926, Gilliat-Smith 1753 (K, W "fragment").

4.4.5.15 *Cousinia macrolepis* Boiss. & Hausskn. in Boiss., Fl. Or. 3: 505 (1875). \equiv *Arctium macrolepis* (Boiss. & Hausskn.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Iraq, Sulaymaniyah, "In monte Pir Omar Gudrun Kurdistaniae Persicae", 4 – 5000', Jun. 1867, Haussknecht 570 (G!; isotypes G!, B!, JE!, W!).

Note. – The sheet with three labels designated as "*C. macrolepis*" is selected as lectotype.

= *C. gigantosphaera* Rech. f., Anz. Math.-Nat. Kl. Österr. Acad. Wiss. 101: 345 (1964). – Holotype: Iraq, Kurdistan, Asma near Sulaimaniyah, slope above Casino, poor oak scrub, 13. VII. 1961, Wheeler-Haines s. n. (E!; isotype W!), **syn. nov.**

Illustration. – Fig. 8, C.

Plant up to 50 cm high, densely arachnoid-tomentose or \pm glabrescent. Stems divaricately branched from base or higher, densely leafy to apex. Leaves leathery, tomentose on both sides; basal leaves up to 25 × 15 cm including spines, obovate, oblong-lanceolate to lanceolate, dentate to deeply pinnatisect with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate-elliptic to broadly lanceolate, spiny-lobed, decurrent to form winged stems, upper leaves enclosing lower part of the involucre. Capitula 4 – 8 cm broad with appendages, usually arachnoid-tomentose. Phyllaries 80 – 100 or more; outer ones similar to uppermost leaves but gradually smaller; middle ones densely imbricate; free part of middle phyllaries abruptly expanded above into a usually keeled, concave or apically recurved, deltoid, rhomboid- or sagittate-lanceolate

appendage, appendage 15 – 25 mm long, 8 – 15 mm broad, attenuate into a short spine at apex, arachnoid-tomentose, with 3 – 8 prickles on both sides. Receptacular bristles rough. Flowers 70 – 160; corolla purple (dirty white in some herbarium material), 28 – 35 mm long; anthers concolorous. Achenes 4 – 5.5 mm long.

Flowering period. – May to June.

Taxonomic remarks. – *Cousinia macrolepis* and *C. gigantosphaera*, both described from around Sulaimaniyeh, are characteristic in having uppermost leaves enclosing the leaf-like outer phyllaries, and differ from each other mainly in the shape of the phyllaries (deltoid vs. rhomboid- or sagittate-lanceolate). The two species are connected by intermediate form and can not be maintained as separate.

Distribution and habitat. – NE Iraq (province Sulaimaniyeh; Fig. 11, D), in oak forests.

Specimens seen. – Iraq: Sulaimaniyeh: Haibat Sultan Dagh (Mt.), N of Koi Sanjaq, 950 m, 7. V. 1959 *Al Rawi et al* 28264 (K); Pir-i Mukrurn Dagh rocks, 1100 - 1200 m, 19. IX. 1933, *Eig & Duodevani* 510 (W); Piere Magroun, hillside with oak scrub and vinefields, 18. VII. 1961, *Wheeler Haines* 2042 (E, K, W); Piere Magroun, stony slope, 5000 ft, 22. 10. 1960, *Wheeler Haines et al.* 1860 (E, K, W); Talan Region near Dokan, 7. VII. 1972, *Karim* 39293 (K); Dokan, 26. V. 1961, *Wheeler Haines* s. n. (E); Azmir (Asme) Mt., 9. VII. 1972, *Karim* 39320 (E, K).

– Iran: Azerbaijan: 8 km N of Mirabad on road to Piranshahr, close to a big river, 1300 - 1400 m, 29. V. 1978, *Runemark & Mozaffarian* 29148 (TARI); 30 km from Sardasht to Piranshahr, 1300 m, 21. VII. 1998, *Ghahreman & Attar* 22009 (TUH).

4.4.5.16 *Cousinia sagittata* C. Winkl. & Strauss., *Acta Horti Petropolitani* 14: 233 (1897). – Holotype: Iran, "prope Sultanabad, in collibus", VIII. 1890, Strauss (JE!).

Plant up to 60 cm high, arachnoid-tomentose or ±glabrescent. Stems branched from base or higher, usually densely leafy to apex. Leaves leathery or herbaceous, tomentose on both sides, glabrescent above and tomentose beneath, or ±glabrescent on both surfaces; basal leaves up to 25 × 15 cm including spines, oblong-lanceolate to broadly lanceolate, finely dentate to deeply pinnatifid with spiny-dentate lobes, rarely lyrate; stem leaves sessile, gradually smaller and less divided towards the apex, ovate-elliptic, oblong to broadly lanceolate, spiny-lobed, usually decurrent to form winged stems, upper leaves usually enclosing the involucre (at least in their lower parts). Capitula 4 – 9 cm broad with appendages, glabrous, ±glabrescent or arachnoid-tomentose. Phyllaries 50 - 100 (-120); outer ones similar to uppermost leaves; middle ones densely imbricate; free part of middle phyllaries abruptly expanded above into a usually keeled, slightly to completely recurved, rhomboid-deltoid to lanceolate-deltoid appendage, appendage 15 – 35 mm long, 8 – 20 mm broad, attenuate into a strong spine at apex, arachnoid-tomentose or glabrous, without or with up to 5 tiny spines on both sides. Receptacular bristles rough or rarely smooth. Flowers 60 – 150; corolla rose, purple or white, 20 – 30 mm long; anthers usually concolorous, sometimes purple at apex. Achenes 5 – 7 mm long.

Key to the subspecies of *C. sagittata*

1. Leaves and phyllaries densely canescent-tomentose; appendages usually slightly recurved. Flowers white, rarely purple (provinces Markazi and western part of Esfahan) subsp. *iranica*
 – Leaves and phyllaries sparsely arachnoid-tomentose; appendages slightly to strongly recurved. Flowers purple, rose or white (province Luristan) subsp. *sagittata*

4.4.5.16.1 *Cousinia sagittata* subsp. *sagittata*

= *C. rhombiformis* C. Winkl. & Strauss., Acta Horti Petropolitani 14: 232 (1897). –Holotype: Iran, "Sultanabad, inter Shuturum Kuh et Kuhe Sass, Sefidab", 24. VI. 1889, Strauss s.n. (JE!; isotype "fragment" B!, W!), **syn. nov.**

= *C. phyllocephala* Bornm. & Gauba, Feddes Repert. 36: 330 (1934). – Lectotype (designated here): Iran, "Luristaniae in montosis ad Khoremabad", VIII. 1933, Madani in Gauba 50 (B!; isotype W!), **syn. nov.**

= *C. köieana* Bornm. in Köie, Beitr. Fl. Südwest-Irans 1 (Danish Sci. Invest. Iran Pt. 4): 26 (1945). Lectotype (designated here): Iran, Luristan, Bicheh, 50 km östl. von Khorramabad, 1600 m, 21. V. 1937, Köie 794 (B!; isotype C), **syn. nov.**

= *C. köieana* Bornm. var. *adenoloba* Bornm. in Köie, Beitr. Fl. Südwest-Irans 1 (Danish Sci. Invest. Iran Pt. 4): 29 (1945). –Lectotype (designated here): Iran, Luristan, 50 km östl. von Bicheh, 1200 – 1600 m, 28. V. 1937, Köie 798 (B!; isotype C).

= *C. khorramabadensis* Bornm. in Köie, Beitr. Fl. Südwest-Irans 1 (Danish Sci. Invest. Iran Pt. 4): 25 (1945), emend. Rech. f., Fl. Iranica 90: 239 (1972). –Lectotype: Iran, "Ninjiu, 25 km südöstl. von Khorramabad", 1900 m, 9. V. 1937, Köie 800 (B!; isotype C), **syn. nov.**

= *C. khorramabadensis* var. *purpurea* Attar & Ghahreman, Iran. Journ. Bot. 9: 164 (2002). – Type: Iran, Lorestan, Aligoudarz to Dalani, 33° 11' N, 49° 30' E, 24. VII. 2001, Ghahreman, Attar & Mehdigholi 27591 (TUH!).

Note. – There exist two sheets with no. 27591 but no holotype was designated by the authors.

Illustration. – Fig. 9, A.

Leaves and phyllaries sparsely arachnoid-tomentose; appendages slightly to strongly recurved. Flowers purple, rose or white.

Flowering period. – May to August.

Taxonomic remarks. – *Cousinia sagittata* subsp. *sagittata*, *C. rhombiformis*, *C. phyllocephala*, *C. köieana* and *C. khorramabadensis*, all distributed in mountainous areas of Luristan province

(Iran), are characteristic in having uppermost leaves partly to completely enclosing the outer imbricate phyllaries. They differ from each other in the texture of their leaves (herbaceous to leathery), the shape of the apex of the phyllaries (slightly to completely recurved) and the degree of enclosure of the capitula by the uppermost leaves. All these characters vary continuously and none of the above taxa can be maintained as separate species.

Distribution and habitat. – Endemic to W Iran, province Luristan (Fig. 11, E), on stony slopes, mountain sides and in oak forests.

Specimens seen. – Iran: Luristan: 35 km N of Borojerd, *Gaubá & Sabeti* 1419 (W); Khorram-Abad, NW of Kuh-e Sefid, 1600 - 1900 m, *Veiskarami* 22598 (TUH); Khorram-Abad, on the road of Sefid-Dasht, after Aznacryt, 1850 m, 18. VI. 1998, *Ghahreman & Attar* 21838 (TUH); Khorram-Abad, on the road of Sefid-Dasht, after Azna crypt, 1850 m, 18. VI. 1998, *Ghahreman, Attar & Ghaffari* 21837 (TUH); Azna, Daratakht, 1820 - 1960 m, 9. VII. 1997, *Jamzad, Ahmadi & Karimi* 76852 (TARI); NW of Khorram-Abad, Kuh-e Sefid, 1600 - 1900 m, *Veiskarami* 22602 (TUH); Inter Khorramabad et Sefid-Dasht, Baghbanan, 60 km a Khorramabad, 1800 m, 12. VI. 1974, *Iranshahr* 34001-E (IRAN, W); Khorram-abad towards Kooouh-e Hashtad Pahlou, 20 km . Khorramabad, 1700 m, 16. VII. 1992, *Delghandi & Tehrani* 9183 (IRAN); 50 km E Khorramabad orientem versus, substr. calc., 1200 - 1400 m, 14. - 16. VII. 1948, *Rechinger* 5760 (B, E, K, TARI, W); E of Alashtar, [33° 56.742' N, 48° 21.675' E], 2165 m, 29. VI. 2005, *Mehregan* 18 (JGM); Mts. west of Doroud, [33° 28.827' N, 49° 01.105' E], 2235 m, 23. VI. 2005, *Mehregan*10 (JGM); 15 km from Khorram-Abad on the road to Keshvar, 1500 m, 18. VI. 1998, *Ghahreman & Attar*, 21827 (M, TUH); 39 km on road from Khorramabad to Nowjian and Keshvar, 2150 m, 27. VI. 1977, *Runemark & Lazari* 26012 & 26054 (TARI), Mts. S of the road, 2300 - 2550 m, 28. VI. 1977, *Runemark & Lazari* 26124 (TARI); In jugo Chariveh Shah 32 km E khorramabad, substr. calc., 2050 m, 11. VI. 1974, *Rechinger* 47730 (B, M, W); Baghbanan 55 km SE Khorramabad versus Sefid Dasht, in quercetis (*Q. brantii*) devastatis, substr. calc., 1950 m, 12. VI. 1974, *Rechinger* 47823 (B, W); Dow Rud, in declivibus aridis ad introitum faucium fluvii Dez, substr. calc., 1500 - 1600 m, 17. VI. 1974, *Rechinger* 48197 (B, M, W); Inter Khorram-Abad and Doroud, Zagheh, 1950 m, 17. VI. 1998, *Ghahreman, Attar & Ghaffari* 21825 (TUH); 30 km W Dorud versus Khorramabad, 1750 m, 11. VI. 1974, *Iranshahr* 34025-E (W); Inter Dorud et Khorramabad, Gardaneh Togha, prope Zagheh, Microwave station, 1900 m, 11. VI. 1974, *Iranshahr* 9187 (IRAN); Dorud, 6. VI. 1941, *Koelz* 18098 (W), 8. VI. 1941, *Koelz* 18141 (W); Dorud, neck mt. between Saravand and Gahar lake, 2300 - 3500 m, 17. VIII. 1982, *Mozaffarian & Sardabi* 42345 (TARI); Shuturankuh, 2 - 5. VII. 1890, *Strauss* s. n. (K); SchuturanKuh, 1899, *Strauss*, s. n. (JE); SchuturanKuh, 25. VI. 1905, *Strauss* s. n. (B, JE); Oshtorankuh, above the village Tihun, 2000 - 2500 m, 12. VII. 1981, *Assadi & Mozaffarian* 37050 & 37081 (TARI); SchuturanKuh, prope Kali Rustam (Ghaleh Rostam), fauce Dere-Tschah, 21. VII. 1889, *Strauss*, s. n. (JE); Oshtorankuh protected region, 31. V. - 4. VI. 2000, *Djavadi & Ghanbari* 29549 & 29550 (IRAN); Oshtorankuh protected region, inter Saravand et lacus Gahar, 16. VI. 1974, *Iranshahr* 34000-E, (IRAN); Dorud, Oshtorankuh, S slope. opposite to Gahar lake, 2380 - 3200 m, 16. VIII. 1982, *Mozaffarian & Sardabi* 42281 (TARI); Mts. south of Doroud (Oshtorankouh), [33° 21.547' N, 49° 12.210' E], 2500 m, 25. VI. 2005, *Mehregan* 11 (JGM); Kalvar, 5000 ft, 5. VI. 1940, *Koelz* 15995 (E, W); Prope Mowdere, VIII. 1890, *Strauss* s. n. (B, WU); ca. 40 km S of Doroud, at Bisheh, 1250 - 1600 m, 11. VII. 1981, *Assadi & Mozaffarian* 37024 (TARI); Bisheh, 1200 - 1400 m, 14. - 16. VII. 1948, *Rechinger* 5744 (IRAN, W); In declivibus saxosis inter Azna et Dow Rud, 1600 - 1900 m, 15. - 16. VI. 1974, *Rechinger* 48031 (B, E, K, M, W, WU); Aligoudarz to Dalani, [33° 11' N, 49° 30' E], 24. VII. 2001, *Ghahreman, Attar & Mehdigholi* 27590 (TUH); Before Azna, Darreh Takht, 1900 m, 19. VI. 1998, *Ghahreman, Attar & Ghaffari* 21851 (TUH); Between Azna and Doroud, 1700 m, 31. V. - 4. VI. 2000, *Djavadi & Ghanbari*, 29560 (IRAN).

4.4.5.16.2 *Cousinia sagittata* subsp. *iranica* (C. Winkl. & Strauss.) Mehregan, **comb. et stat. nov.** ≡ *C. iranica* C. Winkl. & Strauss., Acta Horti Petropolitani 14: 233 (1897). – Lectotype (designated here): Iran, “prope Sultanabad in monte Raswend”, 28. VII. 1892, Strauss 236 (JE!; isotypes JE!, B!).

Note. – The sheet with two plants is here chosen as lectotype.

= *C. straussii* Hausskn. & C. Winkl., Acta Horti Petropolitani 14: 235 (1897). –Lectotype (designated here): Iran, “Sultanabad prope Girdu”, 3. VII. 1892 “1891”, Strauss 204 (JE!; isotype JE!), syntype: Sultanabad, prope Mowdereh, 20.VI. 1892, Strauss s. n. (JE!).

Illustration. – Fig. 9, B.

Leaves and phyllaries densely canescent-tomentose; appendages usually slightly recurved. Flowers white, rarely purple.

Flowering period. – May to August.

Taxonomic remarks. – Type material of *C. sagittata* subsp. *iranica* and *C. straussii* is very similar. The only notable difference is that the uppermost leaves of subsp. *iranica* enclose the capitulum more strongly. Irrespective of this, *C. straussii* can not be segregated from subsp. *iranica* as a separate taxon. *Cousinia sagittata* subsp. *iranica* is distributed in the mountain range parallel and to the east of the mountain range where *C. sagittata* subsp. *sagittata* is distributed. The two are connected by intermediate forms. Subspecies *iranica* has leaves and phyllaries which are more densely canescent-tomentose than in subsp. *sagittata*, its uppermost leaves usually enclose the involucre less, and the phyllaries are less recurved at the apex.

Distribution and habitat. – Endemic to W Iran, provinces Markazi and western part of Esfahan (Fig. 11, F), on stony slopes, mountain sides.

Specimens seen. – Iran: Markazi: 100 km SW Hamedan v. Sultanabad, 1800 m, 10. VI. 1937, *Koie* 795, 796 & 801 (B); Toureh, Besri, NE slopes of Kuh-e Aladagh, 2100 - 3100 m, 11. VII. 1985, *Mozaffarian* 64067 & 64161 (TARI); Ad stationen viae ferrae Fuzieh ad occidentem urbis Sultanabad, 13. VII. 1948, *Rechinger & Rechinger* 5744 (K, W); Arak, Khan-e Miran, Kuh-e Sefid, 2500 - 2850 m, 6. VII. 1985 *Mozaffarian* 63737 (TARI); Sefid Khany mt., 2100 - 2600 m, 16. VII. 1984, *Mozaffarian* 48204 (TARI); Arak towards Sefidkhani, 29. V. 1985, *Ghahreman* 9182 (IRAN); In dit. urb. Sultanabad, Chaladjistan, V. 1899, *Strauss* 15 (B); Arak to Boroujerd, Sendjan, 1800 m, 4. - 6. VI. 1997, *Djavadi* 15186 (IRAN); Arak, 1. VI. 1967, *Kelet* 13432 (IRAN); Mt. Chal-Khaloun, 2050 m, 19. VI. 1998, *Ghahreman, Attar & Ghaffari* 21880 (TUH); Rasvand, *Gauba* k2488 (W); In monte Raswend, 1899, *Strauss* 13 & 14 (B); S of Shazand, Mt. Rasvand, [33° 49.169' N, 49° 29.876' E], 2160m, 24. VII. 2005, *Mehregan* 41 (JGM); Abbas Abad, Kuh-e Rasvand, 25. VII. 1995, *Assadi* 75038 (TARI); Ditionis Sultanabad in monte Raswend, VII. 1897, *Strauss* s. n. (B, JE); In monte Raswend, 22. VI. 1891, *Strauss* s. n. (B, JE); Road of Shahzand, 1950 m, 17. VI. 1998, *Ghahreman, Attar & Ghaffari* 21822 (TUH); M. Schahzinde, VII. 1897, *Strauss*, s. n. (B); Mt. Shahzand, Abbas Abad, 2050 m, 19. VI. 1998, *Ghahreman, Attar & Ghaffari*, 21881 (TUH); Kuh Schahsinde, 19. VII. 1902, *Strauss* 400 (B, JE); Kuh-e Shahzende, 1700 - 1800 m, 31. V. - 4. VI. 2000,

Djavadi & Ghanbari 29557 (IRAN); Shahzand, Hafteh-o Emarat, Anbarteh and Tajereh, Kuh-e Sero, 2150 - 2950 m, 8. VII. 1985 *Mozaffarian* 63849 (TARI); Moudar, 2000 m, 31. V. - 4. VI. 2000, *Djavadi & Ghanbari* 29559 (IRAN); prope Mowdere, VIII. 1890, *Strauss* 291 (JE, W); Gerdou, 1700 - 1800 m, 31. V. - 4. VI. 2000, *Djavadi & Ghanbari*, 29558 (IRAN); Girdü, 2. VI. 1889, *Strauss* 239 (JE); Gerdu Region, 2000 m, 19. VI. 1998, *Ghahreman, Attar & Ghaffari* 21882 (TUH); Khomeyn to Arak, road of Emarat, 2100 m, 29. VI. 1998, *Ghahreman et al.* 21879 (M); Mt. with microwave station NE of Varche (between Arak and Khomein), 2700 m, 3. VII. 1977, *Runemark & Lazari* 26574 (TARI); Esfahan: Golpayegan, Hendeh, 2200 - 2800 m, 27. VI. 1969, *Iranshahr* 13463-E (IRAN, W); Golpayegan, Hendeh, 1970 m, 31. V. - 4. VI. 2000, *Djavadi & Ghanbari* 29545 (IRAN); Golpaigan, 1899, *Strauss* 213 (B, JE).

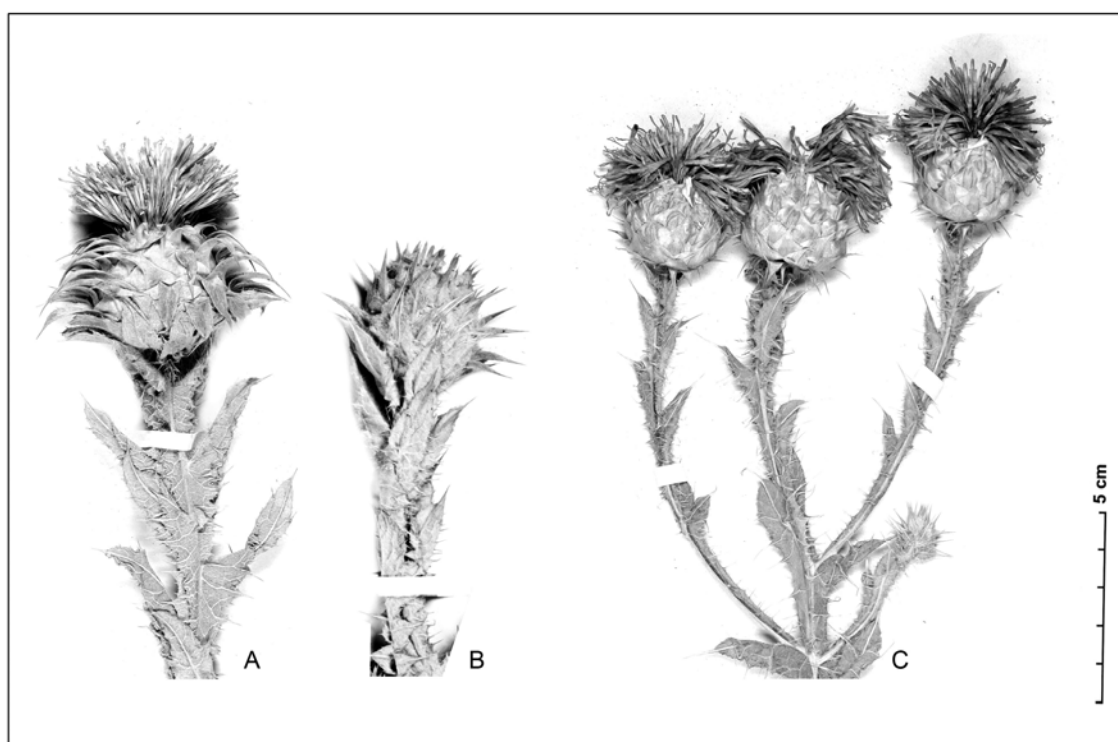


Fig. 9. – A. *C. sagittata* subsp. *sagittata* [Rechinger 48031 (B100158854, B)]; B. *C. sagittata* subsp. *iranica* [Strauss 236 (B100157164, B)]; C. *C. chlorosphaera* [Strauss s.n. (B100093354, B)]. Photographs provided by BGBM.

4.4.5.17 *Cousinia chlorosphaera* Bornm., Beih. Bot. Centrbl. 28: 253 (1911). – Lectotype (designated here): Iran, Luristan: "Ditionis Kermanschah, in trajectu Ushturan, Paß von Uschturan", 19. VI. 1906, Strauss s. n. (B100088374, B!; isotype JE!).

= *C. chlorosphaera* f. *straminea* Bornm, Beih. Bot. Centrbl. 32: 405 (1914). – Lectotype (designated here): Iran, "in m. Kuh-i-Gerru", VII. 1908, Strauss s. n. (lecto B100093354, B!; iso JE!).

= *C. chlorosphaera* β *producta* Bornm, Beih. Bot. Centrbl. 32: 405 (1914). – Lectotype (designated here): Iran, "in m. Kuh-i-Gerru", VII. 1908, Strauss s. n. (lecto B100088373, B!; iso JE!).

= *C. hamadanensis* Rech. f., Fl. Iranica 139a: 142 (1979). –Holotype: Hamedan, Nahavand to Malayer, 28 km S of Nahavand, monts. Gerrau (Yalkow), 1800 – 2400 m, 16. VII. 1974, Terme & Moussavi 33895-E = 5055-IRAN (W!; isotype IRAN!), **syn. nov.**

Illustration. – Fig. 9, C.

Plant usually many-stemmed, up to 50 cm high, arachnoid-tomentose. Stems branched from base or higher, usually densely leafy to apex. Leaves leathery or leathery-herbaceous, tomentose or ±glabrescent on both surfaces; basal leaves up to 25 × 7 cm including spines, oblong-lanceolate, coarsely dentate to pinnatifid with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate-elliptic, oblong-ovate to lanceolate, spiny-lobed, decurrent to form winged stems. Capitula 1.5 – 3.5 cm broad with appendages, glabrous or glabrescent. Phyllaries 60 – 90, coriaceous at least in upper half; middle ones densely imbricate; free part of middle phyllaries abruptly expanded above into a usually keeled, apically slightly recurved or erect, broadly rhomboid-deltoid or rhomboid-flabellate appendage, appendage 5 – 15 mm long, 6 – 14 mm broad, sharply attenuate into a spine at apex, glabrous, without or rarely with up to 2 tiny spines on both sides. Receptacular bristles rough. Flowers 60 – 100; corolla rose, purple or pale purple, 18 – 22 mm long; anthers rose. Achenes unknown.

Flowering period. – June to August.

Taxonomic remarks. – The type material of *C. chlorosphaera* was collected by Strauss in Iran, province Luristan, most probably on the old road from Arak (Sultan-Abad) to Kermanshah at the pass from Oshtorinan to Nourabad (Ditionis Kermanschah, in trajectu Ushturan, Paß von Uschturan). This pass crosses the mountain range today know as Garrin (Gerrau, Kuh-e Gerru). We studied all available material collected from the Garrin mountain range, and found that the area houses one species of sect. *Cynaroides* with relatively little morphological variation. Type material of both *C. chlorosphaera* and *C. hamadanensis* was collected in the same mountain range. As we could not find any differences between the type material of these two species, we regard *C. hamadanensis* as a synonym of *C. chlorosphaera*.

Distribution and habitat. – Endemic to W Iran, provinces Luristan and southern part of Hamedan (Fig. 11, G), in open areas, stony slopes and mountain sides.

Specimens seen. – Iran: Hamadan: ca. 20 km S of Nahavand, Kuh-e Garu, above Cheshme-Gamasb, 1800 - 2200 m, 9. VII. 1981, *Assadi & Mozaffarian* 36912 (TARI); Nahavand, Borzol, Gian, Sarab-e Gian, Kih-e Garrin, 1950 - 2700 m, 14. VII. 1988, *Mozaffarian* 65082 (TARI); Nahavand, Borzol, on the road to Nurabad, above Gamasb, Kuh-e Garin, 2500 - 3400 m, 27. VII. 1995, *Assadi* 75116 (TARI); Nahavand, Gamasb, 1520 m, 27. - 30. VI. 1998, *Djavadi & Ghanbari* 20369 (IRAN); Nahavand, Garrin mnts., 1800 m, 10. VII. 1997, *Ghahreman & Attar* 20551 (TUH); In dit. urb. Sultanabad, in m. Elwend, 1899 *Strauss* 10 (B); Luristan: Inter Boroudjerd et Kermanschah, VI. 1926, *Cavara*, s. n.(B); Boroujerd, W of Kolidar village, Mt. Mishparvar, [33° 50.355' N, 48° 39.365' E], 2500 – 2900 m, 9. VII. 2005, *Mehregan* 35, 36 & 37 (JGM); Boroujerd, W of Vanayee village, [33° 53.696' N, 48° 34.667' E], 2100 – 2350 m, 2. VII. 2005, *Mehregan* 27 & 28 (JGM); Mts. E of Alashtar, 33° 57.290' N, 48° 22.905' E], 2700 – 2750 m, 29. VI. 2005,

Mehregan 19 & 20 (JGM); Nour-Abad to Oshtorinan, S of Isalam-Abad, [34° 01.641' N, 48° 16.835' E], 2600 - 3000 m, 1. VII. 2005, *Mehregan* 25 & 26 (JGM); Borujerd towards Nahavand, Kouh-e Garin, 1800 - 2300 m, 21. VII. 1992, *Delghani & Tehrani*, 9030 (IRAN).

4.4.5.18 *Cousinia pergamacea* Boiss. & Hausskn. in Boiss., Fl. Or. 3: 513 (1875). ≡ *Arctium pergamaceum* (Boiss. & Hausskn.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Iran, “in dumetis montis Teriter prope Pendjavin Kurdistaniae Persicae”, 7000', VIII. 1867, Haussknecht 570a (G!; isotypes G!, P!, JE!, W!).

Note. – The specimen with four labels is here selected as is lectotype.

Plant up to 80 cm high, arachnoid-tomentose or glabrescent. Stems branched from base or higher. Leaves leathery or herbaceous, tomentose on both sides or glabrescent above and tomentose to ±glabrescent beneath; basal leaves up to 40 × 15 cm including spines, obovate, ovate, lanceolate to oblong-lanceolate, undivided to deeply sinuate-lobate with spiny-dentate lobes; stem leaves sessile, rarely distinctly attenuate at base, gradually smaller and less divided towards the apex, oblong-ovate to lanceolate, spiny-lobed, usually long decurrent to form winged stems. Capitula 1.5 – 5 cm broad with appendages, glabrous, sparsely arachnoid or glabrescent. Phyllaries 50 – 140; middle ones imbricate, with prominent yellow midrib; free part of middle phyllaries abruptly expanded above into a usually flat, erect, deltoid or deltoid-sagittate appendage, at least two times broader than base, appendage 5 – 17 mm long, 5 – 15 mm broad, attenuate into a spine at apex, usually glabrous, without or with up to 4 prickles or spines on both sides. Receptacular bristles rough. Flowers 40 – 110; corolla yellow, 20 – 27 mm long; anthers rose or yellow. Achenes 4 - 6 mm long.

Key to the subspecies of *C. pergamacea*

1. Appendages usually without or rarely with very tiny appressed prickles on both sides subsp. *pergamacea*
- Appendages with ± erect and distinct spines on both sides subsp. *sardashtensis*

4.4.5.18.1 *Cousinia pergamacea* subsp. *pergamacea*

= *C. wheeler-hainesii* Rech. f., Anz. Math.-Nat. Kl. Österr. Akad. Wiss. 101: 353 (1964). – Holotype: Iraq, Kurdistan, Penjwin, in cut oak scrub above town, 19. VII. 1961, Wheeler-Haines W-2041 (E!; isotypes E!, W!, K!), **syn. nov.**

= *C. fursei* Rech. f., Fl. Iranica 90: 247 (1972). – Holotype: Iran, Azerbaijan, 20' E Marivan (Dez Shahpur), among oak scrub in clearings, 6000 ft., 24. VII. 1962, Furse 3421 (K!).

= *C. millefontana* Rech. f., Fl. Iranica 90: 248 (1972). – Holotype: Iran, Kurdistan, Montes Chehel Cheshmaeh, 44 km NE Marivan (Dezh Shahpur), substr. Tonschiefer, 2000 m, 7. VII. 1971, Rechinger 43052 (W!; isotypes M!, K!, E!), **syn. nov.**

= *C. caroli-henrici* Attar & Ghahreman, Rostaniha 7 (Suppl. 2): 317 (2006). – Holotype: Iran, Kurdistan, Baneh, Attar & Ghahreman, 22455 (TUH), **syn. nov.**

Note. – We did not see the type material of *C. caroli-henrici*. Instead, we examined herbarium material collected from type locality (*Mehregan* 208 (JGM), *Rechinger* 49174 (W)) which completely match the description of *C. caroli-henrici*.

Illustration. – Fig. 10, A.

Appendages usually without or rarely with tiny appressed prickles on both sides.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia pergamacea* subsp. *pergamacea*, *C. wheeler-hainesii*, *C. fursei*, *C. millefontana* and *C. caroli-henrici* all described from a relatively small mountain area of Iranian and Iraqi Kurdistan and the southwestern part of Iranian Azerbaijan (Fig. 00), have imbricate phyllaries with deltoid or deltoid-sagittate appendages and yellow flowers. The size of the appendages varies continuously from small to large (5 – 17 mm long, 5 – 15 mm broad). None of these taxa can be maintained as separate.

The dense indumentum and tiny spiny appendages of *C. caroli-henrici* are part of the variation of subsp. *pergamacea*.

Distribution and habitat. – Endemic to NE Iraq and W Iran (Fig. 11, H), on stony slopes and mountain sides, usually in oak forests.

Specimens seen. – Iraq: Sulaimaniya: In ditione pagi Penjwin, in glareosis serpentinis jugi Malakawa, 1400 m, 19. - 20. VI. 1957, *Rechinger* 10429 (E, M, W); Mela Kowa (on Sulaimaniyah-Penjwin highway), 1320 m, 20. VI. 1957, *Al Rawi* 22433 (K); In ditione pagi Penjwin, 1600 m, 19. - 20. VI. 1957, *Rechinger* 12238 (W).

– Iran: Azerbaijan: In declivibus saxosis vallis 36 km S Mahabad, substr. schist. 1750 m, 1750 m, 8. VII. 1974, *Rechinger* 49060 (B, E, K, M, W); 81 - 83 km S Mahabad, 1840 - 1930 m, 16. X. 1960, *Pabot* 5504 (IRAN); 25 km on road from Sardasht to Baneh, 1400 m, 20. X. 1977, *Runemark & Mozaffarian* 25936 (TARI); Inter Mahabad et Sardasht, 37 km Atrid vers. Sardasht, 1750 m, 8. VII. 1973, *Zehzad & Siami* 3443 (TARI); Kurdistan: Montes Chehel Cheshmaeh, 44 km NE Marivan (Dezh Shahpur), substr. Tonschiefer, 2000 m, 7. VII. 1971, *Lamond* 4577 (E); Baneh, 2000 - 2200 m, 7. VIII. 1967, *Iranshahr & Terme* 12198E = 9181 (IRAN, W); Marivan, Mian Dagh, 2000 m, 13. VI. 1972, *Mirzayan & Abae* 34035E = 9115 (IRAN); Marivan to Saqqez, 50 km to Saqqez, 2000 m, 6. VII. 1971, *Terme* 9114 (IRAN); Marivan, 1800 - 2100 m, 4. VIII. 1967, *Iranshahr & Terme* 12219E = 9006 (IRAN); Marivan to Baneh, 20 km after Marivan, after Chenareh, 1320 m, *Ghahreman & Attar* 20557 (M); Saqqez to Baneh, Khan pass, 2100 - 2150 m, 27. VII. 1998, *Mozaffarian & Massoumi* 78199 (TARI); ca. 50 km N of Sanandaj, between Sarabghamish village and Kuh-e Chehelcheshmeh, 2100 m, 30. VII. 1995, *Assadi* 75278 (TARI); 45 km on road from Saqqez to Baneh, 1900 m, 20. X. 1977, *Runemark & Mozaffarian* 25927 (TARI); Marivan to Saghez, 12 km to Chenareh, [35° 32', 46° 18' E], 1370 m, 25. VI. 2003, *Assadi* 85036 (TARI); 50 km from Baneh to Sardasht, 1510 m, 30. V. 1978, *Runemark & Mozaffarian* 29256 (TARI); ca. 20 km to Baneh on the road from Marivan (NE2), 1500 m, 25. VI. 2003, *Assadi* 85115 (TARI); Baneh, ca. 10 km on the road from Suteh to Sonnateh to Saqqez, after Haji-Mohammadan, 1950 - 2150 m, 13. VII. 1991, *Mozaffarian* 70058 (TARI); Marivan to Baneh, ca. 19 km from Tusiran to Ghamchian, 1900 m, 28. VII. 1995, *Mozaffarian* 74843 (TARI); Marivan to sanandaj, from old road, Gardaneh Garan, 1400 - 1850 m, 8. VII. 1995, *Ghahreman & Mozaffarian* 18314 (TUH); 20 km E of Marivan, 1410 m, 16. VI. 1999, *Ghahreman & Attar* 22481 (TUH); 20 km from Marivan to Baneh, after

Chenareh, 1320 m, *Ghahreman & Attar* 20557 (TUH); 50 km from Baneh to Marivan, 1600 m, 9. VII. 1995, *Ghahreman & Attar* 20672 (TUH); 70 km from Baneh to Marivan, 1900 m, 9. VII. 1995, *Ghahreman & Attar* 19673 & 19672 (TUH); In declivibus austro-occid. jugi Gardaneh-ye Khan Hasan Saralan prope Baneh, 2050 m, 9. VII. 1974, *Rechinger* 49174 (W); Baneh, Mt. E of Baneh, 2200 m, 2. VIII. 2001, *Mehregan* 208 (JGM).

4.4.5.18.2 *Cousinia pergamacea* subsp. *sardashtensis* (Rech. f.) Mehregan, com. et stat. nov. ≡ *C. sardashtensis* Rech. f., *Fl. Iranica* 139a: 139 (1979). –Holotype: Iran, Azerbaijan, Sardasht, in declivibus siccis. substr. schist., [36' 09° N, 45' 29° E], 1500 m, 9.VII.1974, *Rechinger* 49113 (W!; isotypes B!, E!, K!).

Illustration. – Fig. 10, B.

Appendages with ± erect and distinct spines on both sides.

Flowering period. – July.

Taxonomic remarks. – *Cousinia pergamacea* subsp. *sardashtensis*, distributed in southern parts of Iranian Azerbaijan, differs from subsp. *pergamacea* only in having spines on both sides of the phyllary appendages.

Distribution and habitat. – Endemic to W Iran (Fig. 11, I), on stony slopes and mountain sides, usually in oak forests.

Specimens seen. – Iran: Azerbaijan: ca. 40 km from Mahabad to Sardasht, 1600 m, 13. VII. 1991, *Mozaffarian* 70049 (TARI); Inter Mahabad et Sardasht, 37 km Atrid vers. Sardasht, 1750 m, 8. VII. 1973, *Zehzad & Siami* 3443 (W).

4.4.5.19 *Cousinia concinna* Boiss. & Hausskn., in Boiss., Fl. Or. 3: 513 (1875). ≡ *Arctium concinnum* (Boiss. & Hausskn.) O. Kuntze, *Revis. Gen.* 1: 307 (1891). – Lectotype (designated here): Iran, “in dumosis Kurdistaniae Persicae inter Masibin et Awiheng”, 7 – 10000', VIII. 1867, Haussknecht 568b (G-BOIS!; isotypes JE!, G-BOIS!).

Note. – The sheet with only a single specimen and a handwritten label “*C. concinna*” is here selected as lectotype.

Illustration. – Fig. 10, C.

Biennial or perennial, monocarpic, up to 70 cm high, arachnoid-tomentose or ±glabrescent. Stems branched from base or higher. Leaves leathery or ±herbaceous, glabrescent above and tomentose beneath; basal leaves up to 15 × 5 cm including spines, lanceolate to oblong-lanceolate or lyrate, sinuate-lobate to deeply pinnatisect, with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, lanceolate to linear-lanceolate, spiny-lobed, cuneate at base, usually long decurrent to form winged stems. Capitula 1.5 – 2.5 cm broad with appendages, glabrous or glabrescent. Phyllaries 100 – 120; middle ones imbricate, with prominent yellow midrib; free part of

middle phyllaries constricted at base, expanded above into a concave or flat, erect, deltoid or deltoid-sagittate appendage, as broad as to less than 1.5 times broader than the base, 5 – 8 mm long, 3 – 6 mm broad, attenuate into a spine at apex, usually glabrous or ±glabrescent, margins entire. Receptacular bristles rough. Flowers 40 – 120; corolla rose, purple, white or yellowish-white, 19 – 24 mm long; anthers rose or purple. Achenes 4 - 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – Similar to *C. pergamacea*, but differs in having smaller phyllaries and usually rose, purple or white but never yellow flowers. The two species are distributed in adjacent areas.

Distribution and habitat. – Endemic to W Iran (Fig. 11, J), on stony slopes, in open areas and mountain sides, usually in oak forests.

Specimens seen. – Iran: Kurdistan: 72 km from Sanandaj towards Bijar, 1950 m, 1. VII. 1971, *Terme* 9003 (IRAN); Sanandaj towards Hamadan, pass Salavat Abad, 2400 m, 2. VII. 1971, *Terme* 9004 (IRAN); 42 km S of Sanandaj, Gardaneh Morvarid, 1800 - 1970 m, 17. VI. 1987, *Hamzehee* 1160 (TARI); 28 km from Sanandaj to Divandarreh, 1930 m, 16. VI. 1992, *Attar et al.* 14296 (TUH); Inter Sanandaj et Saqez, 6 km N Divandare, in altoplanitie argillosa, 30. VIII. 1957, *Rechinger* 14737 (B, E, K, M, W); Saqez to Divandarreh, Rashid Abad, 1980 m, 18. VII. 1997, *Ghahreman et al.* 20543 (TUH); Kamyaran to Sanandaj, 20 km to sanandaj, Kerr-e Neck, 1320 m, 11. VII. 1997, *Ghahreman & Attar* 20560 (TUH); 15 km from Sanandaj to Divandarreh, 1320 m, 18. VII. 1997, *Ghahreman & Attar* 20560 (TUH); 3 km Divandarre to Saqez, 1980 m, 18. VII. 1997, *Ghahreman et al.* 20572 (M, TUH); Between Kamyaran and Marivan, [35° 06.535' N, 46° 33.755' E], 1500 m, 5. VII. 2005, *Mehregan & Assadi* 32 (JGM); Between Kamyaran and Marivan, [35° 11.563' N, 46° 28.008' E], 1815 m, 5. VII. 2005, *Mehregan & Assadi* 33 (JGM); Between Kamyaran and Marivan, [35° 13.087' N, 46° 27.355' E], 1675 m, 5. VII. 2005, *Mehregan & Assadi* 34 (JGM); In saxosis et ad versuras 47 km W Bijar versus Divandarreh, 2000 m, 2. VII. 1971, *Rechinger* 42653 (B, TARI, W) & 1950 m, *Lamond* 4428 (E); In graminosis siccis jugi prope Salavatabad 25 km E Sanandaj, 2300 m, 3. VI. 1971, *Rechinger* 42752 (W); In jugo Ariz 20 km W Sanandaj, 2200 m, 4. VII. 1971, *Rechinger* 42859 (W); Ad versuras 80 km W Sanandaj versus Marivan (Dezh Shahpur), 1700 m, 5. VII. 1971, *Rechinger* 42894 (K, W); In jugo prope Salavatabad E. Sanandaj, 2300 m, 28. VI. 1974, *Rechinger* 48500 (B, M, W); Kowleh 65 km N Sanandaj versus Divandarreh, 1950 m, 28. VI. 1974, *Rechinger* 48511 (B, M, W); 11 km to Kamiaran, from Sanandaj, 1800 - 2000 m, 15. VI. 1987, *Assadi* 60654 (TARI); ca. 50 km NW of Sanandaj, mountainy region Sarel, 2300 m, 27. VII. 1992, *Mozaffarian* 71596 (TARI); Sanandaj to Marivan, Gardaneh-e Ariz, 2140 m, 28. VII. 1992, *Mozaffarian* 71607 (TARI); Gardaneh-e Salavat Abad, 2100 m, 24. VII. 1995, *Mozaffarian* 74767 (TARI); 11 km to Kamiaran, from Sanandaj, 1700 - 2200 m, 29. VII. 1995, *Assadi* 75191 (TARI); Above Kamyaran, Savaneh village, 1720 - 1900 m, 30. VI. 1998, *Assadi* 78809 (TARI); Between Sanandaj and Divandarreh, Before Zaghe Pass, 2200 m, 30. VI. 1998, *Assadi* 78852 (TARI); Kamyaran to Paveh, Palangan village, E slope of Kuh-e Shahu, 1100 - 2000 m, 22. VII. 2003, *Mozaffarian* 83800 (TARI); 23 km from Sanandaj to Marivan, [35° 19' N, 46° 58' E], 2100 m, 24. VI. 2003, *Assadi* 84934 (TARI).



Fig. 10. – A. *C. pergamacea* subsp. *pergamacea* [Rechinger 49060 (B100158870, B)]; B. *C. pergamacea* subsp. *sardashtensis* [Rechinger 49113 (B100094011, B)]; C. *C. concinna* [Rechinger 48511 (B100157182, B)]; D. *C. araneosa* [Terme et al. 13431 (IRAN)]. Photographs for A-C provided by BGBM. Photograph D by I. Mehregan.

4.4.5.20 *Cousinia araneosa* DC., Prodr. 6: 556 (1838). ≡ *Arctium araneosum* (DC.) O. Kuntze, Revis. Gen. 1: 307 (1891). – Lectotype (designated here): Iran, "Persia", 1837, Aucher-Eloy 3495 (G!; isotype P!).

= *C. kornhuberi* Heimerl in Stapf, Denkschr. Akad. Wiss. Math.-Nat. Kl. 50: 62 (1885) – Lectotype (designated here): Iran, "in declivibus montis Elwend Persiae boreali-occidentalis", 4. VII. 1882, Pichler (W!; isotypes B!, K!, WU!), **syn. nov.**

= *C. elwendensis* Bornm., Beih. Bot. Centrbl. 28: 255 (1911). – Holotype: Iran, Hamadan, "in acumine montis Elwend", 8. VI. 1905, Strauss s. n. (JE!).

= *C. ecbatanensis* Bornm., Österr. Bot. Zeitschr. 62: 184 (1912). – Lectotype (designated here): Iran, "in agro Ecbatanensi (Media), prope Hamadan, in siccis", 23. VI. 1882, Pichler s. n. (B100093337, B!; isotypes JE!, K!, W!, WU!) **syn. nov.**

= *C. medorum* Bornm. & Gauba in Bornm., Feddes Repert. 40: 345 (1936). – Lectotype (designated here): Iran, Hamadan (Ecbatana), in declivitatibus montis Elwend (Alwand) supra vicum Silvar, 15. VII. 1935, Gauba 643 (B100093443, B!; isotypes B!, JE!, K!).

= *C. pichleriana* Bornm. ex Rech. f., Fl. Iranica 139a: 141 (1979). ≡ *C. ecbatanensis* f. *inermis* Bornm., Feddes Repert. 46: 282 (1939). – Lectotype (designated here): Iran, Hamadan, "Weg nach Dowlatabad", 31. V. 1882, Pichler s. n. (W!).

Note. – There is no plant material on the sheet B100157214 (Designated as holotype by Rechinger).

= *C. parsana* Ghahreman, Iranshahr & F. Attar, Iran. Journ. Bot.8: 16 (1999). –Holotype: Iran, Hamadan, above Ecbatan Dam, 1800 m, Ghahreman & Attar 20553 (TUH!; isotype TUH!), **syn. nov.**

Illustration. – Fig. 10, D.

Plant up to 100 cm high, arachnoid-tomentose. Stems branched from base or higher. Leaves leathery, tomentose on both sides; basal leaves up to 40 × 10 cm including spines, oblong-lanceolate, sublyrate-pinnatifid or sinuate-lobate with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, oblong-ovate to lanceolate, spiny-lobed, decurrent to form winged stems. Capitula 2.5 – 7.5 cm broad with appendages, arachnoid-tomentose or ±glabrescent. Phyllaries 50 – 140; middle ones imbricate, rarely imbricate-spreading, usually yellowish; free part of middle phyllaries abruptly expanded above into a usually keeled, erect or sometimes recurved, rhomboid-lanceolate, deltoid-lanceolate or spatulate appendage, appendage 10 – 20 mm long, 9 – 15 mm broad, attenuate into a spine at apex, arachnoid-tomentose at least along margins, without or with up to 2 spines on both sides. Receptacular bristles rough. Flowers (40-) 50 – 230; corolla rose, pale rose, purple or white, 19 – 27 mm long; anthers rose, purple or white. Achenes 4 - 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – The type material of *C. araneosa* was collected by Aucher-Eloy from an unknown locality in Iran. Comparison of the Aucher-Eloy specimens with other material from Iran revealed that similar specimens have been collected only in the Alvand mountain range in province Hamedan (Fig. 000;). This finding is supported by the distribution of Heimerl 's *C. kornhuberi* which we regard as identical with *C. araneosa*. All material of sect. *Cynaroides* collected from the Alvand mountain range shows continuous variation. Specimens from open areas and lower slopes are relatively small, have smaller and more divided leaves, smaller capitula and phyllaries with longer and sometimes spiny appendages (type material of *C. araneosa*, *C. ecbatanensis*, *C. pichleriana* and *C. parsana*), whereas material from higher slopes and alpine altitudes is relatively larger and has larger and less divided leaves, larger capitula with shorter phyllaries (type material of *C. kornhuberi*, *C. elwendensis* and *C. medorum*). None of these taxa can be maintained as separate species.

Cousinia elwendensis was described from an immature specimen collected at Mt. Alvand (Elwend). Our field studies along with our study of specimens collected at the type locality showed that the type material of *C. elwendensis* is an immature specimen of *C. araneosa*.

The type material of *C. ecbatanensis* includes plants with phyllaries with appendages which are either entire or spiny. This material was collected in the same area and, as already noted by Bornmüller (l.c.), has these different forms of phyllaries even within a single population.

Cousinia pichleriana was described by Rechinger based on specimens with entire appendages, and *C. ecbatanensis* sensu Rechinger refers to plants with spiny appendages.

Cousinia parsana was described based on material with spiny appendages collected from Ecbatan Dam, also the type locality of *C. ecbatanensis*.

Distribution and habitat. – Endemic to W Iran, province Hamedan (Alvand Mt. range; Fig. 16, A), in open areas, stony slopes and mountain sides.

Specimens seen. – Iran: Hamedan: Mont Alvand, 2900 m, 11. VII. 1977, Afzal-Rafii & Zehzad 73-7-77 (G); E of Hamadan, exposed level terrain in clay or granite sand among *Hulthemia*, 1830 m, 9. VII. 1966, Archibald 2609 (E, K); Hamadan, aus Ostfuß des Elwend (Alwand), 12. VIII. 1935, Gauba 641 (B, JE); Hamadan, Elwend (Alwand) Geb. beim Dorf Abasabad, 24. VIII. 1935, Gauba 642 (B, W); Tschamane Abr (Wolkanwiese), VII. 1935, Gauba s. n. (B); Mnts. Alvande, near Shahrestaneh, 2360 m, 9. VII. 1997, Ghahreman & Attar 20550 (TUH); Road of Malayer, Ecbatan Dam, 3. VI. 1999, 3. VI. 1999, Ghahreman & Attar 22371 & 22372 (TUH); Alvand mnts, 1800 m, 10. VII. 1997, Ghahreman et al. 20566 (TUH); Ghahavand, 1650 m, 3. VII. 1988, Mozaffarian 64477 (TARI); Hamedan to Abbasabad, Gondehin, Kuh-e Almogholagh, 2200 - 2800 m, 9. VII. 1988, Mozaffarian 64965 (TARI); Kuh-e Alvand from Abero and Simin valleys (Kuh-e Kolah Ghazi) 2200 - 3100 m, 13. VII. 1988, Mozaffarian 65047 (TARI); Neck Mt. between Ganjnameh and Serkan, 2500 - 2700 m, 23. VII. 1995, Mozaffarian 74761 (TARI); Hamedan, Chamane Abr, Sabeti 1407 (W); Mt. Elwand, 1889, Strauss s.n. (JE); Abbas Abad, Kuh-e Alvand, 2100 - 3300 m, 11. VII. 1974, Terme & Moussavi 33898-E (IRAN, W); Shahnaz (Ecbatan) Dam, Yalfan (montis), 1980 - 2200 m, 12. VII. 1974, Terme & Moussavi 33982-E (IRAN, W); 15 - 20 km from Hamadan, Yalfan (Mt.), 1950 - 2200 m, 10. VI. 1987, Terme, Delghandi & Karavar 13431 (IRAN); Hamadan to Tuyserkan, 12 km to Ganjnameh, 2100 - 3300 m, 5. VIII. 1992, Terme, Moussavi & Tehrani 9056 (IRAN).

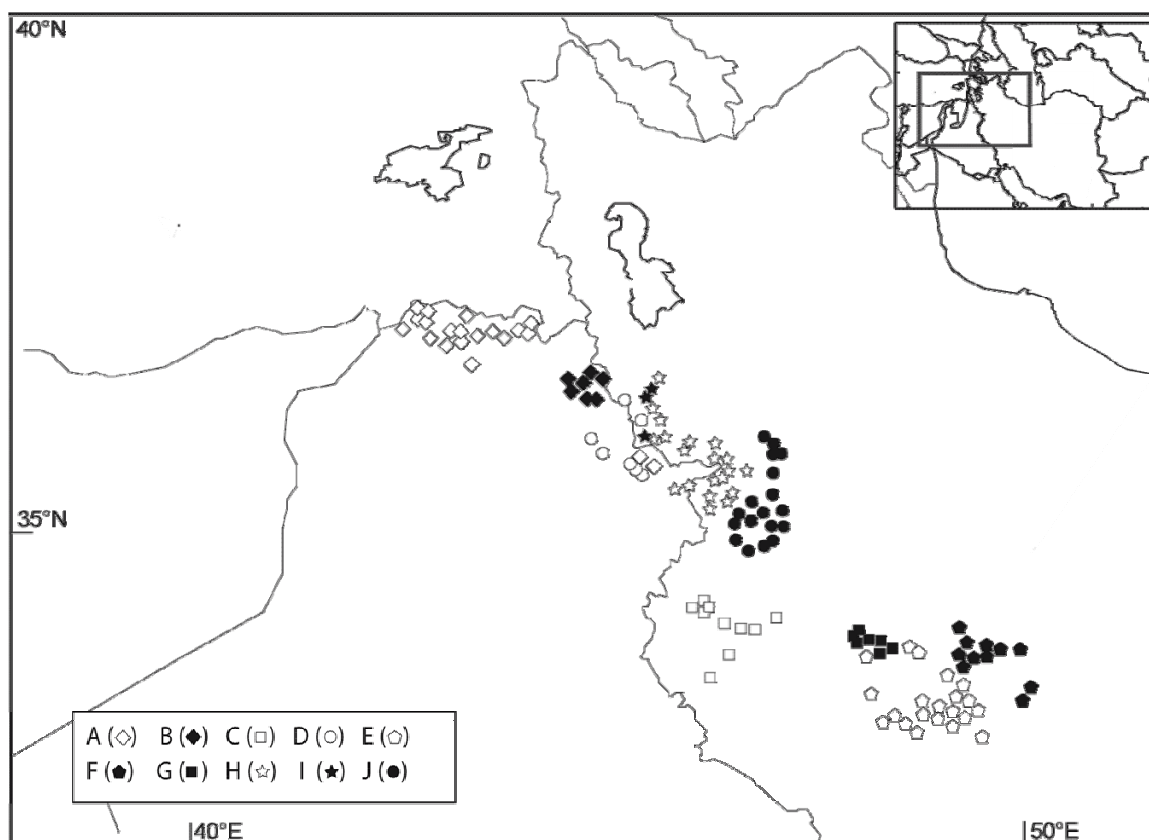


Fig. 11. – Distribution of A. *C. odontolepis* subsp. *odontolepis*; B. *C. odontolepis* subsp. *kurdica*; C. *C. noeana*; D. *C. macrolepis*; E. *C. sagittata* subsp. *sagittata*; F. *C. sagittata* subsp. *iranica*; G. *C. chlorosphaera*; H. *C. pergamacea* subsp. *pergamacea*; I. *C. pergamacea* subsp. *sardashtensis*; J. *C. concinna*. Each symbol indicates the locality of a single collection or several collections made from the same or nearby localities.

4.4.5.21 *Cousinia keredjensis* Bornm. & Gauba in Bornm., Feddes Repert. 36: 328 (1934). – Lectotype (designated here): Iran, Keredj, in declivibus meridionalibus montis Elburs sparsim quidem sed non raro, 1400 – 1600 m, 16. VI. 1934, Gauba 18 (B100093387, B!; isotypes B!, JE!).

Illustration. – Fig. 14, A.

Plant up to 60 cm high, white arachnoid-tomentose, \pm glabrescent. Stems usually branched from the base or higher. Leaves leathery-herbaceous, with prominent white midrib and veins, \pm arachnoid-tomentose on both surfaces; basal leaves usually petiolate, up to 25 \times 5 cm including spines, shortly petiolate, broadly oblong to lanceolate, sinuate-lobate, with spiny-dentate lobes; stem leaves sessile, usually abruptly smaller and less divided towards the apex, oblong, ovate to broadly lanceolate, spiny-lobed, usually long decurrent to form winged stems. Capitula 3.5 – 6 cm broad with appendages, sparsely arachnoid-tomentose, glabrescent or glabrous. Phyllaries 90 – 140, imbricate, with prominent white midrib; middle ones \pm straight or slightly bent outward; free part of middle phyllaries abruptly expanded above into a keeled, deltoid-ovate to deltoid-lanceolate appendage, appendage 12 – 20 mm long, 7 – 15 mm broad, gradually attenuate into a long spine at apex, usually sparsely arachnoid-tomentose, glabrescent, usually with 2 – 3 spines at both

sides. Receptacular bristles smooth. Flowers 70 – 110; corolla pale rose, purple or lilac, 22 – 27 mm long; anthers concolorous. Achenes 4 – 5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia keredjensis* is similar to *C. araneosa* p.p. and differs mainly in having longer spines at the apex and on the margins of the appendages.

Distribution and habitat. – Endemic to N Iran (Fig. 16, B), on rocky slopes.

Specimens seen. – Iran: Tehran: Karadj, Kuh-e Dashteh, 2000 - 2500 m, 19. VI. 1979, *Assadi & Mozaffarian* 32774 (TARI); W of Tehran, Suleghun Valley, 1500 - 2000 m, 31. VI. 1979, *Assadi & Mozaffarian* 32627 (TARI); Mts. NE of Tehran, Souleghun valley,,1900 m, 19. VII. 1980, *Assadi, Mozaffarian & Jamzad* 33614 (TARI); Karaj, Kuh-e Dashteh, 1600 - 2300 m, 25. VII. 1995, *Djavadi* 9051 (IRAN); Chalus road, after Sadd-e Amir-Kabir, 1770 m, 20. VIII. 1996, *Djavadi* 9050 (IRAN); Sarvedar, Karaj valley, 1500 m, 5. VI. 1974, *Foroughi et al.* 12320 (TARI, W); Keredj, 1500 m, 5. VII 1934, *Gaub* 18 (B); Keredj, 2200 m, *Gaub*,1413 (W); Road of Karaj, Kuh-Dashteh, 1550 m, 13. VI. 1998, *Ghahreman & Attar* 21807 (TUH); W of Tehran, Sangan, 24. VI. 1986, *Jamzad* 57089 (TARI); In ditione oppidi Keredj, 1600 - 2200 m, 30. V. 1937, *Rechinger* 606 (W); Karaj valley, 2 km S of Khuzan Kala, 1750 m, 18. VII. 1976, *Runemark, Rezayean & Pak-Tinat* 21705 (TARI); Above Ariamehr Botanic Garden, Vardavard valley, 1700 m, 17. VI. 1974, *Wendelbo, Assadi & Shirdelpour* 12525, 12526 & 12527 (TARI).

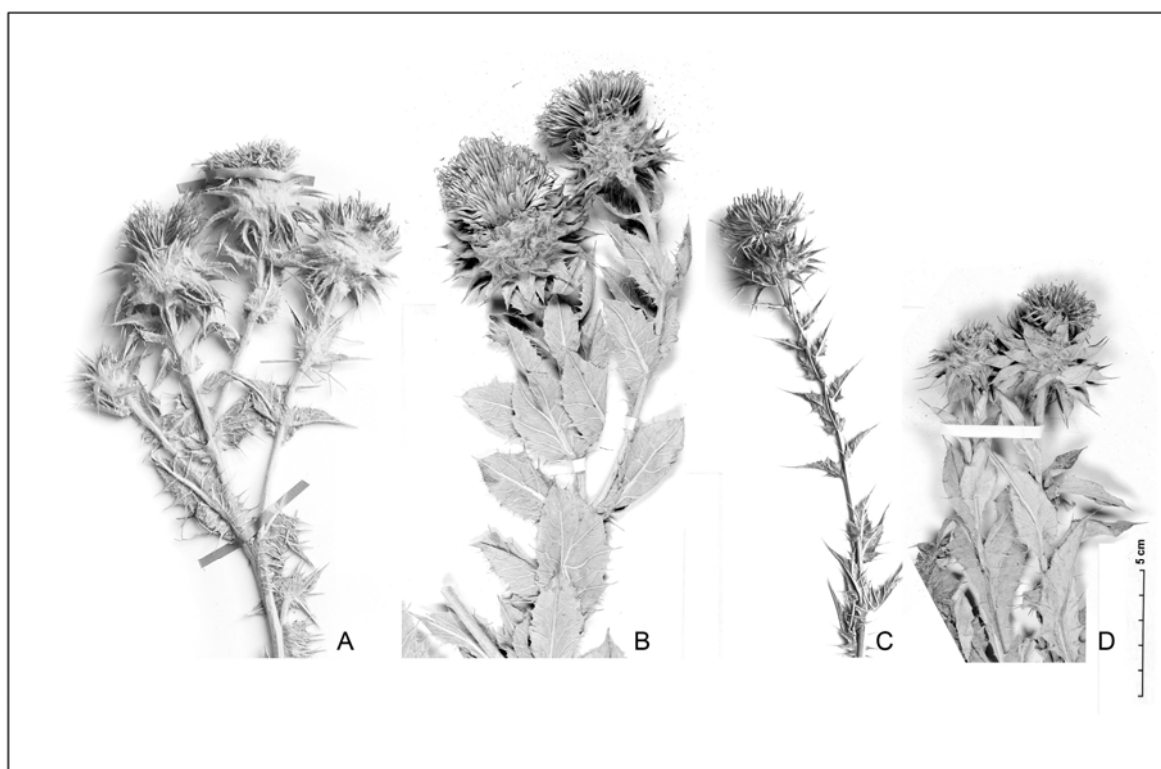


Fig. 12. – A. *C. algurdina* [Rechinger 11465 (E)]; B. *C. canescens* [Rechinger 32865 (B100157229, B)]; C. *hakkarica* [Davis 45467 (E)]; D. *C. macrocephala* [Fedossejew s.n. (B100158871, B)]. Photographs B & D provided by BGBM. Photographs A & C by I. Mehregan.

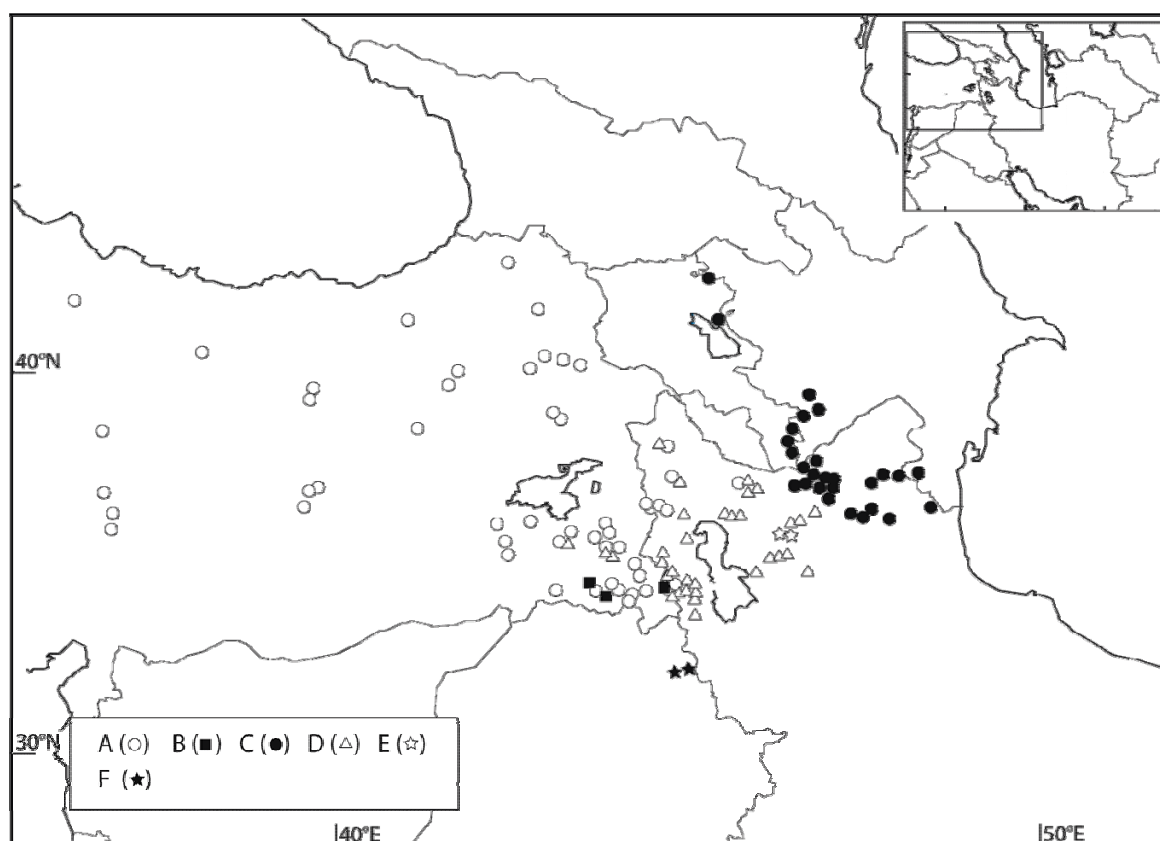


Fig. 13. – Distribution of species of *C.* sect. *Cynaroideae* – A. *C. canescens*; B. *C. hakkarica*; C. *C. macrocephala*; D. *C. grandis*; E. *C. gilliatii*; F. *C. algurdina*. Each symbol indicates the locality of a single collection or several collections made from the same or nearby localities.

4.4.5.22 *Cousinia kotschyi* Boiss., Diagn. Pl. Orient. Ser. 1, 6: 120 (1846). – Lectotype (designated here): Iran, "in collibus aridis ad radices montis Kuh-Daëna in Persia australi", 6. VII. 1842, Kotschy 568 (G00105149, G-BOIS!; isotypes B!, G!, E!, P!, K!, W!).

Plant up to 50 cm high, white archnoid-tomentose, rarely \pm glabrescent. Stems usually branched from the base or higher. Leaves leathery, white archnoid-tomentose on both surfaces or glabrescent above; basal leaves up to 25 \times 6 cm including spines, lanceolate or oblong-lanceolate to linear, sinuate-lobate to deeply pinnatisect, with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate to lanceolate, spiny-lobed, usually long decurrent to form winged stems especially in lower part, sometimes rounded to cuneate at base. Capitula 3.5 – 6 cm broad with appendages, archnoid-tomentose or glabrescent, rarely glabrous. Phyllaries 50 – 120, with prominent midrib, very variable in form and size, recurved, \pm spreading or tightly imbricate; middle ones recurved, \pm spreading, spreading-erect or erect; free part of middle phyllaries slightly or abruptly expanded above into a usually keeled, flabellate, obovate-deltoid, rhomboid, sagittate, ovate, rhomboid-lanceolate to linear appendage, appendage 10 – 25 mm long, 3 – 18 mm broad, gradually or abruptly attenuate into a spine at apex, usually archnoid-tomentose, rarely glabrescent or glabrous, with 1 – 3 spines at both sides. Receptacular

bristles rough or smooth. Flowers 25 – 70; corolla purple, yellow, or white, 18 – 23 mm long; anthers concolorous. Achenes 3 – 4 mm long.

Key to the subspecies of *C. kotschyi*

1. Phyllaries with imbricate, broad appendages (western, northern and northeastern slopes of Dena Mt. range) subsp. *khansaricus*
 - Phyllaries with spreading-imbricate to \pm spreading, broad to narrow appendages (Kerman, Yazd, and southern slopes of Dena Mt. range) subsp. *kotschyi*

4.4.5.22.1 *Cousinia kotschyi* subsp. *kotschyi*

= *C. farsistanica* Bornm., Österr. Bot. Zeitschr. 62: 185 (1912). – Holotype: Iran, Fars, “in monte Kuh Tschah Siah prope Siwaend (nordöstlich von Persepolis)”, 16. VII. 1885, Stapf s. n. (WU!; isotypes B!, K!), **syn. nov.**

= *C. persopolitanus* Attar & Ghahreman, Nordic J. Bot. 23: 589 (2005). – Holotype: Iran, Fars, Abadeh to Shirin-Khosro, after Saghad, 2250 m, 15. VII. 1999, Ghahreman & Attar, 22509 (TUH!; isotype TUH!), **syn. nov.**

= *C. pariziana* Parsa, Fl. de l’Iran 10: 110 (1980). as “*C. parviziana*” – Lectotype (designated here): Iran, Kerman, Pariz, VI. 1957, Anonyme Collector 10026 (K!; holotype in hb-Parsa, destroyed), **syn. nov.**

Note. – Type material of *C. pariziana*, collected from the village “Pariz”, province Kerman, now deposited at K, was labelled by Parsa as “*C. pariziana*” and should be known under this name. The specific epithet “*parviziana*” in Parsa’s Flore de l’Iran published by one of his colleagues in Iran is a mistake.

Illustration. – Fig. 14, B.

Phyllaries with imbricate, broad appendages; terminal spine not longer than half the diameter of the capitulum diameter. Flowers purple or yellow, rarely white. Anthers purple, yellow or white.

Flowering period. – May to August.

Taxonomic remarks. – *Cousinia kotschyi* subsp. *kotschyi* was described from an unknown locality in the large Dena mountain range which stretches from C and SW Iran towards S Iran and includes parts of the provinces Esfahan, Bakhtiari, Kuhgiluyeh and Boirahmad and Fars. In order to identify the type locality, we compared the type material of subsp. *kotschyi* with other material collected in the Dena mountain range and neighbouring areas. We found that some specimens collected from the southern slopes of Dena (province Fars) best match the type material. *Cousinia kotschyi* subsp. *kotschyi* is very variable and widely distributed in S Iran. Capitula vary from having tightly imbricated phyllaries with broad, flabellate to rhomboid appendages and purple flowers (northwestern part of the

distribution area, incl. *C. khansaricus*) to having spreading or recurved phyllaries with linear appendages and white flowers (eastern to southeastern part of the distribution area; incl. type material of *C. farsistanica* and *C. persopolitanus*). None of the species named can be maintained as separate. Type material of *C. pariziana* from SE Iran has very narrow phyllaries but falls within the variation of subsp. *kotschyi*.

Distribution and habitat. – Endemic to S Iran (Kerman, Yazd, and southern slopes of Dena Mt. range; Fig. 16, C), on stony slopes and open area.

Specimens seen. – Iran: Fars: Ad radices m. Kuh-Delu, pr. u. Schiras, VII. 1842, *Kotschy* s.n. (P); 10 km from Sarvestan on the road to Fassa, post Chenar, 1800 - 1850 m, 29. V. 1991, *Jamzad, Taheri & Javidtash* 69372 (TARI); 10 km SE of Sarvestan, Posht-e Chenar, 1650 - 1750 m, 4. VI. 1983, *Mozaffarian* 46727 (TARI); 100 km NE Shiraz, N Tashk, 7. VI. 1970, *Wsylikowa* 14875E (W); 13 km from Ardekan (Sepidan) on the road to Yasoudj, 2400 m, 1. VIII. 1978, *Assadi & Mozaffarian* 31113 (TARI); 15 - 20 km from Shiraz to Esfahan, 1600 - 1900 m, 16. VI. 2002, *Assadi & Ranjbar* 82982 (TARI); 16 km from Fasa on the road to Jahrom, last road, 1800 m, 2. VII. 1999, *Ghahreman & Attar* 22531 (TUH); 3 km W of Saadatabad, 1800 m, 22. V. 1964, *Grant* 15834 (W); 30 km W of Shiraz, on the road to Kazeroun, [29° 40' N, 52° 15' E], 1800 m, 25. V. 1959, *Wendelbo* 835 (W); 49 km from Sourmagh towards Dehbid, 2210 m, 29. VI. 1989, *Zehzad et al.* 66869 (TARI); 75 km to Abadeh on the road from Shiraz, 2000 m, 16. VI. 2002, *Assadi & Ranjbar* 83017 (TARI); 80 km W of Shiraz, 5 km E of Mian Kotal, 2200 m, 28. VI. 1964, *Grant* 15866 (W); Abadeh, Bavanat, Sourian (Mt.), 24. VI. 1969, *Terme & Izadyar* 8771 (IRAN); Abadeh, between Soghad and Shirin-Khosrov, 15 km, 2250 m, 5. VII. 1999, *Ghahreman & Attar* 22508 (TUH); Abadeh, Bovanat, Sourian (montis), 24. VI. 1969, *Terme & Izadyar* 14876E (IRAN, W); Abadeh, Eghlid, 2250 m, 10. VI. 1992, *Mozaffarian* 71330 (TARI); Ardekan (Sepidan), 2500 m, 18. VII. 1983, *Assadi & Abouhamzeh* 46302 (TARI); Ardekan, 10 km from Ardakan to Komhar, 2600 - 3300 m, 18. VII. 1983, *Assadi & Abouhamzeh* 46338 (TARI); Before Seadat Shahr, between Surian and Fenjan, 30 km to Surian, 2560 m, 3. VII. 1999, *Ghahreman, Attar & Mehdigholi* 22514 (TUH); ca. 25 km NE of Abadeh-Tashk, between Tujerdi and Bagh-e Safa, [30° 11' N, 53° 22' E], 2177 m, 15. VI. 2002, *Assadi & Ranjbar* 82977 (TARI); ca. 30 km NE of Abadeh-Tashk, between Tujerdi and Bagh-e Safa, [29° 53' N, 54° 01' E], 2077 m, 15. VI. 2002, *Assadi & Ranjbar* 82960 (TARI); Kuh Tschah Siah bei Siwend NW Persepolis, 16. VII. 1885, *Stapf* 2821 = 2813 (K); NW of Shiraz, open W facing slopes, in clay among limestone boulders, 2740 m, 23. VII. 1966, *Archibald* 2815 (E, K); S of Estahbanat, Kuh-e Bash, 1700 - 2200 m, 7. VI. 1983, *Mozaffarian* 47016 (TARI); Saadatshahr, Pasargad to Sirbanu, Kuh-e Mousa Khan, 2250 - 2700 m, 15. VI. 1992, *Mozaffarian* 71524 (TARI); Shiraz to Abadeh, Saadatabad, 28. VI. 1969, *Terme & Izadyar* 14875E (IRAN, W); Shiraz to Pasargad, 2060 m, 3. VII. 1999, *Ghahreman & Attar* 22521 (TUH); Shiraz, Kieshalden bei d.Imamzadeh von Sabs Boushan (Sabz-Poushan), 29. V. 1885, *Stapf* 2383 (K); Shiraz, Fuß der Kuh Sabs Boushan (Sabz-Poushan), 29. V. 1885, *Stapf* s.n. (K); Shiraz, 40 km on the road to Ardekan, 2130 m, 31. VII. 1978, *Assadi & Mozaffarian* 31049 (TARI); Bamu protected Area, Darreh Chap, 1650 - 1900 m, 30. V. 1975, *Wendelbo & Foroughi* 17528A (TARI); Dashte Arzhan, E slope of Kuh-e Tasak, from Bonrud and Zanganeh, 2250 - 3000 m, 11. VI. 1992, *Mozaffarian* 71369 (TARI); Shiraz, Khane-Zenian, Zakherd, 2050 m, 11. VI. 1992, *Mozaffarian* 71362 (TARI); Parke Bamu, (protected Area), 1750 - 2000 m, 14. VI. 1992, *Mozaffarian* 71478 (TARI); Kerman: 40 km NE of Sirjan, 2130 m, 7. V. 1961, *Pabot* 134 c (G); 63 km to Anar on the road from Shahre Babak, 2200 m, 4. VI. 1986, *Assadi & Bagosha* 56453 (TARI); NE Sirjan, 7. V. 1961, *Pabot* 6869 (IRAN); Yazd: ca. 30 km SW of Marvast, Baghe-Shadi, [29° 48' N, 54° 08' E], 2148 m, 15. VI. 2002, *Assadi & Ranjbar* 82945 (TARI); Harat, Bakhtiari and Baghe Shahdy, 2050 m, 18. VI. 1997, *Mozaffarian* 77801 & 77805 (TARI).

4.4.5.22.2 *Cousinia kotschyi* subsp. *khansaricus* (Attar & Ghahreman) Mehregan, **stat. & comb. nov.** ≡ *C. khansaricus* Attar & Ghahreman, *Nordic J. Bot.* 23: 592 (2005). – Holotype: Iran, "Esfahan, Khansar", 2400 m, 27. VI. 1997, Ghahreman & Attar 20037 (holo TUH!).

Note. – Khansar (Esfahan, Iran) is outside the distribution range of *C. kotschyi*, and our search for more material of this species from Khansar failed. Examination of other specimens from the type locality and neighbouring areas revealed two more sheets collected by the same collectors under the same number (Ghahreman & Attar 20037, TUH). These two sheets did not match the description of *C. khansaricus* and were identified as *C. silybooides* by us. We found material similar to the type material of *C. khansaricus* in a more southern area in province Bakhtiari well inside the distribution range of *C. kotschyi*, where more material was collected by Ghahreman & Attar one day later than the type (Ghahreman & Attar 20567 TUH collected on 28. VI. 1997 at Bakhtiari, Lordegan). Therefore, the correct type locality of *C. khansaricus* seems to be somewhere in Bakhtiari, most probably Lordegan, and the material was mistakenly numbered with material of *C. silybooides* from Khansar (Esfahan).

Illustration. – Fig. 14, C.

Phyllaries with spreading-imbricate to ±spreading, broad to narrow appendages; terminal spine usually longer than half the diameter of the capitulum. Flowers yellow or white. Anthers usually white, rarely yellow.

Flowering period. – June to August.

Taxonomic remarks. – All material from the western, northern and northeastern parts of the Dena mountain range, including the type material of subsp. *khansaricus*, is very similar to *C. kotschyi*, and intermediate forms are frequent (see *C. kotschyi*). We therefore consider it appropriate to reduce the recently published *C. khansaricus* to a subspecies of *C. kotschyi*.

Distribution and habitat. – Endemic to Iran, western, northern and northeastern parts of Dena mountain range, province Esfahan, Bakhtiari, Kuhgiluyeh & Boirahmad and Fars (Fig. 16, D), on stony slopes and in oak forests.

Specimens seen. – Iran: Ad latera in meridiem spectantia m. Kuh - Daena (Dena), 10. VII. 1842, *Kotschy* 795 (B, E, JE, K, M, P, W); Esfahan: 10 km to Semirom on the road from Shahreza, 2600 m, 14. VII. 1983, *Assadi & Abouhamzeh* 46024 (TARI); Khafr, Kuh-e Dena, 2500 m, 16. VIII. 1972, *Riazi* 6765 (TARI); Kuhe Dena, Khafr, 2500 m, 12. VIII. 1972, *Riazi* 6765 (IRAN, W); N of Kuh-e Dena, Abmalakh, 2000 - 2600 m, 5. VIII. 1978, *Assadi & Mozaffarian* 31349 (TARI); N-side of Kuh-e Dena, near Noghol, 2500 m, 14. VII. 1983, *Assadi & Abouhamzeh* 46072 (TARI); Near Semirom, Abshar, 2300 m, 8. VIII. 1978, *Assadi & Mozaffarian* 31587 (TARI); Bakhtiari: 40 km S Gandoman (Dorabun), 1920 m, 8. VII. 1959, *Pabot* XXX IX h & b (G); Borujen to Dorahan, after Godar-e Kabk, Kuh-e Doudelu, 2300 - 2700 m, 29. VI. 1986, *Mozaffarian* 57231 (TARI); Falard, 2 km Dalvara, 2000 m, 4. VI. 1973, *Iranshahr & Moussavi* 33924E (IRAN, W); Goushaki to Gandoman, 5. VI. 1973, *Iranshahr & Moussavi* 33916E (IRAN, W); Lordegan to Goushaki, 21 km Lorgegan, 1700 m, 5. VI. 1973, *Iranshahr & Moussavi* 33923E (W); Lordegan, Rocky valley of Kuh-e Rig, oppsite to Kuhian and Chellegah, 2000 - 2400 m, 8. VII. 1986, *Mozaffarian* 57603 (TARI); Road from Lordegan to Sarkhon, between Abchenar and Bougar

(around Karoun river), 1100 - 1350 m, 28. VI. 1986, *Mozaffarian* 54983 (TARI); 49 km from Sourmagh towards Dehbid, 2210 m, 18. VI. 1972, *Babakhanlou & Rezaian* 24079 (TARI); Abadeh, Eghlid, Dasht-e Namdan, neck Mt. between Sedeh and Cherkas, 2300 - 2600 m, 10. VI. 1992, *Mozaffarian* 71348 (TARI); Eghlid, Dasht-e Namdan, road from Daryacheh-e Kaftar to Sirbanu, Kuh-e Baraftab, 2350 - 2900 m, 15. VI. 1992, *Mozaffarian* 71542 (TARI); Shiraz to Tale khosravi, Chaleh-Kalagh, 24. VIII. 1949, *Behboudi* 1219E (IRAN, W); Boyer-Ahmad: Yasouj, Bizhan pass, 2800 m, 1. VII. 1999, *Ghahreman, Attar & Mehdigholi* 22501 (TUH).

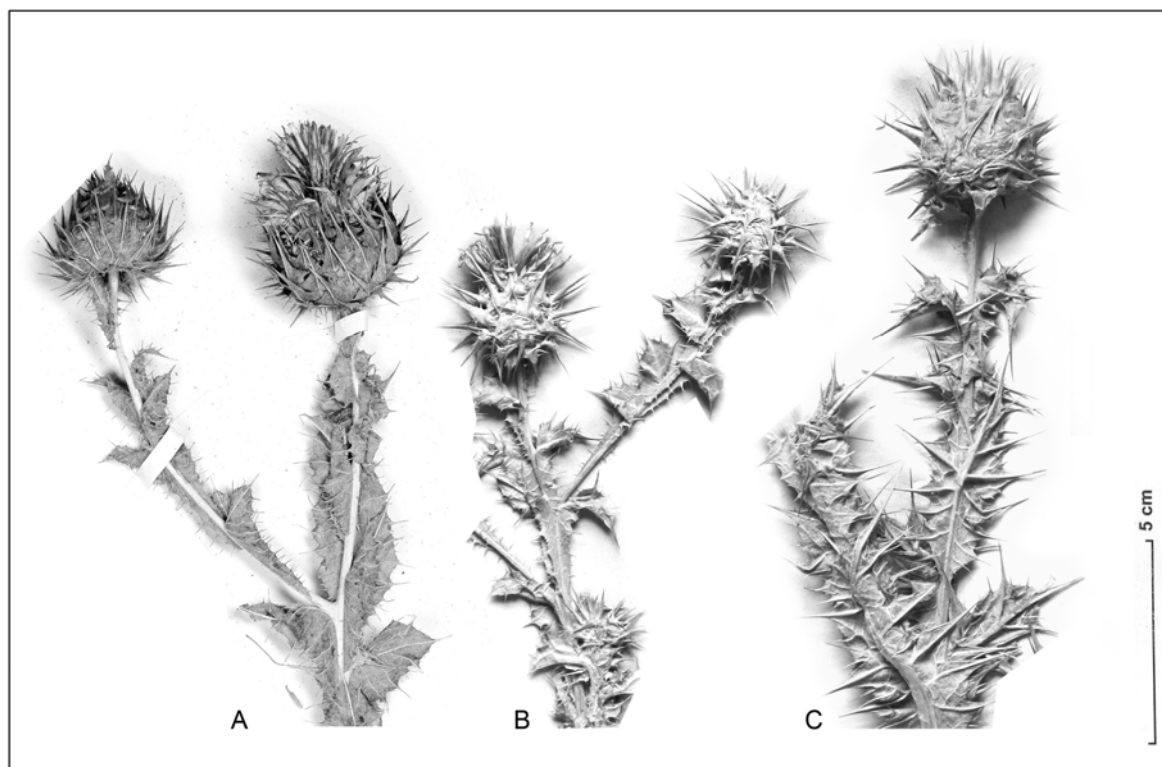


Fig. 14. – A. *C. keredjensis* [Gaubá 18 (B100093387, B)]; B. *C. kotschy* subsp. *kotschy* [Stapf 2821 (K)]; C. *C. kotschy* subsp. *khansaricus* [Kotschy 795 (K)]. Photograph A provided by BGBM. Photograph B & C by I. Mehregan.

4.4.5.23 *Cousinia lordeganensis* Mehregan, *sp. nov.*

– Holotype: Iran, Bakhtiari, Gandoman to Lordegan, 1900 m, 30. VI. 1998, Ghahreman, Attar & Ghaffari 21884 (TUH!; isotype TUH!).

Illustration. – Fig. 15.

Verisimiliter biennis vel perennis monocarpica, pausicaulis. Tota planta canescenti-tomentosa. *Caulis* usque ad 80 cm altus, simplex vel in medio vel supra pausiraosus. *Folia* omnia coriacea; basalia ambitu oblongo-lanceolata, sinuato-lobata. *Capitulae* usque 3 – 4 cm diam., ca. 70-florae; *phyllaria* erecto-patentia, 110 – 120; *phyllaria* intermedia ca. 15 mm longa, 4 – 5 mm lata, linear-lanceolata. *Corolla* alba. *Antherarum* tubus concolorous.

Plant up to 80 cm high, completely canescent-tomentose. Stems usually simple or branched from the middle or higher. Leaves leathery, silver arachnoid-tomentose on both surfaces; basal leaves up to 20 × 7 cm including spines, oblong to lanceolate, sinuate-lobate, with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, ovate, oblong, to lanceolate, spiny-lobed, long decurrent to form winged stem. Capitula 3 – 4 cm broad with appendages, densely arachnoid-tomentose. Phyllaries 110 – 120, ±spreading-erect, straight, with prominent midrib; middle ones ±straight; free part of middle phyllaries gradually expanded above into a ±keeled, linear–lanceolate appendage, appendage ca. 15 mm long, 4 – 5 mm broad, gradually attenuate into a spine at apex, white arachnoid-tomentose, smooth at margin. Receptacular bristles unknown. Flowers ca. 70; corolla white, ca. 20 mm long (immature); anthers concolorous. Achenes unknown (immature).

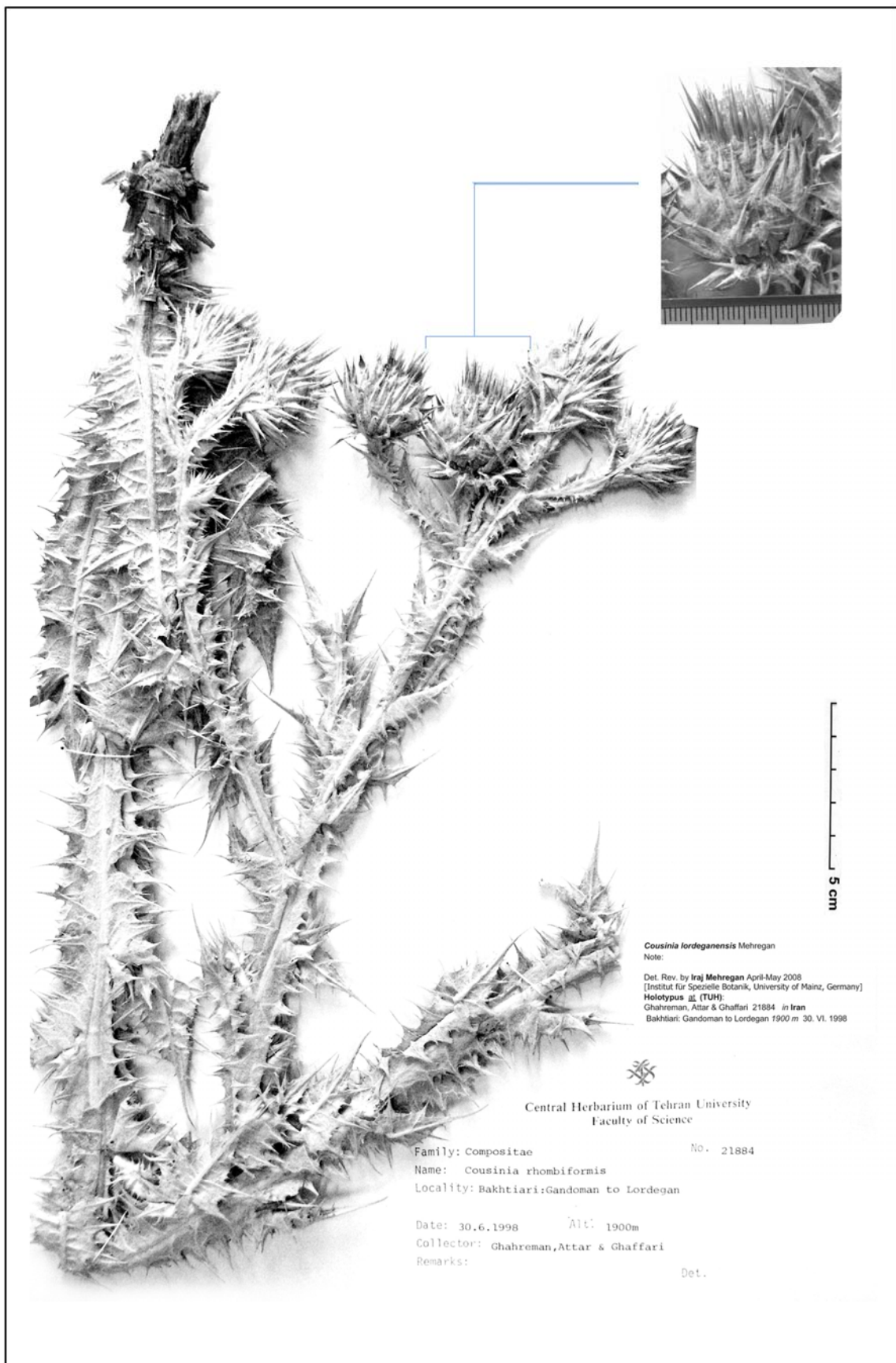
Flowering period. – June to July.

Etymology. – The specific epithet refers to "Lordegan", where the type was collected.

Taxonomic remarks. – The new species is similar to *C. silyboides* subsp. *zardkuhensis*, but distinguishable from it by having up to 80 cm tall and stronger stems (vs. to ca. 40 cm), ±spreading-erect phyllaries with ±straight, linear–lanceolate appendages which are entire and slightly constricted at the base, and flowers with white anthers (vs. not recurved, spreading to erect phyllaries with curved, lanceolate appendages which are spiny at the margin and clearly constricted at the base, and flowers with purple anthers).

Distribution and habitat. – Endemic to central SW Iran (Fig. 16, G), on rocky slopes.

Specimens seen. – Iran: Bakhtiari: Lordegan, after Tunnel Abvanak, 1900 m, 28. VI. 1997, *Gahreman & Attar* 20567 (TUH).



Cousinia lordeganensis Mehregan
 Note:
 Det. Rev. by **Iraj Mehregan** April-May 2008
 [Institut für Spezielle Botanik, University of Mainz, Germany]
Holotypus *st.* (TUH):
 Ghahreman, Attar & Ghaffari 21884 in Iran
 Bakhtiari: Gandoman to Lordegan 1900 m 30. VI. 1998



Central Herbarium of Tehran University
 Faculty of Science

Family: Compositae No. 21884
 Name: *Cousinia rhombiformis*
 Locality: Bakhtiari: Gandoman to Lordegan
 Date: 30.6.1998 Alt: 1900m
 Collector: Ghahreman, Attar & Ghaffari
 Remarks: Det.

Fig. 15. – *C. lordeganensis* [Ghahreman, Attar & Ghaffari 21884 (TUH)]. Photograph by I. Mehregan.

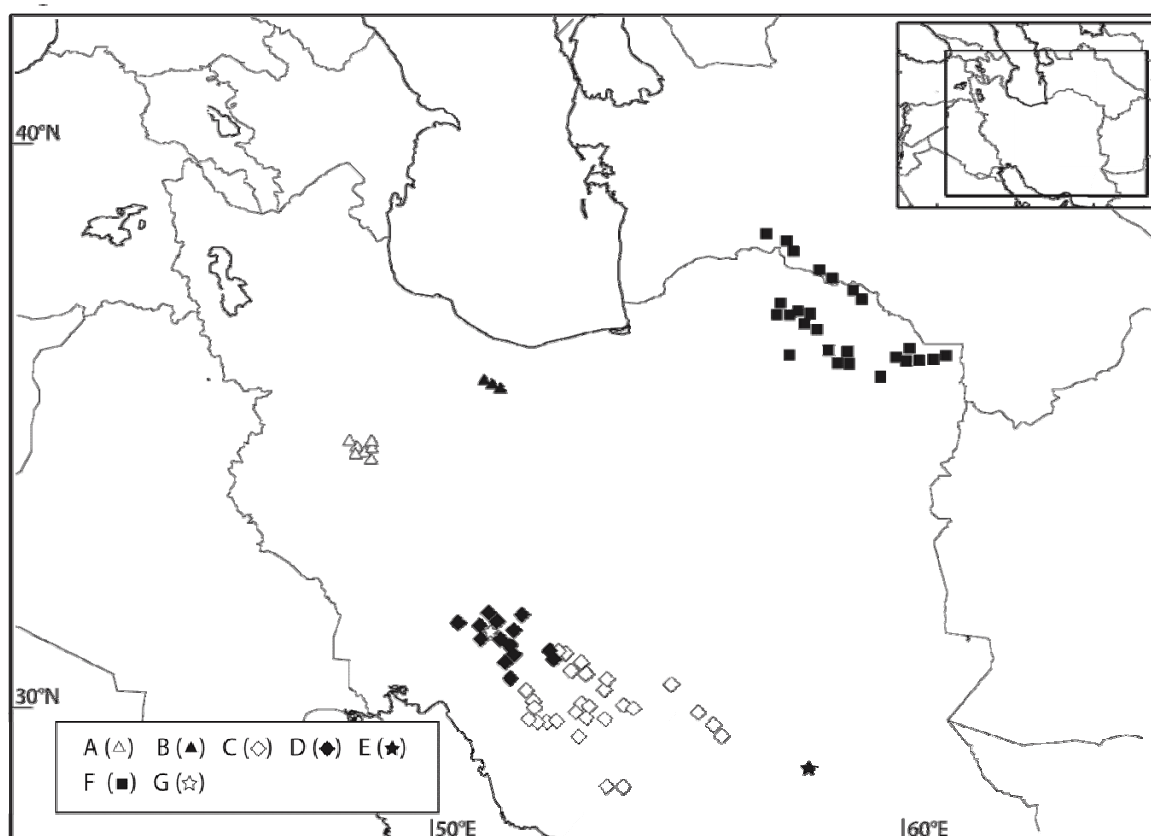


Fig. 16. – Distribution of A. *C. araneosa*; B. *C. keredjensis*; C. *C. kotschyi* subsp. *kotschyi*; D. *C. kotschyi* subsp. *khansaricus*; E. *C. sarzehensis*; F. *C. verbascifolia*; G. *C. lordeganensis*. Each symbol indicates the locality of a single collection or several collections made from the same or nearby localities.

4.4.5.24 *Cousinia cynaroides* (M.B.) C. A. Mey., Verz. Pfl. Cauc. 230 (1831). ≡ *Carthamus cynaroides* M. B., Besch. Länd. Terek Kasp. 195 (1800). ≡ *Onobroma cynaroides* (M. B.) Spreng., Syst. Veg. ed. 3: 392 (1826). ≡ *Arctium cynarodes* (M. B.) O. Kuntze, Revis. Gen. 1: 307 (1891). – Type: Azerbaijan, inter Kuba et Schamachi (Shemakha), "ex montibus Schirvancir", 1796, Marschall von Bieberstein s. n. (LE!).

Illustration. – Fig. 17, A.

Plant up to 45 cm high, densely arachnoid-canescens. Stems usually branched from the middle or higher. Leaves leathery or ±herbaceous, arachnoid-tomentose on both surfaces or ±glabrescent above and arachnoid-tomentose beneath; basal leaves up to 14 × 4.5 cm including spines, lanceolate to oblong-lanceolate, deeply sinuate-lobate with spiny-dentate lobes; stem leaves sessile, gradually smaller and less divided towards the apex, lanceolate, spiny-lobed, cuneate at base, often long decurrent to form winged stems. Capitula 4 – 7.5 cm broad with appendages, arachnoid or ±glabrescent. Phyllaries 50 – 70; middle ones spreading, sometimes slightly recurved; free part of middle phyllaries expanded above into a keeled, slightly recurved, lanceolate to oblong-lanceolate appendage, appendage 10 – 27 mm long, 4 – 8 mm broad, gradually attenuate into a spine at apex, usually arachnoid-tomentose, with 1 - 4 spines on both sides. Receptacular bristles

rough. Flowers 50 – 100; corolla yellow, 20 – 28 mm long; anthers yellow, rarely purple. Achenes 4 - 5 mm long.

Flowering period. – May to July.

Taxonomic remarks. – Similar to *C. calocephala*, distinguishable from it by its densely arachnoid-canescenscent indumentum.

Distribution and habitat. – Endemic to Caucasus and NW Iran (Fig. 19, G), on dry stony slopes.

Specimens seen. – Azerbaijan: Talysch, Meyer s. n. (G-BOIS, P, W); Caucas, VI. 1839, Hohenacker s. n. (E).

– Armenia: Georgia: Swant, cauc. In aridis arenensis, saxosis ditionis, 4500', VI. 1836, Hohenacker s. n. (E, K, M, P, W, WU).

– Iran: Azarbaijan: ca. 17 km from Ardabil to Nir, 1550 m, 30 . VII. 1998, Mozaffarian & Massoumi 78229 (TARI); Ardebil, Namin, Astara Road, 1450 m, 27. VII. 1974, Foroughi & Assadi 13956 (TARI); ca. 20 km from Ardebil to Germi, 1320 m, 16. V. 1993, Ghahreman et al. 17488 (TUH); Between Ardebil and Sar-e Ain, 1650 m, 22. VI. 1999, Attar & Mehdigholi 22569 (TUH); 10 km from Namin to Heyran pass, 1600 m, 22. VI. 1999, Ghahreman & Attar 22568 (TUH); 80 km N of Meshkin-Shahr, near Kangar-Lou, 1000 m, 19. VII. 1999, Ghahreman & Attar 21967 (TUH).

4.4.5.25 *Cousinia calocephala* Jaub. & Spach, Ill. Pl. Or. 2: 96, tab. 178 (1846). ≡ *Arctium calocephalum* (Jaub. & Spach) O. Kuntze, Revis. Gen. 1: 307 (1891). – Holotype: Iran, “in Hyrcania”, Aucher-Eloy 4817 (P!).

Plant up to 60 cm high, arachnoid-tomentose, ±glabrescent. Stems branched from the base or higher. Leaves leathery or herbaceous, arachnoid-tomentose on both sides, or ±glabrescent above; basal leaves up to 25 × 6 cm including spines, lanceolate to oblong-lanceolate, pinnatisect; stem leaves sessile, usually abruptly smaller and less divided towards the apex, ovate to lanceolate, pinnatipartite to spiny-dentate, usually long decurrent to form interrupted wings. Capitula 1.7 – 6 cm broad with appendages, arachnoid or glabrescent. Phyllaries 60 – 100; middle ones ±spreading to recurved, rarely imbricate; free part of middle phyllaries expanded above into a usually ±flat, straight to recurved, deltoid-lanceolate to linear-lanceolate appendage, appendage 6 – 32 mm long, 2 – 6 mm broad, attenuate into a spine at apex, usually glabrous or ±glabrescent, with (0-) 2 – 3 (-5) spine on both sides. Receptacular bristles rough or smooth. Flowers 40 – 140; corolla purple, rose, yellow or dirty white, 18 – 30 mm long; anthers purple, rose or white (in dried material). Achenes 3 – 5 mm long.

Taxonomic remarks. – *Cousinia calocephala* is widely and discontinuously distributed in Iran and Turkey. Intermediate forms between *C. calocephala* and *C. adnata*, *C. vanensis*, *C. stroterolepis*, *C. sefidiana*, *C. sabalanica*, *C. behboudiana*, *C. astrocephala* and *C. nana* are frequent, and none of those can be maintained as separate species. We here group the material of *C. calocephala* into three subspecies based on geographical distribution and morphology.

Key to the subspecies of *C. calocephala*

1. Flowers yellow or cream (plants from eastern Elburz) subsp. *behboudiana*
– Not as above 2
2. Phyllaries ±spreading, 2 cm long or more (plants from C Iran, provinces Markazi, Esfahan except western and southern parts and Qom) subsp. *astrocephala*
– Not as above subsp. *calocephala*

4.4.5.25.1 *Cousinia calocephala* subsp. *calocephala*

= *C. squarrosa* Boiss., Diagn. Pl. Orient. Ser. 1, 10: 102 (1846). ≡ *Arctium squarrosus* (Boiss.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Iran, “in valle Schahristonek montis Elburs”, 16. VII. 1843, Kotschy 551 (G00152012, G!; isotypes G!, P!, W!).

= *C. adnata* Bunge, Mem. Acad. Imp. Scienc. St. Pet. 7. Ser. 9: 50 (1855). ≡ *Arctium adnatum* (Bunge) O. Kuntze, Revis. Gen. 1: 307 (1891). – Holotype: Iran, Azarbaijan, “in montosis inter Bagh et Agh-kent, in Persia boreali, inter Teheran et Tabris”, VI. 1859, Bunge & Bienert s. n. (P!; isotype G! “fragment”), **syn. nov.**

= *C. vanensis* Hub.-Mor., Notes R. B. G. Edinb. 32: 55 (1972). – Holotype: Turkey, Van, Toprak kale, hill above Van, 1770 m, 30 VI. 1949, Huber-Morath 8921 (G!), **syn. nov.**

= *C. stroterolepis* Rech. f., Fl. Iranica 90: 250 (1972). – Holotype: Iran, Kurdistan, 114 km N Marivan (Dezh Shahpur) versus Saqqes, 1580 m, 7. VII. 1971, Rechinger 43086-b (W!; isotype B!, K!, M!), **syn. nov.**

= *C. sefidiana* (Pau) Rech. f., An. Jard. Bot. De Madrid, 47: 365 (1990). – *C. cymbolepis* Boiss. var. *sefidiana* Pau, Trab. Mus. Nac. Cienc. Nat. Ser. Bot. 14: 40 (1918). – Holotype: Iran, Bakhtiari, Kuh Safid, alto Karum“, 3000 m, VI. 1899, Martinez de la Escalera s. n. (MA!), **syn. nov.**

= *C. sabalanica* Attar, Ghahreman & Assadi, Nordic J. Bot. 20: 699 (2000). – Holotype: Iran, Azarbaijan, between Sar-Ayn and Ardebil, 1450 m, 22. VI. 1999, Attar & Mehdigholi 22572 (TUH!), **syn. nov.**

Illustration. – Fig. 17, B.

Phyllaries usually recurved. Flowers purple, rose, rarely yellow. Anthers usually concolorous.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia calocephala* subsp. *calocephala* is very variable and widely distributed in Iran and SE Turkey. Its local populations are continuously connected via intermediate forms.

Distribution and habitat. – SE Turkey, N, NW, C and W Iran (Fig. 19, A), on stony slopes.

Specimens seen. – Turkey: Van: 10 km NW of Baskale, hillside, 2500 m, 18. VIII. 1954, *Davis* 24526 (ANK, E); 34 km from Gürpınar (Havasar) to Hosap, dry stony hills, 2150 m, 3. VII. 1966, *Davis* 45967 (E, K, W); 50 km S Gürpınar, 2200 m, 22. VIII. 1984, *Sorger* 84-74-2 (W); Gevas-Euromit, steppe, 9. VII. 1954, *Davis* 22609 (ANK, E, K); Havasar-Van, steppe hills, 30. VII. 1954, *Davis* 23286 & 23288 (ANK, E, K); Hakkari: Jüksekara-Baskala, 57 km, 37° 54' 38", 44° 04' 38", 1950 - 2000 m, 16. VII. 2001, *Karaveliogullari* ZA-8216 (GAZI).

– Iran: Azerbaijan: 10 km from Sarab to Ardebil, 1400 - 1500 m, 3. VII. 2003, *Mehregan* 85779 (TARI); 35 km from Kivi, Firouz Abad, 1180 - 1350 m, 17. VI. 1980, *Mozaffarian & Nowrouzi* 34248 (TARI); 45 km on the road from Zanjan to Bijar, 1550 m, 19. X. 1977, *Runemark & Mozaffarian* 25926 (TARI); Between Shahindege and Takab, Kuh-e Gharadash (Aghdash) from Ghezghapan, 1400 - 2450 m, 4. VII. 1991, *Mozaffarian* 69880 (TARI, TUH); Bostan Abad, Pishiclou to Chiniboulagh, 4 km. Pishiclou, 2150 - 2350 m, 1. VIII. 1984, *Terme & Moussavi* 8846 (IRAN); ca. 18 km from deviation Zanjan-Mianeh to Mahnesan, 1800 m, 25. VII. 1998, *Mozaffarian & Massoumi* 78161 (TARI); ca. 20 km to Khalkhal on the road from Kivi, 1600 m, 23. VI. 1988, *Assadi & Shahsavari* 65973 (TARI); Entre Maineh et Kivi, Topghara vers Yaleh-gharshi, 1400 - 1600 m, 19. VI. 1978, *Terme, Moussavi & Habibi* 8821 (IRAN); Khalkhal (Mt.), 2. IX. 1968, *Alava & Mojib* 8826 (IRAN); Mianeh, Varzeghan, Souly-Darreh, 1550 - 1920 m, 4. VII. 1983, *Moussavi, Habibi & Tehrani* 13433 (IRAN); Mianeh to Tabriz, 1600 m, 31. V. 1973, *Sabeti* 4124 (TARI); Near Nazagheh, 7 km from Kharaju toward S side of Kuh-e Sahand, 1850 m, 6. VII. 1978, *Assadi & Mozaffarian* 30711 (TARI); Rezaiyeh vers. Mahabad, 120 km S Rezaiyeh, 1250 m, 16. VI. 1971, *Iranshahr* 33990E (IRAN, W); Shahindezh, Halasii, 20. VII. 1976, 7642 (TARI); Takab, 2100 m, 20. VII. 1976, *Siami & Zehzad* 7640 (TARI); 25 km to Soltanieh-Ghaydar, 1750 m, 2. VII. 1974, *Terme & Moussavi* 33897E (IRAN, W); Zanjan, Mahnesan to Takab, Belgheis Mt., 2750 - 2800 m, 26. VII. 1998, *Mozaffarian & Massoumi* 78173 (TARI); 19 km from Zanjan on the road to Bijar, 1940 m, 16. VII. 1974, *Assadi & Amini* 13555 (E, W); 12 km NW Mahabad towards Miandoab, 1300 m, 16. VI. 1971, *Iranshahr* 8829 (IRAN); 20 - 25 km from Takab to Shahindezh, 2000 m, 27. VII. 1998, *Mozaffarian & Massoumi* 78190 (TARI); 30 km to Ahar on the road from Tabriz, 1600 - 2000 m, 17. VII. 1977, *Assadi & Sardabi* 24416 (TARI); 5 km SW Mahabad, 1390 m, 16. X. 1960, *Pabot* 5486 (G); 93 km ESE Tabriz versus Mianeh, 1700 m, 14. VII. 1971, *Rechinger* 42214 (W); Ad versuras et in agris derelictis 16 km NW Mahabad, 1280 m versus Miandoab, 1300 m, 16. VI. 1971, *Rechinger* 42189 (W); Ardebil to Khalkhal, Meresht to Arpachai, 2050 - 2300 m, 30. VII. 1998, *Mozaffarian & Massoumi* 78237 & 78238 (TARI); ca. 25 km from Ardebil to Khalkhal, 1670 m, 30. VII. 1998, *Mozaffarian & Massoumi* 78234 (TARI); Hills S of Tabriz, VI. 1929, *Gilliat-Smith* 2549 (K); Khalkhal to Masouleh, after Majelan, 1450 - 2300 m, 31. VII. 1998, *Mozaffarian & Massoumi* 78259 (TARI); Rezaiyeh to Mahabad, 16 km NW of Mahabad, 1280 m, 15. VI. 1971, *Lamond* 4202 (E); Saqqez to Tabriz, ca. 11 km N of Saqqez, 1500 m, 8. VII. 1971, *Lamond* 4620 (E); Saqqez, between Sonate and Divandarreh, Kuh-e Ghaleh, neck Munt between Bashmagh and Jafarabad, 2300 m, 14. VII. 1991, *Mozaffarian* 70067 (TARI); Sarab, Landjewan, 2000 m, 26. VII. 1970, *Izadyar* 13732E (IRAN, W); Prope Tabris, 1350 - 1500 m, 25. VI. 1924, *Grossheim* 2 (B); Zanjan: 120 km W of Zanjan towards Bidjar, 1500 m, 30. VI. 1971, *Terme* 33989E (IRAN, W); 140 km SE Zanjan to Hamadan, mts. Takht, 2150 - 2560 m, 5. VII. 1974, *Terme & Moussavi* 33896E (IRAN, W); 20 km from Abhar to Gheidar, after Kine vars, 1950 m, 25. VII. 1998, *Mozaffarian & Massoumi* 78148 (TARI); 5 km from Abhar to Gheidar, 1600 m, 25. VII. 1998, *Mozaffarian & Massoumi* 78141 (TARI); 57 km SE Zanjan, Col. S Soltanieh, 2070 m, 24. VI. 1960, *Pabot* 3925 (G); 70 km from Zanjan to Bijar, 1700 m, 30. VI. 1971, *Terme* 33998E (IRAN); 82 km SE Zanjan, 1750 m, 24. VI. 1960, *Pabot* 3963 (TARI); Ad versuras 8 - 22 km SW Zanjan versus Bijar, 1800 m, 30. VI. 1971, *Rechinger* 42364 (TARI); Kurdistan: 108 km from Zanjan on the road to Bijar, 1700 m, 30. VI. 1971, *Lamond* 4321 (E); In collibus siccis et ad versuras 11 km N Saqqes, 1550 m, 8. VII. 1971, *Rechinger* 43109 (B, K, W); 40 km

from Divandarreh to Saqqez, 2100 m, 11. VI. 1996, *Mozaffarian* 77157 (TARI); Gourbaba-Ali, 2240 m, 5. VIII. 1967, *Iranshahr & Terme* 8836 (IRAN); In declivibus argillosis 107 - 109 km Zanjan versus Bijar, 1700 m, 30. VI. 1971, *Rechinger* 42439 (B, K, W); Hamadan: 130 km from Hamadan on the road to Ghazvin, 1850 m, 26. VI. 1974, *Assadi & Shirdelpour* 13220 (W); 137 km from Hamadan on the road to Ghazvin, 2170 m, 18. VI. 1974, *Assadi & Amini* 13621 (W); 5 km from Hamadan to Kaboudar-Ahang, 1690 m, 11. VII. 1997, *Ghahreman & Attar* 20552 (TUH); 5 km to Kaboudar-Ahang, 1690 m - 1860 m, 11. VII. 1967, *Ghahreman & Attar* 20556 & 20548 (TUH); After Kaboudar-Ahang, Molla-Bodagh to Chopoghlu, 1900 m, 11. VII. 1997, *Ghahreman & Attar* 20558 (TUH); Gardane Avaj, after Sultan Bolagh, 2300 m, 14. VII. 1999, *Mozaffarian & Massoumi* 79656 (TARI); Kaboutar Ahang, Shirinsou, 1400 m, 27. - 30. VI. 1998, *Djavadi & Ghanbari*, 20386 (IRAN); Razan to Avadj, 7- 8 km to Avadj, 2000 - 2100 m, 21. VII. 1999, *Terme, Eskandari & Falsafi* 32237 (IRAN); Avaj pass, 1900 m, 9. VI. 1997, *Ghahreman & Attar* 20547 (TUH); Ghazvin to Hamedan, just after Avaj, 2100 m, 7. VII. 1981, *Assadi & Mozaffarian* 36632 (TARI); Markazi: Chelesban, 60 km from Saveh in NWW direction, 2280 m, 25. VI. 1974, *Assadi & Shirdelpour* 13190 (E, W); Aq Bulaq, ca. 100 km N Hamedan, [35° 36' N, 48° 27' E], 15. IV. - 1. VII. 1960, *Rioux & Golvan* 489 (W); Montes Karaghan, In jugo Soltan Bolagh inter Avej et Razan, 2200 - 2400 m, 27. VI. 1974, *Rechinger* 48431 (B, W); Lorestan: Shoulabad to Sefid-Dasht, after Shoulabad, 1700 m, VI. 1998, *Ghahreman & Attar* 21875 (TUH); Sefid Dasht to Shulabad, 30 km to Shulabad, 1800 m, 26. VII. 1999, *Attar & Mirtaj* 22607 (TUH); Ad Bürüdjerd, VIII.1899, *Strauss* s. n. (B, JE); Bakhtiari: 5 km from Farsan to Shahrekord, 1880 m, 28. VI. 1997, *Ghahreman & Attar* 20549 (TUH); Ardal, Dashtak to Cherry, 2100 m, 16. VI. 1973, *Iranshahr & Moussavi* 33917E & 33926E (IRAN, W); Barrage de Kuh-Rang, 2500 m, 6. VII. 1959, *Pabot* 2165 (IRAN); Bazoft area, 2 km to Samsami, from Shahriari, 2050 m, 17. VII. 1994, *Zarre* 17789 (TARI, TUH); Brojen, Boldaji, Kuh-e Chiro, Bagh-e Chiro, 2200 - 2600 m, 1. VII. 1986, *Mozaffarian* 57328 (TARI); Darreh Bazoft, Chebed, N slope of Kuh-e Taraz, 1700 - 2300 m, 12. VIII. 1986, *Mozaffarian* 58825 (TARI); Darreh Bazoft, Mavarz, 1750 m, 13. VIII. 1986, *Mozaffarian* 58049 (TARI); Zagrog mts., Kurang (Kouhrang), 8000 ft., 31. VII. 1965, *Timmis* 10 (K); Esfahan: 30 km Daran, Dalan Kuh, Cheshmeh Gorgi, 280 - 2500 m, 25. VI. 1974, *Moussavi & Satei* 33902E (IRAN, W); 30 km Daran, Dalan Kuh, Cheshmeh Gorgi, 2200 m, 8. VII. 1996, *Mozaffarian* 77226 (TARI); Akhoreh to Chaghyourt, Kuhe Cyhalin-Darreh, 2420 - 2700 m, 3. VIII. 1973, *Moussavi & Satei* 33906E (IRAN, W); Fereydoun-Shahr, Choghoyourt, 2550 m, 31. V. - 4. VI. 2000, *Djavadi & Ghanbari* 29551 (IRAN); Khuzistan: Dehdez to Karun river, around Lirsiah, 1000 m, 17. VI. 1995, *Mozaffarian* 74481 (TARI); Mazandaran: Kandavan, Chaloush-Haraz road, Yoush, 1600 m, 11. VII. 1997, *Ghahreman, Attar & Ghahremani* 21221 (TUH); Inter Djabun et Firuzkuh, 2200 m, 29. VI. 1938, *Rechinger* 1159 (B, W); Tehran: Near Alamut, [36° 23' N, 50° 12' E], 1940 m, 26. VII. 2001, *Attar & Mehdigholi* 27629 (TUH); Col de l'Imam Zadeh Hashem, descente sur Ab-e Ali, 2100, 30. VI. 1974 *Klein* 7640 (E); Elburz, above Tehran, 3000 ft(!), 12. VII. 1959, *Agnew* 18 & 15 (E); Abhange bei Getschesär, 2500 m, 24. VIII. 1934, *Gaubä* 10 (B); Keredj, Kuh Nemar bei Pasinand, 1900 m, 3. VI. 1937, *Gaubä* 1575 (B); Elbursgebirge, auf Hangan, 30. VI. 1933, *Gaubä* 46 (B); In lapidosis vallis Lar, pr. pagum Gatschesar, 2200 m, 6. VII. 1902, *Bornmüller* s. n. (B); In valle Lur montium Elburs occid. ad pagum Meidan, 2200 m, 21. VI. 1902, *Bornmüller* 7365 (B); In valle Scheheristanek montium Elburs, 2200 m, 6. - 7. VI. 1902, *Bornmüller* 7371 & 7372 (B); Jugi Elbursensis in montanis inter aples Totschal et Demawend prope Feschend, 1800 - 1900 m, 12. VII. 1902, *Bornmüller* 7367 (B, JE, K, P, W, WU); Jugi Elbursensis in reg. subalpina. in valle Lur ad pagum Getschesär, 2200 m, 4. VII. 1902, *Bornmüller* 7369 (B, E, JE, K, P, W, WU); Jugi Elbursensis in subalpinis ad basin septentr. alpium Totschal, prope Scheheristanek, 2200 m, 10. VI. 1902, *Bornmüller* 7370 (B, P, W, WU) & 10. VI. 1902, *Bornmüller* 7371 (B, E, JE, P); Totschal, in subalpinis supra Ferasad (Farahzad), 1800 - 1900 m, 29. V. 1902, *Bornmüller* 7366 (B); In ditone oppidi Keredj, in valle fluvi Keredj prope Nissa, 2200 m, 20. VIII. - 1. IX. 1948, *Rechinger & Rechinger* 6726 (B, E, K, M, W); Montes Elburz: In saxosis summi montis Kuh dashteh c. 30 km a Tehran occidentum versus, 2400 - 2500 m, 28. VI. 1977, *Rechinger* 57297 (B, M); 10' W of Firuzkuh, 6 - 8000 ft., 2. VII. 1962, *Furse* 3060 (K, W); 104 km E of Tehran, 2310 m, 5. VII. 1972, *Amin &*

Arazm 4161 (TARI); 116 km NW of Karaj, 2070 m, 7. VII. 1972, *Foroughian* 4168 (TARI); 20 - 35 km from Firouzkuh towards Semnan, 1800 - 2200 m, 5. VIII. 1975, *Moussavi & Karavar* 8830 (IRAN); 20 km from Firouz-Kuh to Semnan, 2050 m, 28. VII. 1996, *Djavadi, Ghaffari & Bakhsheshi* 8928 (IRAN); 22 km Firuz Kuh toward Rodehen, near Chehel-Cheshmeh, 2300 m, 12. VII. 1974, *Renz & Iranshahr* 16616E (IRAN, W); 30 km from Tehran on the road to Shemshak, 1930 m, 12. VI. 1973, *Babakhanlou & Amin* 4226 (TARI); 40 km from Karaj on the road to Chalous, 1980 m, 23. VI. 1973, *Babakhanlou & Amin* 4235 (TARI); 5 km before the pass from Tehran to Chalus, 2400 m, 2. VII. 1969, *Andersen & Petersen* 175 (E, K, W); 7 km E of Firouzkuh, 1900 m, 11. VII. 1972, *Babakhanlou & Amin* 4163 (TARI); 81 km W of Karaj, 1680 m, 28. VI. 1972, *Foroughian & Hariri* 4152 (TARI); 88 km after Firouzkuh on the road to Semnan, Gorsfand, 2200 m, 17. VIII. 1973, *Amin* 4225 (TARI); Alamout, Akbar Abad, 1850 m, 28. VII. 1970, *Foroughi* 747 (TARI); Between Tehran and Karaj, Vardasht, 4. VII. 1977, *Assadi* 25427 (TARI); ca. 27 km from Firuzkuh to Damavand, 2100 m, 9. VII. 1998, *Mozaffarian* 78032 (TARI); Chalous road, Kandowan, 2750 m, 21. VIII. 1996, *Djavadi* 8852 (IRAN); Chalous road, Shahrestanak, 2220 - 2340 m, 20. VIII. 1996, *Djavadi* 8851 (IRAN); Chalus road, S slope of Kandavan, 2600 m, 19. VII. 1990, *Ghahreman & Mozaffarian* 9784 (TUH); Damavand, Ghareh-Ghaj, Sefid Kamar, 2000 m, 23. VI. 1985, *Mozaffarian* 53958 (TARI); Damawand, Chenar, 2050 - 2300 m, 9. VII. 1998, *Mozaffarian* 78009 (TARI); Doab, Karadj valley, 2060 m, 19. VII. 1972, *Rahmanian* 4055 (TARI, W); Elburz mts, S side, W of Firuzkuh, 7000 ft., 23. VI. 1960, *Furse & Synge* 612 (K); Farahzad, Youjeh-Zar, 2200 m, 3. VII. 1972, *Dini & Bazargan* 4237 (TARI); Firouzkuh road, Deh-e Chenar, 2150 m, 4. VII. 1971, *Djavadi & Ghanbari* 8850 (IRAN); Firouzkuh, 5 km to Sarbandan, 2200 m, 4. VII. 1972, *Dini & Arazm* 4141 (TARI); Arjmand, 2200 m, 14. VIII. 1085, *Mozaffarian* 54116 (TARI); Firouzkuh, Eyvanehkey, 2200 m, 4. VII. 1972, *Arazm & Dini* 4171 (TARI); Lazour, Kariz, 2500 m, 14. VIII. 1985, *Mozaffarian* 54188 (TARI); Firouzkuh, Sarbandan, 2250 m, 4. VII. 1972, *Dini & Arazm* 4111 (TARI); Firouzkuh, Seyed Abad, 2250 m, 5. VII. 1972, *Dini & Arazm* 4133 (TARI); Firouzkuh, siding of Eyvanehkey, 2100 - 2200 m, 3. VII. 1972, *Dini & Arazm* 4105 (TARI); Firuzkuh (Sarbandan), 2050 m, 4. VIII. 1973, *Amin* 4082 (W); In valle fluvi Keredj, ad cascades, *Gaub* 1412 (W); Karaj valley, Assemvarak, 2450 m, 25. VIII. 1974, *Wendelbo, Foroughi & Assadi* 14462 (W); 15 km NE Karaj, Mt. Atashgah, 1800 - 1850 m, 27. VI. 1974, *Alava & Moussavi* 33886E (IRAN, W); Karaj, Shahrestanak, 2000 - 2500 m, 11. VIII. 1983, *Mozaffarian* 45445 (TARI); Kolak-Chal, 2100 m, 24. VI. 1974, *Amin & Bazargan* 19263 (TARI); Kuh-e Dasht prope Keredj, 2400 m, *Gaub* 1411 (W); Kuh-e Tochal, Galeh-Kileh towards Shahrestanak, 2000 - 2500 m, 2. VII. 1973, *Terme & Satei* 33910E (IRAN); Lashgarak toward Fasham, 6 km Fasham, 1870 m, 2. VII. 1975, *Moussavi* 33817E (IRAN, W); Mts. NE of Tehran, Suleghun valley, 1900 m, 19. VII. 1974, *Assadi, Mozaffarian & jamzad* 33589 (TARI); Near Takharz, in Elburz, 6000 ft., 28. VI. 1936, *Trott* 501 (K); 104 km E of Tehran, 2350 m, 10. VII. 1972, *Dini & Arazm* 2282 (TARI); Pas-Ghaleh to Kuh-e Tochal, 2070 - 2400 m, 25. VI. 1974, *Alava & Terme* 33890E (IRAN); Pass between Qazvin and Manjil, 1500 m, 13. VII. 1975, *Wendelbo & Assadi* 18284, (TARI); Road from Firouzkuh to Semnan, W side of Bashm pass, 2200 m, 18. VII. 1974, *Wendelbo & Cobham* 13660 (TARI, W); Road of Ghazvin, 2060 m, 26. VI. 1972, *Foroughian & Hariri* 4096 (TARI); S slopes of Tuchal, 2900 - 3650 m, 22. VII. 1998, *Mozaffarian* 78285 (TARI); Taleghan, 2100 m, 18. VII. 1972, *Foroughian* 4205 (TARI); Taleghan to Gachsar, Darreh-pey, 2200 - 2250 m, 25. VII. 1990, *Terme & Moussavi* 8844 (IRAN); Taleghan to Gachsar, Gareh-oheh, 2200 - 2500 m, 26. VII. 1990, *Terme & Moussavi* 8845 (IRAN); 123 km NW of Karaj, 2500 m, 16. VII. 1972, *Foroughi* 23623 (TARI); Taleghan, Darreh-Pey to Garab, Kuh-e Garab, 2200 - 2450 m, 13. VIII. 1991, *Terme, Moussavi & Tehrani* 8847 (IRAN); Taleghan, Mt. between Ganedeh and Jovestan, 2080 m, 15. VII. 1972, *Foroughian* 4202 (TARI); Tochal, 2950 m, 20. VI. 1993, *Attar* 17078 (TUH); Valat-Rud, [36° 04' N, 51° 23' E], 2450 m, 15. VII. 1971, *Edmondson* 683 (E, IRAN, W); Zardeband, 2800 m, 22. VI. 1974, *Amin & Bazargan* 19164 (TARI); 116 km E Teheran, 2150 m, 11. VII. 1960, *Pabot* 4308 (G); Semnan: In jugo Baschm, 2400 m, 29. -30. VI. 1937, *Rechinger* 1967 (B, W); 12 km NE of Shahmirzad, 2400 m, 26. VII. 1982, *Assadi & Mozaffarian* 40388 (TARI); 2 km N of Shahmirzad, mnts. above the village Sufian, 2400 - 2800 m, 22. VII. 2001, *Assadi & Ranjbar* 82042 (TARI); 31 km from Firouzkuh to Semnan,

Gardaneh Bashm, 2600 m, 26. VII. 1982, *Assadi & Mozaffarian* 40330 (TARI); 31 km from Shahmirzad towards Sari, Has-Kouh, 2250 - 2350 m, 14. VII. 1988, *Terme & Karavar* 8930 (IRAN); 35 km from Shahmirzad to Fuladmahalleh, 2300 m, 27. VII. 1982, *Assadi & Mozaffarian* 40418 (TARI) & 2350 - 2500 m, 9. VII. 1974, *Renz & Iranshahr* 34008E & 16614E (IRAN, W); 40 km Shahmirzad to Fulad Mahalleh, 2200 m, 9. VII. 1974, *Renz & Iranshahr* 16629 (IRAN, W); 59 km from Semnan on the road to Sari, 2400 - 2800 m, 25. VII. 1976, *Assadi & Massoumi*, 1536 (TARI); 75 km from Semnan vers Sari, Parvar protected area, 2000 - 2150 m, 9. VIII. 1978, *Terme, Moussavi & Tehrani* 8834 (IRAN); ca. 35 km from Firouzkuh to Semnan, 2020 m, 10. VII. 1998, *Mozaffarian* 78040 (TARI); ca. 50 km N of Semnan, near Tang-e Parvar, 2200 m, 30. VII. 1982, *Assadi & Mozaffarian* 40756 (TARI); Highest pass between Jashm and Shahmirzad, 2900 m, 15. VII. 2003, *Assadi* 85407 (TARI); Shahmirzad toward Fulad Mahalleh, 30 km NE of Shahmirzad, Parvar protected area, 2100 m, 21. VII. 1975, *Moussavi & Karavar* 33781E (IRAN, W); Shahmirzad, Gharm Cheshmeh (5 km NW Shahmirzad), 2200 - 2400 m, 20. VII. 1975, *Moussavi & Karavar* 33808E (IRAN, W).

The specimens *Attar* 26089 (TUH) from Tehran (Sohanak hills, 1990) and Alava & Moussavi 8824/3 (IRAN) from Tehran (Karaj, 15 km NE Karaj, Mt. Atashgah, 1800 - 1850 m, 27. VI. 1974) are intermediate between *C. calocephala* and *C. keredjensis*.

The specimen *Ghahreman, Attar & Ghaffari* 21861 (TUH) from Luristan (Khorramabad, 18 km from Cheshmeh Par to Shoulabad, 2300 m, 26. VII. 1999) is intermediate between *C. calocephala* and *C. sagittata*.

Djavadi, Ghaffari & Bakhsheshi 8928 (IRAN) and *Assadi* 85407 (TARI) from Semnan clearly belong to *C. calocephala* but have middle phyllaries with entire (vs. spiny) appendages.

4.4.5.25.2 Cousinia calocephala subsp. behboudiana (Rech. f. & Esfand.) Mehregan, **comb. & stat. nov.** ≡ *C. behboudiana* Rech. f. & Esfand., Ann. Nat. Mus. Wien 57: 81 (1950). – Holotype: Iran, Tehran, Damavand, Marounak, 2200 m, 11. VII. 1948, Behboudi 169-E (W!; isotype IRAN!).

= *C. calocephala* Jaub. & Spach var. *albiflora* Bornm., Bull. Herb. Boiss. 2. Seri. 220 (1907). – Holotype: Iran, Tehran, Ditionis oppidi Demavend in planitie arida lapidosa, 2200 – 2300 m, 20. VII. 1902, Bornmüller 7369 (B100157191, B!).

= *C. calocephala* Jaub. & Spach var. *albiflora* Bornm. f. *minor* Bornm., Bull. Herb. Boiss. 2. Seri. 220 (1907). – Holotype: Iran, Tehran, Ditionis oppidi Demavend in planitie arida lapidosa, 2200 – 2300 m, 20. VII. 1902, Bornmüller 7374 (B100157192, B!).

= *C. calocephala* Jaub. & Spach var. *lachnolepis* Bornm., Bornm., Fedd. Repert. 41: 311 (1937). – Type: Iran, Elburs, Demavend, auf der Route Dorf Demavend zum Thar-See antraf, 2500 m, 19. VII. 1935, Bornmüller 467 (B100157196, B!).

Illustration. – Fig. 17, C.

Phyllaries usually \pm spreading, \pm straight. Flowers yellow or cream. Anthers concolorous or purple at apex.

Flowering period. – June to August.

Taxonomic remarks. – Differing from subsp. *calocephala* in being smaller and having usually yellow flowers.

Distribution and habitat. – Endemic to eastern Elburz Mt. range (19, B), on rocky slopes.

Specimens seen. – Iran: Tehran: Demavend, bei Ab-i.garm, 1. VIII. 1902, *Brüns* s. n. (B); 10 km S Firouzkuh, Ziba Dasht, 1700 m, 28. V. 1973, *Bazargan & Arazm* 4085 (TARI); 14 km S of Damavand, Akhorbadin, 1650 - 1800 m, 22. VI. 1985, *Mozaffarian* 53866 (TARI); 2 km from Ab Ali to Tehran, 2080 - 2440 m, 16. VII. 1972, *Dini & Arazm* 4188 (TARI); 20 km E of Tehran, 1700 m, 9. VII. 1960, *Pabot* 4047 (TARI); 25 km E of Tehran, 1950 m, 21. VI. 1972, *Dini & Arazm* 4135 (TARI); 41 km N Tehran (Shemshak), 2000 m, 19. VI. 1973, *Amin* 4165 (W); 70 km E of Tehran, 1900 m, 11. VII. 1969, *Cronquist* 10718 (K, TARI, W); 7km from Lashgarak to Gardaneh Ghouchak, 1850 m, 2. VII. 1975, *Moussavi* 8778 (IRAN); Ab Ali, 2080 - 2440 m, 17. VII. 1972, *Dini & Arazm* 4144 (TARI); Ab Ali, 12. VII. 1968, *Bonvan* 9827 (TARI); Ab Sard, 10. VII. 1968, *Bonvan* 9580 (TARI); Ab-e Ali, Sarpolak, 17. VI. 1967, *unknown* 11663 (TUH); ca. 20 km NE of Tehran, above the village Afjeh, 2000 m, 4. VII. 1985, *Assadi & Jamzad* 55258 (TARI); ca. 5 km from Jajroud to Tehran, 1500 - 1600 m, 9. VII. 1998, *Mozaffarian* 78004 (TARI); ca. 6 km to Damavand, Hesar (Hossainabad), 1800 m, 1. VI. 1978, *Mozaffarian* 32488 (TARI); Damavand, 1700 m, 8. VII. 1972, *Dini & Arazm* 4156 (TARI, W); Damavand, 12 km S of Damavand, Akhorbadin, 1750 - 2000 m, 11. VI. 1982, *Mozaffarian* 39872 (TARI); ca. 12 km S of Damavand, Akhobadin, 1700 - 1800 m, 15. VII. 1983, *Mozaffarian* 45331 (TARI); Gilavand, 4 km to Mara, near Akhor-badin, 2000 m, 25. VI. 1972, *Dini & Arazm* 4239 (TARI); Damavand, road from chenar to Daryacheh Tar, 2700 - 2750 m, 9. VII. 1998, *Mozaffarian* 78019 (TARI); Damavand, stony mts. N of Vel, 1900 - 2000 m, 15. VII. 1978, *Mozaffarian* 32379 (TARI); S of Demavand, Above Ab-e Ali, [35° 45' N, 51° 55'], 2300 m, 19. VII. 1959, *Wendelbo* 1382 (W); Firouzkuh, 1950 m, 24. VI. 1972, *Dini & Arazm* 4134 (TARI); Firouzkuh road, Rostam Abad road, Mt. Arabha, 2550 m, 27. VI. 1972, *Dini & Arazm* 4195 (TARI); Firouzkuh, 4 km (to Tehran), 1950 m, 24. VI. 1972, *Dini & Arazm* 4187 (TARI); Firouzkuh, near Gol Ahang, 1750 m, 24. VI. 1972, *Dini & Arazm* 4144 (TARI); Firuzkuh, 1750 m, 24. VII. 1972, *Dini & Arazm* 4149 (W); Firuzkuh road to Ab-e Sard, Deh-e Chenar towards Daryacheh-e Tar, 2140 - 2750 m, 4. VII. 1995, *Djavadi & Ghaffari* 8858 (IRAN); Firuzkuh road to Ab-e Sard, between Deh-e Chenar and Daryacheh-e Tar, 2320 m, 17. VII. 1995, *Ghaffari & Djavadi* 8781/1-(IRAN); Jajroud, 1650 m, 21. VII. 1972, *Arazm* 4191 (TARI, W); Jajroud, 1700 m, 22. VII. 1972, *Dini & Arazm* 4103 (TARI, W); Lashgarak toward Gardaneh-e Ghouchak (16 km N Tehran), 1780 m, 2. VII. 1975, *Moussavi* 33814E (IRAN, W); Lashgarak toward Gardaneh-e Ghouchak (7 km from Lashgarak), 1850 m, 2. VII. 1975, *Moussavi* 33869E (IRAN, W); Montes Elburz centr., in ditione lacus Thar, 2500 m, *Gauba & Esfandiari* 1410 (W); Mt. Emamzadeh Hashem, 24. VI. 2002, *Attar & Mehdigholi* 28692 (TUH); Near Sorkh-e Hesar, Se Pay-e mnts., 1320 m, 18. VI. 1990, *Pouladian* 21342 (TUH); Shemshak, Emameh, 2000 m, 19. VI. 1973, *Amin* 4165 (TARI); Mazandaran: 4 km S of Renyeh, on E slope Mt. Demavand, 2200 m, 27. VII. 1964, *Grant* 16515 (W); Near Rineh, 2500 m, 16. VII. 1998, *Ghahreman & Attar* 21970, (M, TUH); Rineh to Ab-e Garm-e Larijan, 2100 m, 22. VI. 1996, *Djavadi & Ghanbari* 8857 (IRAN); Haraz road, above Rineh, 2350 m, 26. IX. 1978, *Assadi & Salehi* 31755 (TARI); Haraz road, Abgarm-e Larijan, 2090 m, 27. VII. 1996, *Djavadi & Bakhsheshi*, 9456 (IRAN); In the pass NW of Tehran, against Amol, Rockside, 2100 m, 5. VII. 1969, *Andersen & Petersen* 232 (E, K, W); Ad basin montium prope Reneh, 1400 - 1500 m, 28. VII. 1902, *Bornmüller* 7364 (B).

4.4.5.25.3 *Cousinia calocephala* subsp. *astrocephala* (Hauskn. & Bornm.) Mehregan, **comb. & stat. nov.** ≡ *C. astrocephala* Hauskn. & Bornm., Beih. Bot. Cntrbl. 30: 160 (1906). – Lectotype (designated here): Iran, “Sultanabad, in monte Schahsinde”, 18. VII. 1902, Strauss s.n. (B100157251, B!; isotype JE!).

= *C. cynaroides* (M.B.) C. A. Mey. β *viridior* Bornm., Beih. Bot. Centrbl. 32: 406 (1914). – Lectotype (designated here): Iran, “in m. Kuh-i-Kohrud”, VI. 1908, Strauss s. n. (B100157223, B!; isotype JE!).

= *C. nana* Attar, Ghahreman & Assadi, Nordic J. Bot. 20: 698 (2000). – Holotype: Iran, Arak, Mayghan, Davoudabad, 1650 m, 12. VII. 1985, Mozaffarian 64185 (TARI!), **syn. nov.**

Note. – The type locality “9 - 10 km E of Aybak-Abad towards Davood Abad, 1650 m” in the original publication does not match the type label but refers to herbarium material collected by Akhani under no. 14347 (TUH).

= *C. bornmülleri* auct non C. Winkl., Fl. Iranica 90: 231 (1972).

Illustration. – Fig. 17, D.

Capitula large. Phyllaries usually ±spreading, with ± straight appendages, appendages 2 cm or more long. Flowers purple or white. Anthers usually purple.

Flowering period. – (May-) June and July (-August).

Taxonomic remarks. – *Cousinia calocephala* subsp. *astrocephala* is distributed in C Iran and differs from subsp. *calocephala* in having larger capitula with usually ± straight appendages.

Distribution and habitat. – Endemic to C Iran, provinces Markazi, Esfahan and Qom (Fig. 19, C), on rocky slopes.

Specimens seen. – Iran: Esfahan: VI. 2001, *Pour Mohammadi* 27609 (TUH); Ardestan, Yaryan, 2550 m, 8. VII. 1971, *Foroughi* 1864 (TARI); Delijan, 1420 m, 27. X. 1971, *Sabeti*, 2901 (TARI); Kashan, Ghamsar towards Ghohroud, road to Esfahan, after Reza-Abad, 3100 m, 5. VI. 1999, *Assadi, Jamzad & Azizian* 80046 (TARI); Kuh-e Karkas (Kuh-i Kargiz), in declivibus supra Tar, [33° 27' N, 51° 48' E], 27. V. 1974, *Rechinger* 46553 (W); Natanz, Karkas mt., 3000 - 3300 m, 26. VI. 1975, *Foroughi & Assadi* 18086 (TARI); Natanz, Tameh, 2000 m, 20. VI. 1988, *Hashemi & Badiei* 34279 (IRAN); Near Meymeh, 1600 m, 1. VII. 1997, *Ghahreman, Attar & Sheikh* 20542 (TUH); Near Meymeh, 2200 m, 29. VI. 1999, *Ghahreman & Attar* 22491 (TUH); Varian, near Ardestan, 2000 m, 25. VI. 1975, *Foroughi & Assadi* 18042 (TARI); Inter Sultanabad et Kaschan, ad Dschekab, VI. 1899, *Strauss* s.n. (B); Kashan (Mooteh protected region), Muteh (Mooteh), 1950 m, 30. V. 1974, *Rechinger* 46814 (W); Natanz, Karkas mt., 2700 m, 9. VII. 1972, *Foroughi* 4376 (TARI, W); Karmejegan, 50 km S of Qom, Karmojgan, 1900 m, 12. VI. 1974, *Amin & Bazargan* 18960 (TARI, W); Markazi: 83 km from saveh on the road to Hamedan, 1850 m, 26. VI. 1974, *Assadi & Shirdelpour* 13194 (E, TARI, W); 86 km from saveh on the road to Tafresh, 2000 m, 24. VI. 1974, *Assadi & Shirdelpour* 13145 (E, TARI, W); Between Mashad-Ardahal and Narragh, 2150 m, 25. VII. 2000, *Ghahreman, Attar & Mahdigholi* 25108 (TUH); Bifurcation of Tafresh and Dastgerd, 30 km to Tafresh, 1870 m, 17. VI. 1998, *Ghahreman, Attar & Ghaffari* 21811 (IRAN, TUH); Saveh,

beginning of the road, Nubaran to Kahlou to Tafresh, 1635 m, 23. VI. 1993, *Mozaffarian* 72072 (TARI); Tafresh, Gardaneh-e Noghreh Kamar, 1750 m, 24. VI. 1993, *Mozaffarian* 72092 (TARI); Tehran to Arak, ca. 30 km to Arak, near Ebrahim Abad, "Haftad Gholeh Protected Area", 1800 - 2200 m, 25 - 26. V. 2000, *Zarre et al.* 682 (M); Arak, Haftad-Gholleh, Chek Ab, 2100 - 2500 m, 12. VI. 1984, *Mozaffarian & Massoumi* 47862 (TARI); Mahallat, Bagher Abad, Tang-e Badam, 1900 - 2100 m, 14. VI. 1984, *Mozaffarian & Massoumi*, 47990 (TARI); Saveh, beginning of the road, Nubaran to Kahlou to Tafresh, 1635 m, 23. VI. 1993, *Mozaffarian* 72072 (TARI); Tafresh, neck mt. of Noghreh-Kamar, on the road to Ashtian, 2200 - 2400 m, 16. VI. 1984, *Mozaffarian & Massoumi* 48159 (TARI); Arak (Sultanabad), ad stationem viae ferrae Nungird inter Sultanabad et Kum (Qom), 16. VII. 1948, *Rechinger & Rechinger* 5791 (G, W); In declivibus siccis ad viam 62 km NE Arak versus Qom, 1350 m, 18. VI. 1974, *Rechinger* 48272 (B, E, K, M, W); W of Kavir-e Meyghan, 5 km NE of Meyghan village, near the margin of Arak salt lake, 11. VI. 1985, *Akhani* 867 (TARI); N of Kavir-e Meyghan, 9 - 10 km E of Aybak-Abad towards Davood Abad, 1650 m, 12. VII. 1990, *Akhani* 14347 (TUH); Qom: Ferdow, Margheh-Peymal, 2480 m, 3. VII. 1984, *Moussavi & Tehrani* 34278 (IRAN).

Specimen *Mozaffarian* 63784 (TARI) from province Markazi (Arak, Anjadan, 2000 - 2400 m, 7. VII. 1985) is an intermediate form between *C. calocephala* subsp. *astrocephala* and *C. sagittata*.

Specimen *Ghahreman & Attar* 22532 (TUH) from province Esfahan (Near Meymeh, 2200 m, 30. VI. 1999) is intermediate between *C. calocephala* subsp. *astrocephala* and *C. silyboides*.

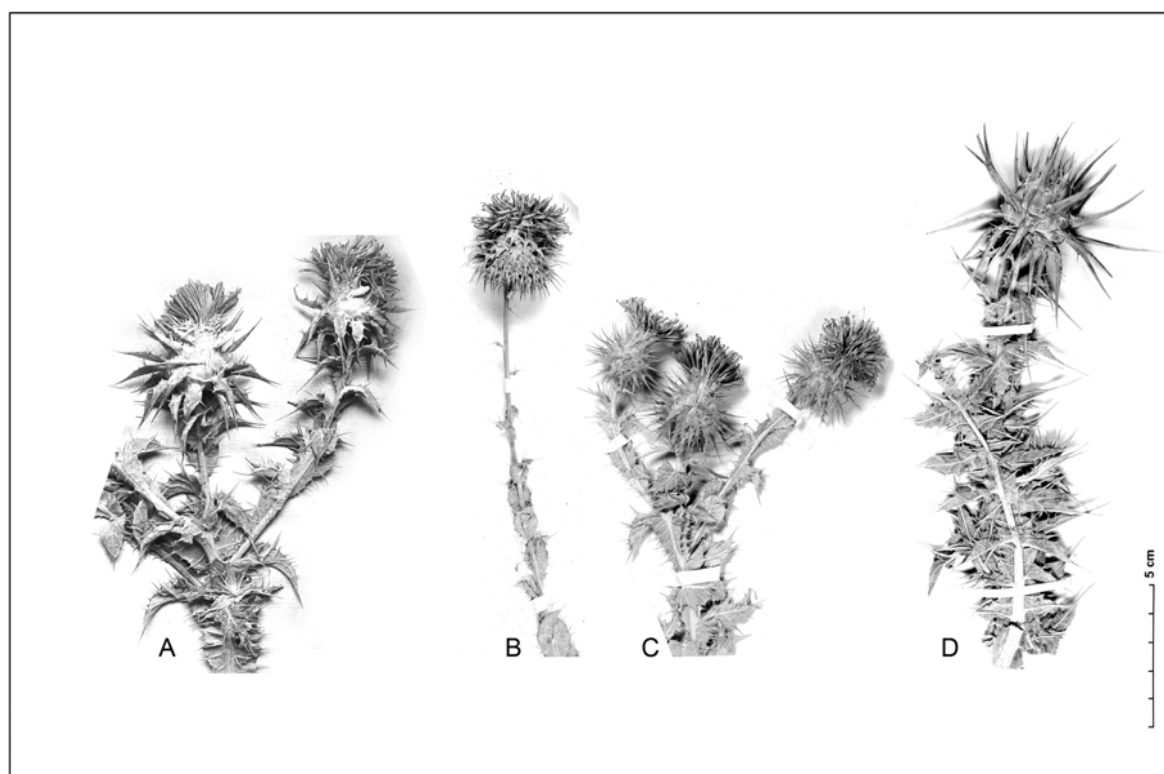


Fig. 17. – A. *C. cynaroides* [Hohenacker s. n. (K)]; B. *C. calocephala* subsp. *calocephala* [Bornmüller 7369 (B100157210, B)]; C. *C. calocephala* subsp. *behboudiana* [Bornmüller 7369 (B100157191, B)]; D. *C. calocephala* subsp. *astrocephala* [Strauss s.n. (B100157251, B)]. Photograph A by I Mehregan. Photograph B-D provided by BGBM.

4.4.5.26 *Cousinia lurorum* (Bornm.) Bornm., Feddes Repert. 40: 346 (1936). As “var. *typica*” ≡ *C. calocephala* Jaub. & Spach. var. *subintegriloba* Bornm., Beih. Bot. Centrbl. 28, 2: 255 (1911). ≡ *C. cymbolepis* Boiss. var. *subintegriloba* (Bornm.) Bornm., Beih. Bot. Cntrbl. 32, 2: 407 (1914). – Holotype: Iran, Kermanshah, “bei Sahneh”, 3. VI. 1909, Strauss s. n. (B100093391, B!).

= *C. lurorum* (Bornm.) Bornm. var. *recurvata* Bornm., Feddes Repert. 40: 347 (1936). – Lectotype (designated here): Iran, Kermanshah, “ad pagum Sahne (Route Kengower-Kermanschah)”, 3. VI. 1909, Strauss 612 (B100158892, B!; isotype JE!).

= *C. lurorum* (Bornm.) Bornm. var. *lancigera* Bornm., Feddes Repert. 40: 348 (1936). – Lectotype (designated here): Iran, Kermanshah, Sungur, “Kuh-i-Emrullah”, 3. VI. 1908, Strauss s. n. (B100158893, B!; isotypes B!, JE!).

= *C. sanandajensis* Rech. f., Fl. Iranica 90: 235 (1972). – Holotype: Iran, Kurdistan, 30' East of Sanandaj, very dry bare, earthy fallow, 5500 ft, 20. VI. 1962, Furse 3304 (K!; isotypes W!, E!), **syn. nov.**

= *C. dalahuensis* Attar & Ghahreman, Iran. Journ. Bot. 8 (2): 264 (2000). – Holotype: Iran, Kermanshah, Gahvareh, Tang-e Khamoush, 1500 m, 4. VII. 1996, Attar & Mirtajodini 19918 (TUH!); paratype: Iran, Kermanshah, Mahidasht region, Bujan pass, 1300 m, Attar & Mirtajodini 19929 (TUH!), **syn. nov.**

Illustration. – Fig. 18, A.

Plant up to 40 cm high, arachnoid-tomentose, or ±glabrescent. Stems branched from the base or higher. Leaves leathery-herbaceous, arachnoid-tomentose on both sides, or ±glabrescent above; basal leaves up to 10 × 3 cm including spines, lanceolate to oblong-lanceolate, sinuate-dentate to pinnatipartite; stem leaves sessile, usually gradually smaller and less divided towards the apex, lanceolate to linear-lanceolate, usually spiny-lobed, long decurrent to form interrupted winged stems. Capitula 1.5 – 3.5 cm broad with appendages, ±arachnoid, glabrescent. Phyllaries 60 – 100, inflated-imbricate or ±spreading; middle ones ±straight or slightly recurved, with prominent midrib; free part of middle phyllaries slightly or abruptly expanded above into a slightly keeled, ±erect or slightly recurved, deltoid to lanceolate appendage, appendage 5 – 10 mm long, 2 – 5 mm broad, attenuate into a spine at apex, arachnoid-tomentose, or ±glabrescent, without or with one (-2) tiny spine on both sides. Receptacular bristles rough. Flowers usually 30 – 70; corolla purple or pink, 17 – 20 mm long; anthers concolorous. Achenes 4 – 5 mm long.

Flowering period. – June and July.

Taxonomic remarks. – *Cousinia lurorum*, *C. sanandajensis* and *C. dalahuensis*, characteristic in having small capitula (1 – 1.5 cm in diam. excl. phyllaries), distributed in mountain W of Iran, are connected with many intermediate forms. Phyllaries are variable and usually have spreading-erect, rarely recurved or appressed, deltoid to lanceolate appendages.

Distribution and habitat. – Endemic to W Iran, provinces Kermanshah, Hamedan and Kurdistan (Fig. 19, D), on stony slopes.

Specimens seen. Iran: – Kermanshah: Kuh-e Parow (Siruleh), 1200 - 2200 m, 17. VIII. 1973, *Moussavi & Satei* 33912-E (IRAN); Ad Songur: in monte Küh-i Emrullah, 3. VI. 1908, *Strauss* s. n. (B); Hamadan: Assadabad, 1750 m, V. 1960, *Arefi* 11670 (TARI); Assadabad pass, 2400 m, 28. VI. 1998, *Assadi* 78730 (TARI); Gardaneh Assadabad, 2250 - 2750 m, 11. VII. 1976, *Javid & Amin* 33291 (TARI); Gardaneh Assadabad, 2500 m, V. 1960, *Attar et al.* 14200 (TUH); Gardaneh Assadabad, 2100 m, 15. VII. 1997, *Ghahreman et al.* 20571 (TUH); Gardaneh Assadabad to Kuh-e Gharavol Khaneh, 2500 - 2700 m, 10. VII. 1988, *Mozaffarian* 64994 (TARI); Assadabad, 2000 m, 10. VII. 1977, *Zehzad & Rafii* 409 (W); Assadabad pass, 20. VI. 1956, *Sabeti* 62 (W), 1. VI. 1956, *Sabeti* 34013E (W); Mahidasht, Bouzhan, 1450 m, 15. VII. 1997, *Ghahreman et al.* 20568 (TUH); Songhor, Mt. Dalakhani, 2300 m, 31. VII. 2001, *Mehregan* s. n. (TUH); Kurdistan: Ad radices montis Hamzeh Arab, SE Bijar, 2000 m, 1. VII. 1971, *Rechinger* 42513 (W); Divandarreh to Bijar, 1710 m, 18. VII. 1997, *Ghahreman & Attar* 20559 (TUH); Foot of Kuh-e Hamzeh arab, Bijar to Hamedan, 2000 m, 1. VII. 1971, *Rechinger* 4404 (E); Kuh-e Hamzeh arab, 2100 - 2550 m, 7. VII. 1968, *Iranshahr* 13131E (IRAN, W); Near Bijar, 6500 ft., 28. VII. 1968, *Sayer* 26 (K); Sarab, 6 km NE of Gol Tappeh, rocky and SE facing valley near Sarab, 2194 m, 14. VIII. 1973, *Calder* 26 (E); In saxosis (Tonschiefer) 6 km SE Bijar, ad viam versus Hamadan ducentem, 2000 m, 30. VI. 1971, *Rechinger* 42472 (B, M, W).

4.4.5.27 *Cousinia purpurea* C. A. Mey., in DC., Prodr. 6: 555 (1838). ≡ *Arctium purpureum* (C. A. Mey.) O. Kuntze, Revis. Gen. 1: 308 (1891). – Lectotype (designated here): Azerbaijan, in locis lapidosis eremi salsi Armenia inter Nakitschiwan et Kok, 1832, Szovits s. n. (G!; isotypes P!, LE).

Illustration. – Fig. 18, B.

Plant up to 45 cm high, arachnoid-tomentose, ±glabrescent. Stems branched from the base or higher. Leaves leathery, white arachnoid-tomentose beneath and green and ±glabrescent above; basal leaves up to 15 × 5 cm including spines, petiolate, oblanceolate to oblong-lanceolate, sinuate-dentate to pinnatifid; stem leaves sessile, usually gradually smaller and less divided towards the apex, ovate to oblong, spiny-lobed to spiny-dentate, long decurrent to form interrupted winged stems. Capitula 1.7 – 4 cm broad with appendages, ±arachnoid, glabrescent. Phyllaries 60 – 110; middle ones spreading-erect, with prominent yellow midrib; free part of middle phyllaries expanded above into a usually keeled, slightly recurved or apically horizontal, ovate to lanceolate appendage, appendage 5 – 12 mm long, 3 – 5 mm broad, attenuate into a spine at apex, usually glabrous or ±glabrescent, usually with 2 spines on both sides. Receptacular bristles rough. Flowers usually 30 – 60; corolla purple, 20 – 30 mm long; anthers concolorous. Achenes 4 – 5.5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia purpurea* is similar to *C. calocephala* and is characteristic in having phyllaries with typically ovate to lanceolate appendage.

Distribution and habitat. – Endemic to the S Caucasus, probably introduced to NW Iran (Fig. 19, E), on dry slopes.

Specimens seen. – Armenia: Ararat distr., 2 km NE of Vedi village, between villages Urtsadz ant Azizkend, [39° 51' N, 44° 41' E], 985 m, 18. VI. 2002, *OPTIMA* 2003-11399 (B, W); Ararat distr., 8 km NE of Vedi village, between villages Urtsadz ant Azizkend, [39° 57' N, 44° 53' E], 1220 m, 20. VI. 2002, *OPTIMA* 2004-02646 (M, W); In valle fluvii Razdan prope pagum Arzni, in clivis argillosis stepposis, 1250 - 1300 m, 18. VII. 1975, *Greuter* 13023 (E, G); Erivan, in decliv. siccis., 20. VII. 1919, *Grossheim* s. n. (B, G, K); Vajk distr., village Martiros, mountain steppe, 28. VII. 1986, *Gabrieljan et al.* 33 (G, W).

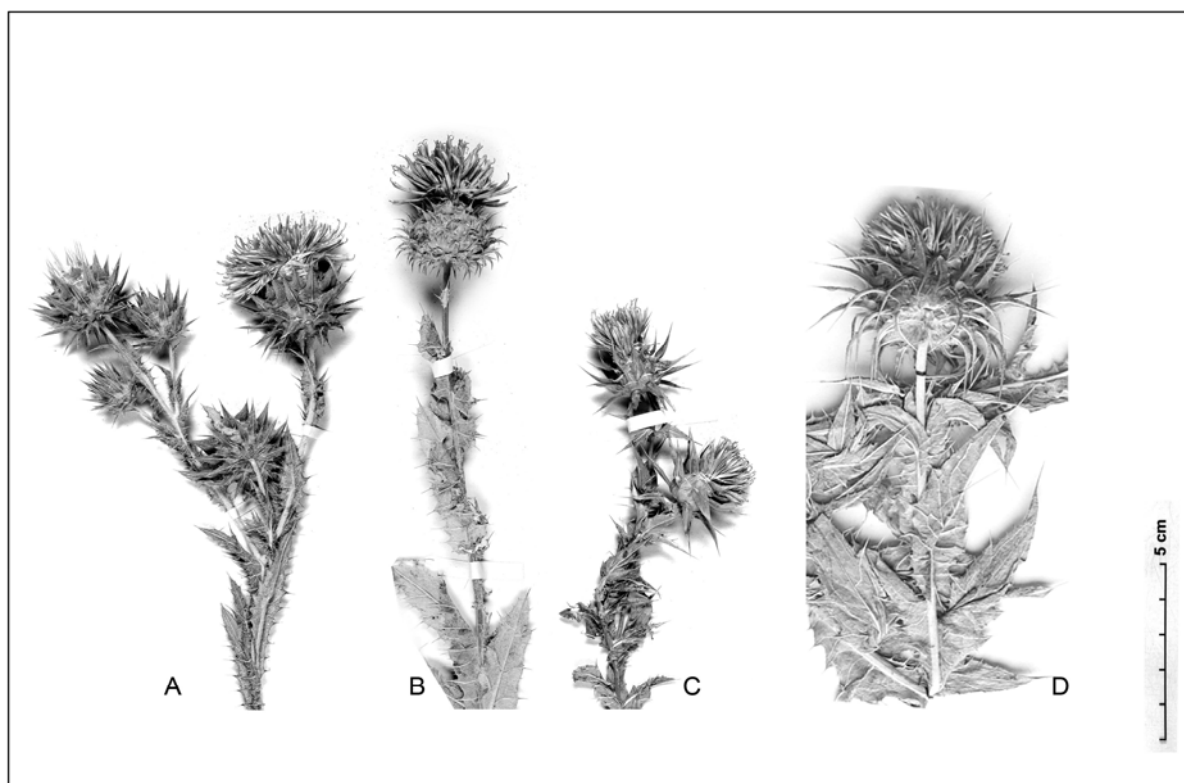


Fig. 18. – A. *C. lurorum* [Rechinger 48472 (B100158845, B)]; B. *C. purpurea* [Grossheim s.n. (B100158853, B)]; C. *C. bobekii* [Rechinger 49031(B100157257, B)]; D. *C. sarzehensis* [Assadi et al. 2103 (E)]. Photographs A-C provided by BGBM. Photograph D by I Mehregan.

4.4.5.28 *Cousinia bobekii* Rech. f., *Fl. Iranica* 90: 238 (1972). – Holotype: Iran, Azerbaijan, Haydarabad ad ripam austro-occidentalem lacus Urmia (Rezayieh), 10. IX. 1956, Bobek 89 (W!; isotype E!).

Illustration. – Fig. 18, C.

Plant up to 40 cm high, arachnoid-tomentose or glabrescent when mature. Stems branched from the base or higher. Leaves leathery-herbaceous, arachnoid-tomentose on both surfaces, glabrescent above and arachnoid-tomentose beneath or glabrescent on both surfaces; basal leaves up to 20 × 6 cm including spines, oblong-lanceolate, deeply pinnatipartite to pinnatisect; stem leaves sessile, gradually smaller and less divided towards

the apex, oblong-ovate to linear-lanceolate, spiny-lobed to spiny-dentate, cuneate at base, short- to long-decurrent to form wings. Capitula 3 – 6.5 cm broad with appendages, arachnoid or ±glabrescent. Phyllaries 50 – 95; middle ones spreading or slightly incurved; free part of middle phyllaries expanded above into a usually keeled, ±straight or slightly incurved, ovate- or rhomboid-lanceolate to linear-lanceolate, rarely sagittate-lanceolate appendage, appendage 9 – 25 mm long, 2 – 7 mm broad, attenuate into a spine at apex, arachnoid-tomentose, ±glabrescent or glabrous, with 1 – 2 tiny spines on both sides. Receptacular bristles smooth. Flowers 40 – 110; corolla yellow or dirty yellow (brown in dried material), 17 – 21 mm long; anthers purple or pale. Achenes 3 – 4.5 mm long.

Flowering period. – June to August.

Taxonomic remarks. – *Cousinia bobekii* is similar to *C. calocephala* but differs in having bright yellow corollas and purple anthers.

Distribution and habitat. – Endemic to NW Iran (Fig. 19, F), on open areas and rocky slopes.

Specimens seen. – Iran: Azerbaijan: *Ghahreman & Attar* 22501 (TUH); 34 km S of Rezaiyeh, inter Balansh et Reshekan (Bashakan?), 1300 m, 15. VI. 1971, *Iranshahr* 8797 (IRAN); 40 km from Ghotour to Khoy, 1400 m, *Ghahreman & Attar* 22008 (TUH); Piranshahr to Oshnavieh, 1400 m, 14. VI. 1999, *Ghahreman & Attar* 22489 (TUH); Uromiyeh to Oshnavieh, 1800 m, 14. VI. 1999, *Ghahreman & Attar* 22456 (TUH); Uromiyeh to Oshnavieh, Darreh Khoroshow, 1400 - 1650 m, 4. VII. 1991, *Delghandi & Abbasi* 15185 (IRAN); Urumieh, road from Darr-e Ghasemlu to Oshnavieh, viviation to Zeiveh, 1800 m, 12. VII. 1991, *Mozaffarian* 70031 (TARI); 20 km NW Naqadeh versus Oshnoviyeh, 1450 m, 8. VII. 1974, *Zehzad & Siami* 3605 (M, TARI, W); 34 km S of Rezaiyeh, inter Balanish et Bashakan, 1350 m, 15. VI. 1971, *Lamond* 4171 (E), *Rechinger* 42121 (B, K, W); Ad litus occidentale lacus c. 20 km E Rezaiyeh, 1340 m, 30. VII. 1974, *Rechinger* 48628 (B, M, W); Ad versuras ad meridiem lacus Rezaiyeh ab Haydarabad austro-occidentem versus, 1400 m, 15. VI. 1971, *Rechinger* 42144 (W); In declivibus siccis inter Oshnoviyeh et Naqadeh, 1500 m, 8. VII. 1974, *Rechinger* 49031 (B, E, K, M, W); Inter Naqadeh et Mahabad, 2. VI. 1974, *Siami* 2262 (W); Lake Rezaiyeh, SW side, [37° 02.5' N, 45° 28' E], 1300 m, 12. VI. 1962, *Jacobs* 6862 (E, K, W).

4.4.5.29 *Cousinia sarzehensis* Attar, Ghahreman & Assadi, *Nordic J. Bot.* 20: 697 (2000). – Holotype: Iran, Kerman, 40 km from Jiroft on road to Kerman: Kuh-e Sarzeh, 2100 – 2500 m, 13 VI. 1977, Assadi & Miller 25326 (TARI!).

Illustration. – Fig. 18, D.

Plant up to 50 cm high, arachnoid-tomentose, ±glabrescent. Stems branched from the middle or higher. Leaves ±herbaceous, arachnoid-tomentose on both surfaces, glabrescent above; basal leaves unknown; stem leaves sessile, gradually smaller and less divided towards the apex, oblong to lanceolate, spiny-lobed to spiny-dentate, cuneate at base, usually long-decurrent to form winged stems. Capitula 6 – 9 cm broad with appendages, arachnoid, glabrescent. Phyllaries 90 – 100; middle ones spreading or slightly recurved; free part of middle phyllaries expanded above into a usually keeled, slightly recurved,

rhomboid-lanceolate appendage, appendage 20 – 38 mm long, 5 – 12 mm broad, attenuate into a spine at apex, arachnoid or \pm glabrescent, with (1-) 2 tiny spines on both sides. Receptacular bristles rough. Flowers 70 – 100; corolla pale purple, 20 – 23 mm long; anthers concolorous. Achenes 4 - 6 mm long.

Flowering period. – June.

Taxonomic remarks. – *Cousinia sarzehensis* is a distinct species without close similarities to other species from the area, including *C. kotschyi* and *C. onopordioides*.

Distribution and habitat. – Endemic to SE Iran (province Kerman; Fig. 16, E), on rocky slopes.

Specimens seen. – Iran: Kerman: Kuh-e Jebal Barez, Kuh-e Sarzeh, 5 km NE of Garraghan, E of road from Jiroft to Deh Bakri, rocky limestone slopes, [28° 55' N, 57° 56' E], 2000 m, 13 VI. 1977, *Assadi, Edmondson & Miller* 2103 (E, W).

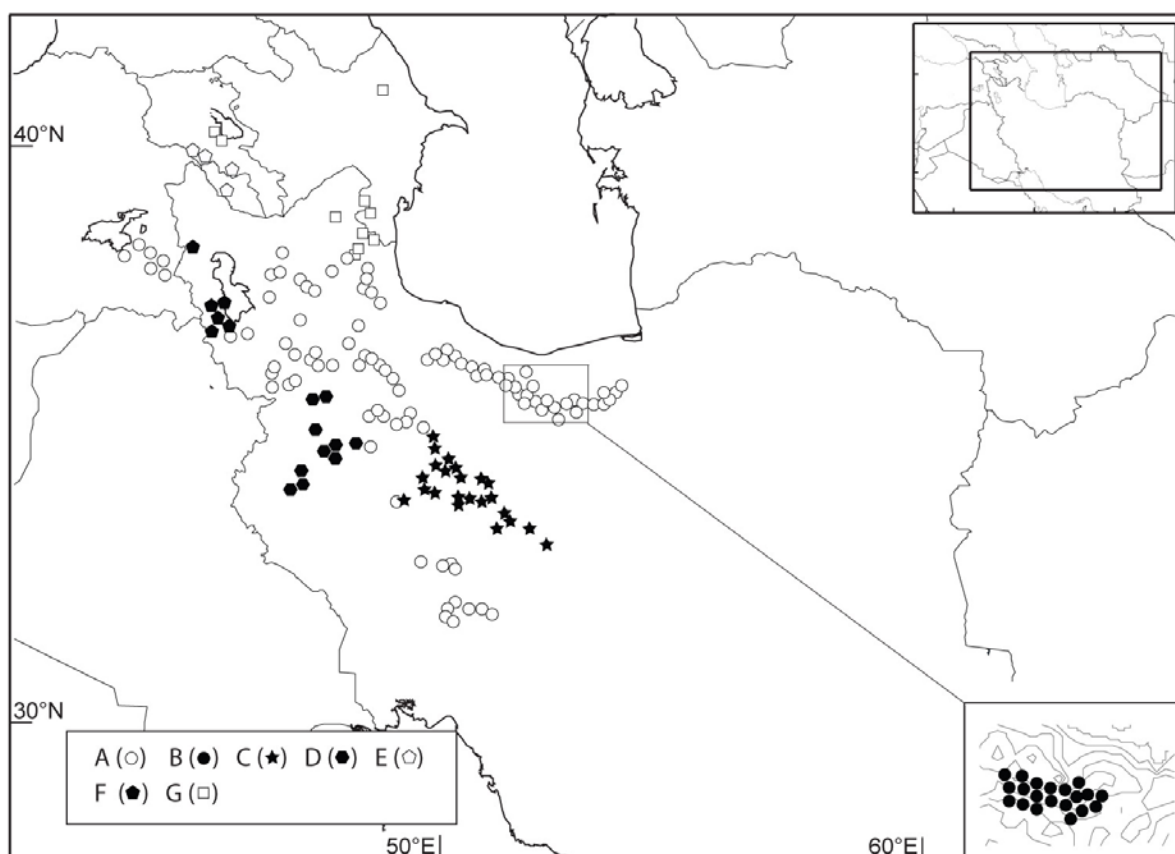


Fig. 19. – Distribution of A. *C. calocephala* subsp. *calocephala*; B. *C. calocephala* subsp. *behboudiana*; C. *C. calocephala* subsp. *atsrocephala*; D. *C. lurorum*; E. *C. purpurea*; F. *C. bobekii*; G. *C. cynaroides*. Each symbol indicates the locality of a single collection or several collections made from the same or nearby localities.

4.4.5.30 *Cousinia onopordioides* Ledeb. in Eichw., Pl. Nov. It. Casp. Cauc. 40 (1831-33). \equiv *Onopordon polyacanthum* Eichw. l. c.: 3 (1831-33). \equiv *Arctium polyacanthum* (Eichw.) Kuntze,

Revis. Gen. 1: 307 (1891). – Lectotype (designated here): Turkmenistan, "In littore orientale Djupkaragan maris Caspii" Eichwald & Karelin "syntype" (LE!; isotypes K! , P!).

= *C. albicaulis* Boiss. & Buhse, Nouv. Mém. Soc. Nat. Mosc. 12: 128 (1860). ≡ *Arctium albicaule* (Boiss. & Buhse) O. Kuntze, Revis. Gen. 1: 307 (1891). – Lectotype (designated here): Iran, "in valle Nika pr. Radkann", 19. VII. 1848, Buhse 1046/6 (P!).

= *C. grandiceps* Bunge, Mém. Acad. Imp. Sciences St.-Petersbourg, VII^e Sér., 9: 54 (1865). ≡ *Arctium grandiceps* (Bunge) O. Kuntze, Revis. Gen. 1: 307 (1891). – Holotype: Iran, Chorassan (Khorassan), inter Schahrud et Nischapur, in montosis ad austrum ab urbe Sebsewar in provincial Chorassan sitis, VI. 1858, Bunge & Bienert s. n. (P!; isotypes K!, P!), **syn. nov.**

= *C. bornmülleri* C. Winkl., Acta Hort Petrop. 14: 235 (1897). – Lectotype: Iran, Kerman, in monte Kuh-i-Dschupar, 3400 m, 10. VI. 1892, Bornmüller 3456 (B100088389, B!; isotypes B!, JE!), **syn. nov.**

= *C. sabzevarensis* Rech. f., Fl. Iranica 139a: 134 (1979). – Holotype: Iran, Khorassan, montes Yoghatay, in jugo 20 km N Sabzevar, 1750 m, 16. VI. 1975, Rechinger 53669 (W!).

= *C. karelinii* Lessg., Bull. Soc. Nat. Mosc.: 159 (1839). ≡ *Arctium karelinii* (Lessg.) Kuntze, Revis. Gen. 1: 308 (1891), **nom. nud.**

Illustration. – Fig. 20, A.

Plant up to 100 cm high, tomentose. Stems branched from the base. Leaves leathery, tomentose on both sides, rarely ±glabrescent; basal leaves up to 30 × 9 cm including spines, narrowly oblanceolate to linear, pinnately-lobed, lobes with spiny-dentate margin and a larger terminal spine; stem leaves sessile, gradually smaller and less divided towards the apex, lanceolate to ovate, spiny-lobed, rounded to cuneate at base, decurrent for up to 10 cm. Capitula 6 – 10 cm broad with appendages, usually arachnoid-tomentose, rarely glabrous. Phyllaries 40 – 100; middle ones spreading, rarely spreading-incurved or -recurved; free part of middle phyllaries expanded above into a (cordate-) ovate-lanceolate to narrowly lanceolate appendage, appendage 25 – 40 mm long, 7 – 15 mm broad, attenuated into a long spine at apex, with 3 – 4 smaller spines on both sides. Receptacular bristles rough or smooth. Flowers 80 – 200; corolla purple to purplish-lilac, 35 – 50 mm long; anthers concolorous or pale. Achenes 5 – 8 mm long.

Flowering period. – May to August.

Taxonomic remarks. – *Cousinia onopordioides* is a morphologically rather uniform and distinct species widely distributed in semi-deserts and arid areas of NE and E Iran, W and S Turkmenistan, Afghanistan and W Pakistan (Rechinger, 1972). It has been described based on material from W Turkmenistan today deposited in LE, K and P. We here select the LE specimen as lectotype. Reports of *C. onopordioides* from the Caucasus may refer to misidentified specimens of *C. macrocephala*. The species shows some variation mainly in

capitulum morphology including number and dimensions of the phyllaries and flower number. Also, the indumentum sometimes can be highly reduced or absent. Tscherneva (1962) and Rechinger (1972) treated *C. albicaulis* as a synonym of *C. onopordioides*. Rechinger later (1979) regarded *C. albicaulis*, known only from its type locality, as a separate species. In our opinion this is not justified and the morphology of this species falls within the variation of *C. onopordioides*.

Cousinia grandiceps, *C. bornmülleri* and *C. sabzevarensis* were described by Bunge based on collections from within the distribution range of *C. onopordioides*. The separation of *C. grandiceps* from *C. onopordioides* based on a lower number of phyllaries (40 – 50) and a higher number of flowers (170 – 180) in *C. grandiceps* is not justified. The figures fall within the range of *C. onopordioides*. *Cousinia bornmülleri* was described based on material with closed capitula from SE Iran, province Kerman. New collections from the neighbourhood of the type locality of *C. bornmülleri* (e.g., *Esfandiar & Pour-Mohammadi* 20545 (TUH)), which completely match the morphology of the type material of *C. bornmülleri*, clearly belong to *C. onopordioides*. The only difference between the type of *C. sabzevarensis* and *C. onopordioides* is the absence of an indumentum in the former. This however, can also be found within *C. onopordioides*.

Distribution and habitat. –Turkmenistan, Iran, Afghanistan and Pakistan (Fig. 21), in open areas, scrublands and on rocky slopes.

Specimens seen. – Turkmenistan: In montibus prope Tschuli, 1400 m, 1. VI. 1897, *Litwinow* 194-A (E, JE); Krasnowodsk, 3. VII. 1880, *Becker* 62 (K); Krasnowodsk, in saxis mont. ad Ufra, 21. X. 1900, *Sintenis* 1310 (B); Uschtscheje Baba-so, 25. VI. 1942, *Kultiasov* 122 (W).

– Iran: Tehran: 17 km from Firouzkuh towards Semnan, 2050 m, 13. VI. 1996, *Djavadi & Ghaffari* 9466 (IRAN); 20 - 35 km SE of Firouzkuh towards Semnan, 1800 - 2200 m, 5. VIII. 1975, *Moussavi & Karavar* 9159 (IRAN); 20 km S of Damavand, between Tamisiun and Aselun, 1550 - 1650 m, 22. VI. 1985, *Mozaffarian* 53885 (TARI); Beginning of the road Semnan, from Firouzkuh, mnts. above Saranza, 2170 m, 15. VII. 2003, *Assadi & Hamdi* 85384 (TARI); Firouzkuh road, between Hableroud and Firouzkuh, 1500 m, 28. VII. 1996, *Djavadi, Ghaffari & Bakhsheshi* 9154 (IRAN); Firouzkuh, beginning of the road to Anzeha, from main road, 2100 m, *Assadi & Abouhamzeh* 66303 (TARI); Firouzkuh, close to Mahabad, between Mahabad and Anzehn, 2000 m, 16. VIII. 1985, *Mozaffarian* 54253 (TARI); Kuh-e Shahr Abad, 2000 - 2400 m, 1. VIII. 1985, *Mozaffarian* 54890 (TARI); Gadouk, Chashm, 27. VIII. 1948, *Behboudi* 5477E = 9169-IRAN (IRAN, W); Kavir protected Region, N side of Siah Kuh, above Cheshmeh Siah, 1800 - 2000 m, 20. IV. 1975, *Wendelbo & Assadi* 16046 (TARI); Shahroud, Chehel Dokhtar to Malek-Aran, Tange Olang, 30. VII. 1972, *Iranshahr & Zargani* 33862E (W); Hohe zu Firuzkuh - Semnan, 2500 m, 20. VIII. 1936, *Gauba* 955 (B); Inter Firuzkuh et jugum Baschm, 1900 - 2200 m, 29. - 30. VI. 1937, *Rechinger* 1966 (B, W); Montes Elburs orient., prope Abr, 1800 m, *Gauba & Sabeti* 1477 (W); 10 km from Shahrud to Azad-Shahr, 1600 m, 2. VI. 1998, *Ghahreman & Attar* 21901 (TUH); 12 km NE of Shahmirzad, 2400 m, 26. VII. 1982, *Assadi & Mozaffarian* 40395 (TARI); 15 km from Shahmirzad to Fuladmahalleh, 1980 m, 11. VII. 1998, *Mozaffarian* 78053 (TARI); 18 km before Khoshyeylagh, on way Shahpasand-Shahroud, 1000 m, 21. VI. 1973, *Andersen & Jensen* 7161 (E); 30 km NW of Shahroud, between Tash and Cahar Bagh, 2200 m, 12. VII. 1976, *Assadi & Massoumi* 21191 (TARI); 31 km from Firouzkuh to Semnan, Gardaneh Bashm, 2600 m, 26. VII. 1982, *Assadi & Mozaffarian* 40332 & 40316 (TARI); 5 km NW of Shahroud, Shah Pasand road, 1630 m, 15. VII. 1965, *Babakhanlou & Pabot* 23711 (TARI); Biarjemand, Ahmad Abad to Zaman Abad, 1150 m, 17. - 21. VI. 1997, *Djavadi* 18966 (IRAN); ca. 2 km N of Shahmirzad, mnts. above the village Sufian, 2400 - 2800 m,

22. VII. 2001, *Assadi & Ranjbar* 82032 (TARI); ca. 50 km N of Semnan, Tang-e Parvar, 2100 m, 27. VII. 1982, *Assadi & Mozaffarian* 40485 (TARI) & 2200 m, 30. VII. 1982, *Assadi & Mozaffarian* 40759 (TARI); Damghan to Shahroud, Gharieh-e Tazareh, 30 km N of Mehman-Doust, Kuhhay-e Sefid-Shekar, 2700 - 3000 m, 22. VII. 1975, *Moussavi & Karavar* 13429 (IRAN); Firouzkuh to Semnan, E side of Bashm pass, 2200 m, 18. VII. 1974, *Wendelbo & Cobham* 13675 (TARI, W); Gorgan to Shahroud, Tchehel-Dokhtar, 30. VII. 1968, *Ershad* 9160 (IRAN); In jugo Khosh_Jaila (Khogh Yeilagh), ca. 70 km ab oppido Shahrud orientem versus, 2000 m, 17. VI. 1948, *Rechinger & al* 5495 (K, W); Semnan: 15 km N of Shahroud, Nekarman, 2000 m, 10. VII. 1976, *Assadi & Massoumi* 21061 (TARI); Shahpasand to Shahroud, between Noodeh and Khosh Yeilagh, 1250 m, 22. VI. 1974, *Wendelbo & Foroughi* 12861 (TARI, W); Kavir protected region, Siah Kuh, in ditione regugii Karvan-Sarai Shah Abbas, [34° 44' N, 52° 10' E], 1300 m, 20. IV. 1975, *Rechinger* 50138 (W); N of Semnan, above Chashm, 2700 m, 23. VII. 2001, *Assadi & Ranjbar* 82078 (TARI); Nezva, Shahmirzad (Bashm) Kuh, S slopes, N of Shahmirzad, [35° 48' N, 53° 19' E], 2300 m, 11. VII. 1959, *Wendelbo* 1379 (IRAN, W); Shahkuh, in desert "Shah Kuh, Mazenderan", 16. VI. 1940, *Koelz* 16264 (E); Shahmirzad, Garm-Cheshmeh (5 km NW of Shahmirzad), Kuh-e Bashm, 2200 - 2400 m, 20. VII. 1975, *Moussavi & Karavar* 9162 (IRAN); Shahmirzad, Garm-Cheshmeh, Kuhhayeh Kahesh, 2120 - 2350 m, 7. VIII. 1978, *Terme, Moussavi & Tehrani* 9172 (IRAN); Shahmirzad, Ghaleh (montis), 1900 - 2000 m, 11. VII. 1988, *Terme & Karavar* 9026 (IRAN); Shahroud towards Bastam, Mojen, Sange Bon, Shah-Kuh (mnts.), 2100 m, 10. VIII. 1988, *Moussavi, Delghandi & Tehrani* 9173 (IRAN); Shahroud, Gharieh-e Tash (mnts.), 2400 - 2600 m, 30. VII. 1975, *Moussavi & Karavar* 9156-IRAN = 33806E (IRAN); Shahrud towards Azadshahr, 1600 m, 2. VI. 1998, *Ghahreman & Attar* 21894 (TUH); Shahrud, after Nekarman to Kelodar, 2100 m, 1. VI. 1998, *Ghahreman & Attar* 21890 (TUH); Shahrud, in alaeo lapidosis fl. Shahrud, 1400 m, 20. - 26. VII. 1948, *Rechinger & Rechinger* 5318 (W); Mnts. NWW of Shahroud, above the village Mojen, 2300 m, 24. VII. 2001, *Assadi & Ranjbar* 82156 (TARI); Mujen, 2050 m, 11. VII. 1998, *Mozaffarian* 78066 & 78067 (TARI); N slopes of Kuh-e Shahvar from Mighan and Turne to Panarvan, 1600 - 2500 m, 13. VII. 1998, *Mozaffarian* 78115 (TARI); Touran protected area, Nahar valley, upper part, Kuh-e Peyghambar, 1400 m, 19. VII. 1976, *Freitag* 13709 (TARI); Kuh-e Peyghambar, [35° 43' N, 56° 45' E], 1300 m, 1. V. 1975, *Rechinger* 50892 (W); Golestan: On the road from Azadshahr to Khosh-Yeylagh, 1600 m, 20. VII. 2003, *Assadi* 85642 (TARI); 49 km from Shah-Pasand on the road to Shahroud, 1400 m, 21. VII. 1976, *Assadi & Massoumi* 21509 (TARI); 69 km from Shah-Pasand on the road to Shahroud, 1950 m, 21. VII. 1976, *Assadi & Massoumi* 21510 (TARI); ca. 35 km from Semnan on the road to Sari, 2100 m, 25. VII. 1976, *Assadi & Massoumi* 21534 (TARI); Khorassan: ca. 40 km N of Ghuchan on the road to Darreh Gaz, 1800 m, 18. VII. 1976, *Assadi & Massoumi* 21430 (TARI); 40 km from Boshrouyeh to Tabas, 1380 m, 30. VI. 2002, *Mozaffarian* 81210 (TARI); 60 from Tabas to Birjand, Deyhuk, 1370 m, 3. VI. 1998, *Ghahreman, Attar & Sheikh* 21735 (TUH); Bushrueh, Sorond to Khoda Afarid, 1500 m, 1. VII. 2002, *Mozaffarian* 81212 (TARI); Ca 28 km S of Sabzevar on the road to Kashmar, 1500 m, 13. VII. 1976, *Assadi & Massoumi* 21233 (TARI); Esfarayen vers. Sabzevar, 5 - 20 km Sabzevar, 17. VI. 1975, *Terme* 33971E (W); Ghouchan to Bajgiran, on the road of Dare-Gaz, 1800 m, 5. VII. 1998, *Ghahreman & Attar* 21923 (TUH); In saxosis montium 27 km S Bejestan, [34° 32' N, 58° 08' N], 1700 - 1750 m, 10. V. 1975, *Rechinger* 51556 (W); Inter Shahrud et Nischapur, pr. Sibzewar, VI. 1858, *Bunge & Bienert* s. n. (K, P); Khaur, on dry slope, 6. VIII. 1940, *Koelz* 16835 (E, W); Montes Yoghasty: In jugo 20 km N Sabzevar, 1750 m, 16. VI. 1975, *Rechinger* 53665 (W); On the road of Ferdous to Tabas, 1100 - 1250 m, 4. VI. 1978, *Rajamand & Bazargan* 31960 (TARI); Pir, 1200 m, *Gabriel* 29 (W); Yazd: Ardakan, Hamane, Kuh-e Hamaneh, 2000 m, 1. VI. 1996, *Mozaffarian* 77574 (TARI); Khormiz, 5 km SW of Mehriz, NE of Kuh-e Khoseh, [31° 33' N, 54° 22' E], 1700 m, 27. V. 1977, *Aryavand et al.* 1484 (E, TARI); Mehriz, Darre Damghan, 2100 - 2500 m, 9. VII. 1996, *Mozaffarian* 77630 (TARI); Shirkuh, Deh-Bala, 10000 - 11000 ft., 12. VIII. 1939, *Davis* 798 (W); Shirkuh, Deh-Bala, 2750 m, 20. V. 1977, *Rajamand & Bazargan* 33112 (TARI); Taft, diviation of Dehbala-Tezerjan to Dehbala, 2130 m, 30. VI. 2002, *Mozaffarian* 81209 (TARI); Taft, neck Mt. between Aliabad and Dehshir, 2550 m, 11. VII. 1996, *Mozaffarian* 77682 (TARI); Tezerjan, 2410 m, 4. VII. 1972,

Foroughi 4386 (TARI); Kerman: unknown 22050 (TUH); Bardsir to Sarkhoun, 1600 m, 17. VI. 1997, *Esfandiar & Pour-Mohammadi* 20545 (TUH); Kuh-e Laleh-Zar, Mt. Hezaran, 23. VI. 1996, *unknown* s.n. (TUH); Mt. Jupar, 2800 m, 17. VIII. 1997, *Mirtajaldini* 21345 (TUH); Zereshk valley, VI. 1999, *Pour-Mohammadi* 24423 (TUH); Baluchestan: Taftan Mt., S-slope, above the village of Torshab, 1900 - 2300 m, 11. III. 1977, *Ruemark, Assadi & Sardabi* 22626 (E, TARI); Taftan Mt. region, Kharestan, 2200 m, 27. V. 1985, *Mozaffarian* 53007 (TARI); Taftan Mt. region, Tamendan valley, 2300 - 2500 m, 30. V. 1985, *Mozaffarian* 53184 (TARI).

– Afghanistan, *Griffith* 3324 (K, P), *Griffith* 395! (K); 1879 - 1880, *Johnston* 64 (K); Ghazni: O-Hänge des Arghandab-Taleb, 5 km O Sange Masha, 2470 m, 27. VI. 1978, *Podlech* 31845 (M); 50 km a Kabul versus Gardez, [33° 37' N, 69° 09' E], 1900 m, 28. VI. 1965, *Rechinger* 31487 (W), Lamond 2142 (E); Balaqala (an der Strasse von Malestan nach Sange Masha), 2650 m, 14. VIII. 1970, *Podlech* 19384 (W); Loman (Lomar) inter Qarabagh et Sang-i Masha, 2400 m, 30. VI. 1962, *Rechinger* 17432 (B, W); Kapisa: Mittleres Panjir-Tal, Darrah-i Zuria nördlich von Safed Jir, 2600 - 3400 m, 24. VIII. 1965, *Podlech* 12584 (K, M, W); Paktia: Ghafurkhel, 14 km N of Gardez on the road toward Kabul, 2650 m, 2. VII. 1970, *Podlech* 18522 (W); Parvan: Panjshir valley, near Safed Jir, dry slopes, 2200 m, 27. VII. 1962, *Hedge & Wendelbo* 5529 (E); Urgun: Urgun, in declivibus saxosis, [32° 52' N, 69° 07' E, 2200 - 2300 m, 10. VI. 1967, *Rechinger* 35881 (E, W).

– Pakistan: Beluchistan, 1851, *Stochs* 1044 (K, P); Baluchistan, *Unknown* 1044 (K); Baluchistan, 1. VI. 1952, *Croakshauk* 304 (K); Baluchistan, 9. VI. 1956, *Diek-Feddie* 20 (K); Baluchistan, 1891-4, *Elliott* s.n. (K); Baluchistan, 6000 ft., 17. VII. 1957, *Nasir* 28447 (K); Kalat, 6700', 20. VI. 1957, *Jafri & Akbar* 1930 (B); Quetta: Hazarganji-Chitan National Park, 15. VI. 1997, *Rafiq & Hayat* HG-97-292 (W); In jugo Khojak, [30° 54' N, 66° 29' E], 2300 m, 8. V. 1965, *Rechinger* 29070 (W); Ziarat, 7 - 8000', 15. VI. 1962, *Stewart* 523 (W); Kalat, 6700', 20. VI. 1957, *Jafri* 1930 (K); Pil, Rift, 6500 ft, 21. VI. 1888, *Lace* 3878 (E); Urak-Tal, 15 miles W of Quetta, V. 1958, *Repp* s.n. (W).



Fig. 20. – A. *C. onopordioides* [Bornmüller 3456 (B100088389, B!)]; B. *C. verbascifolia* [Rechinger 55613 (B100158869, B)]. Photograph provided by BGBM.

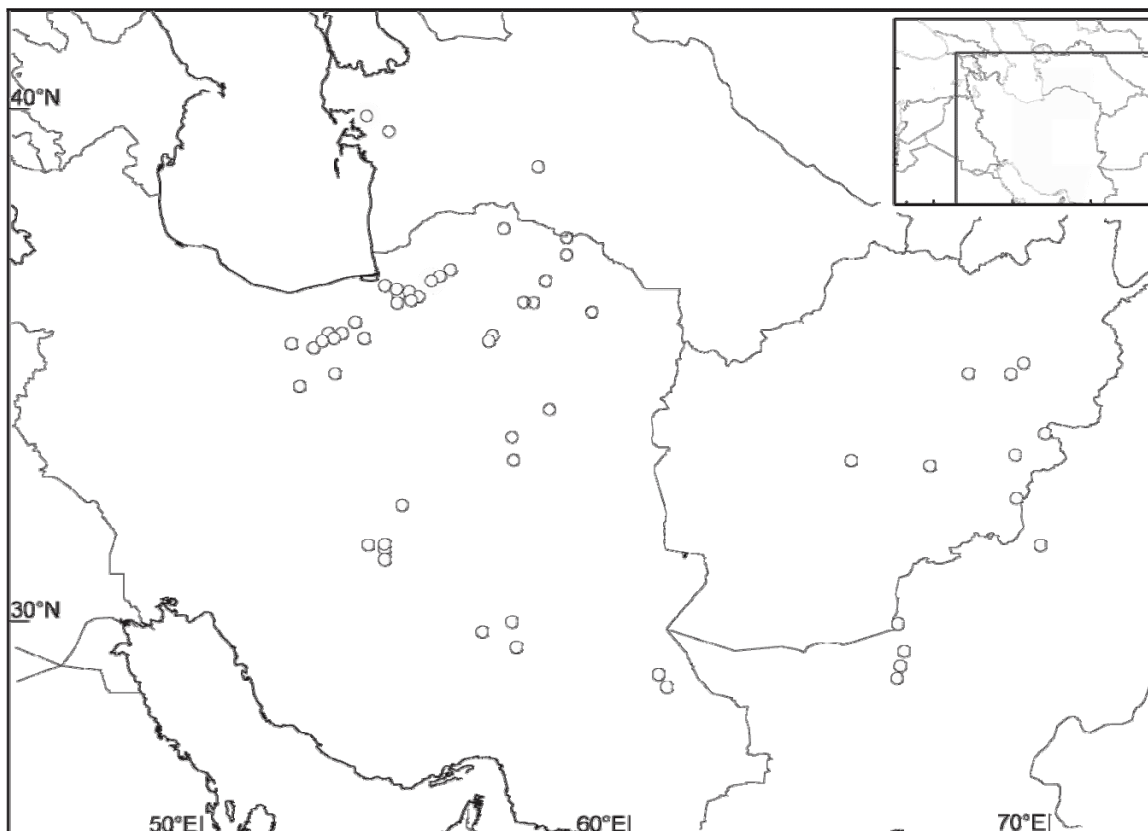


Fig. 21. – Distribution of *C. onopordioides*. Each symbol indicates the locality of a single collection or several collections made from the same or nearby localities.

4.4.5.31 *Cousinia verbascifolia* Bunge, *Mém. Acad. Imp. Sciences St.-Petersbourg*, 7. Sér., 9: 52 (1865). ≡ *Arctium verbascifolium* (Bunge) O. Kuntze, *Revis. Gen.* 1: 308 (1891). – Holotype: Iran, in apricis lapidosis prope Nischapur in provincia Chorassan, Jun. 1858, Bunge & Bienert s. n., (P!; isotypes K!, P!).

= *C. monocephala* Bunge, *Mém. Acad. Imp. Sciences St.-Petersbourg*, 7. Sér., 9: 52 (1865). ≡ *Arctium monocephalum* (Bunge) O. Kuntze, *Revis. Gen.* 1: 308 (1891). – Holotype: Iran, in montosis prope Achmet-Abbad orientem versus ab urbe Mesched in provincial Chorassan, 1958 – 59, Bunge & Bienert s. n. (P!), **syn. nov.**

= *C. lyrata* Bunge, *Mém. Acad. Imp. Sciences St.-Petersbourg*, 7. Sér., 9: 53 (1865). ≡ *Arctium lyratum* (Bunge) O. Kuntze, *Revis. Gen.* 1: 308 (1891); – Holotype: Iran, in lapidosis montium inter Sebsewar et fodinas Calaiti Maadan provinciae Chorassan, 16. VI. 1858, Bunge & Bienert s. n. (P!; isotypes K!, LE, P!), **syn. nov.**

Note. – *Cousinia verbascifolia*, *C. lyrata* and *C. monocephala* were effectively published by Bunge (1865). Because of their simultaneous publication (*C. monocephala*, l. c., p. 52, sp. No. 121; *C. verbascifolia*, l. c., p. 52, sp. No. 122 and *C. lyrata*, l. c., p. 53, sp. No. 123), all three names could be selected as valid (ICBN, 2006). *Cousinia monocephala* was published based on a small and incomplete specimen deposited in P. In comparison with the other two species,

the type of *C. monocephala* is poor. In comparison with *C. lyrata*, material of *C. verbascifolia* is in better condition and therefore *C. verbascifolia* was selected as the valid name.

= *C. caesia* C. Winker, Acta Horti Petropolitani 14: 238 (1897). – Holotype: Turkmenistan, prope pagum Bami, 19. V. 1896, Lipsky 1007 (LE!).

Illustration. – Fig. 20, B.

Plant up to 45 cm high, arachnoid-tomentose. Stems simple or branched from the base. Leaves herbaceous or ±leathery, tomentose to ±glabrescent above and densely tomentose beneath; basal leaves up to 15 × 10 cm, lyrate, with spiny-dentate margin; stem leaves gradually smaller and less divided towards the apex, ovate to broadly-lanceolate, rarely oblanceolate, spiny-lobed to –dentate, cordate to cuneate at base, decurrent for up to 5 cm. Capitula 3 – 10 cm broad with appendages, usually arachnoid-tomentose. Phyllaries 40 – 70; middle ones spreading to spreading-incurved; free part of middle phyllaries expanded above into a cordate or ovate to lanceolate appendage, appendage 10 – 40 mm long, 7 – 15 mm broad, attenuate into a long spine at apex, with 2 – 6 smaller spines on both sides. Receptacular bristles rough or smooth. Flowers 50 – 150; corolla pink, rose or purple, 20 – 35 mm long; anthers concolorous or pale. Achenes 5 – 7 mm long.

Flowering period. – May to July.

Taxonomic remarks. – Variation in material of *C. verbascifolia*, *C. lyrata*, *C. monocephala* and *C. caesia* is continuous. Accordingly, none of these three species can be regarded as distinct. *Cousinia verbascifolia* is very variable in size and form of the capitula and phyllaries. Basal and cauline leaves show little variation and by a good diagnostic character especially in comparison with the sympatric *C. onopordioides*.

Distribution and habitat. – Endemic to Kopetdagh (NE Iran and S Turkmenistan; Fig. 16, F), open areas, scrublands and stony slopes.

Specimens seen. – Turkmenistan: Aschabad-Gouvern., neben Dorf Nochur (nach süd von Bocharden), steinig Abhang, 9. VII. 1982, *Schroeter* 26 (B); Bakharden, Ad locum "Podzemnoie ozero" dictum, 300 m, 16. IX. 1976, *Vasak*, s.n. (W); In montibus prope Tschuli, 1. VI. 1897, *Litwinow* 194 (B, E, P); Aschabad, in montibus supra pagum Firusa, 17. VI. 1900, *Sintenis* 597 (B, E, K). Aschabad, in montibus supra pagum Nephton, 2. VI. 1900, *Sintenis* 442 (B).

– Iran: Khorassan: Shah Jahan Protected Area, Dashte Shah Jahan, in artemisietis argillosis ad pagum Hessari, 1300 m, 16. VI. 1975, *Rechinger* 53586 (B, M, W); In declivibus saxosis inter Gardaneh Perimus S Bojnurd et Esfarayen, substr. calc., 1700 - 1800 m, 15. VI. 1975, *Rechinger* 53572 (E, W); Environs de Sarakhs, 300 m, 24. & 25. VI. 1956, *Schmid* 6264 (E, W); 18 km N of Mashhad on the road to Kalat-e Naderi, 1000 m, 17. VII. 1976, *Assadi & Massoumi* 21349 (TARI); 25 mile Mashhad versus Kalat Naderi, prope Mohamadieh, 1000 m, 21. VII. 1972, *Iranshahr & Zargani* 33860E = 9340-IRAN (IRAN, W); 30 km from Mashhad on the road to Neyshabour, 1100 m, 14. VII. 1976, *Assadi & Massoumi* 21281 (TARI); 53 mile W Sarakhs, 900 m, 14. VII. 1972, *Terme* 33935E = 9341-IRAN (W); 66 km N on mashhad on the road to Kalat-e naderi, 1150 m, 18. VII. 1976, *Assadi & Massoumi* 21398 (TARI); 75 km on the road from Mashhad to Sarakhs, between Abrovan and Mozduran, 850 m, 24. V.

1977, *Runemark & Sardabi* 23313 (TARI); 92 km from Sabzevar on the road to Neyshabour, 1300 m, 13. VII. 1976, *Assadi & Massoumi* 21241 (TARI); Bojnurd vers. Esfarayen, Gardaneh-e Perimus, 1300 - 1400 m, 21. VII. 1975, *Terme* 33955E = 9339-IRAN (IRAN, W); Dargaz, 15 km, Yaghel village, 380 m, 11. VI. 1988, *Vafae* 287 (TARI); Darregaz, Nokhandan, Durungar and Sangsurakh, 860 m, 1. VII. 1999, *Mozaffarian & Massoumi* 79145 (TARI); Esfarayen to Sabzevar, Hesari to Shahe- Jahan, 1300 m, 17. VI. 1975, *Terme* 33968E = 9343-IRAN (W); Shah Jahan mts., region rocky soily, mt. Tourken from deep gorge close to Noushirvan village, 1400 - 2500 m, 8. VI. 1984, *Mozaffarian* 48564 (TARI); Fariman to Shahan, Garmak, 1400 m, 12. VII. 1972, *Iranshahr* 33948E = 9344-IRAN (W); Ghouchan to Sabzevar, near Bifurcation of Sabzevar-Neyshabour, 1600 m, 7. VII. 1998, *Ghahreman & Attar* 21931 (TUH); Mashad to Sarakhs, Abravan, 1000 m, 4. VII. 1998, *Ghahreman & Attar* 21907 (M, TUH); Mashad-Sarakhs road, the hills E of Mozduran, 850 m, 21. V. 1959, *Merton* 3906 (K); Mashhad towards Sarakhs, 65 km to Sarakhs, 600 m, 13. VI. 1996, *Terme, Delghandi & Karavar* 15193 (IRAN, TUH); Mashhad towards Sarakhs, Mozduran, 900 - 1000 m, 1. VII. 2001, *Djavadi & Ghanbari* 29247 (IRAN); Monts. N of Neyshabour, 1450 - 1600 m, 16. VI. 1981, *Assadi & Mozaffarian* 35974 (TARI); Monts. NW of Neyshabour, above Mirabad, 1600 - 1900 m, 17. VI. 1981, *Assadi & Mozaffarian* 36042 (TARI); Sarakhs, 500 m, 4. VII. 1998, *Ghahreman & Attar* 21912 (TUH); SE Fariman, between Shahan- Garmab and Tappeh Naderi, [35° 58' N, 59° 22' E], 1429 m, 16. V. 2003, *Assadi & Amirabadi* 84541 (TARI); In collibus aridis 89 km a Mashhad versus Sarakhs, 800 m, 24. V. 1977, *Rechinger* 55613 (B, M, W); Abdollah Kivi 43 km NE Soltanabad versus Quchan, 1400 m, 17. VI. 1975, *Rechinger* 53713 (W); Tus, in aridis planitis, 8. -9. VI. 1948, *Rechinger* 5249 (B, IRAN, K, W).

4.4.6 Taxa excluded from *C. Sect. Cynaroideae*

1. *C. subinflata* Bornm., Österr. Bot. Zeitschr. 63: 291 (1913). – Holotype: Iran, ditionis oppidi Nehawend in monte Kuh Gerrü, 2. VIII. 1908, Strauss s. n. (JE!; isotype B!).

Cousinia subinflata is an intersectional hybrid between *C. chlorosphaera* and *C. orthoclada* Hausskn. & Bornm. (sect. *Pugioniferae* Bunge).

2. *C. squarrosa* Boiss. var. *integrifolia* Bornm., Bull. Herb. Boiss. 2. Seri: 220 (1907). Iran, "Persia borealis: in valle Scheheristanek montium Elburs", 12. VI. 1902, 2200 m, Bornmüller 7373 (B100157200, B!).

Cousinia squarrosa var. *integrifolia* was described from material with unopened capitula and identified as *Cousinia chamaepeuce* Boiss. (sect. *Sphaerocephalae*) by us.

3. *C. beckeri* Trautv., Acta Horti Petrop. 9: 457 (1886). – Holotype: Turkmenistan, Kopet-Dagh, Kisil-Arwat, a. 1883, Becker 246 (LE!).

Cousinia beckeri is excluded from sect. *Cynaroides* because of its chromosome number of $2x=18$ (vs. $2x=24$; Ghaffari et al. 2000) and the morphology of its phyllaries which have unusually narrow, linear-lanceolate appendages (Trautvetter 1886).

4.5 ACKNOWLEDGEMENTS

4.6 REFERENCES

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