

Systematics and biogeography of *Klasea* (Asteraceae–Cardueae) and a synopsis of the genus

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Klasea, traditionally treated as a section in *Serratula*, is now widely accepted at the generic level. A classification of the genus is presented here, accommodating the 46 species in ten sections based on nuclear ribosomal DNA external and internal transcribed spacer sequence data and morphology. New combinations for five species and ten subspecies are published, and a new hybrid species is described. The genus ranges from the Iberian Peninsula and north Africa through southern and eastern Europe, west and central Asia to the Himalayas, and the Far East of Russia and China. The ancestral area is in west Asia, most probably eastern Anatolia and northern and western Iran. In this region, representatives of all sections are present. The largest section *Klasea* diversified most likely in the mountains of central Asia. A key to all *Klasea* species is provided. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, 152, 435–464.

ADDITIONAL KEYWORDS: ancestral area – Centaureinae – classification – phylogeny – *Serratula* – taxonomy.

INTRODUCTION

Klasea Cass. is an Old World genus of unarmed perennial herbs. Its systematic position has been determined as basal within the subtribe Centaureinae (Wagenitz & Hellwig, 1996), and it is most probably sister to the genera of the *Rhaponticum* group (Martins & Hellwig, 2005). When Cassini (1825) established the genus *Klasea*, he included four species formerly assigned to *Serratula* without validly publishing the new combinations. According to him, *Klasea* is characterized by bisexual homogamous capitula. Lessing (1832) placed *Klasea* as a subgenus in *Rhaponticum*. De Candolle (1838) treated *Klasea* as a section of *Serratula*, and this opinion had been followed for more than a century. An infrageneric classification of the oriental taxa of *Serratula* was given by Boissier (1875). In addition to the sections *Klasea* and *Serratula* ('*Sareta*'), he described the new section *Piptochaete* which contained the single species

S. xeranthemoides M. Bieb. (= *K. erucifolia*) characterized by a caducous pappus consisting of few bristles. The section *Klasea* was divided into four unranked groups on the basis of leaf shape characters. Of these, only 'Auriculatae' is approximately congruent with a later formally recognized group. It has been described as a separate genus *Schumeria* by Iljin (1960). Borisova (1963a, b) followed this generic delimitation and classified the species remaining in *Serratula* into seven sections, three newly described, and several not validly published series. The previously described section *Lepidocephalae* (Zahariadi, 1946) containing the single species *S. caput-najae* Zahariadi (= *K. bulgarica*) was included in *Serratula* sect. *Klasea* 'Heterophyllae'. An overview of the classifications of the supraspecific taxa included in *Klasea* is given in Table 1.

From the middle of the 20th century onwards, many new combinations in *Klasea* have been published (Kitagawa, 1947, 1950; Löve & Löve, 1961; Holub, 1977a, b; Cantó & Rivas-Martínez, 1983; Greuter, 2003; Greuter & von Raab-Straube, 2005; Martins & Hellwig, 2005; Hidalgo *et al.*, 2006). How-

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Table 1. Infrageneric classifications of *Klasea* (*S.* = *Serratula*, *K.* = *Klasea*)

Boissier (1875)	Iljin (1962), Borisova (1963a, b)	This paper
–	<i>Nikitinia</i> Iljin	<i>K.</i> sect. <i>Nikitinia</i>
<i>Leuzea serratuloides</i>	<i>S.</i> sect. <i>Leuzeopsis</i> Boriss.	<i>K.</i> sect. <i>Leuzeopsis</i>
<i>S.</i> sect. <i>Klasea</i> (Cass.) DC. 'Pinnatisectae' p.p.	<i>S.</i> sect. <i>Klasea</i> 'Quinquefoliae'	<i>K.</i> sect. <i>Quinquefoliae</i>
<i>S.</i> sect. <i>Klasea</i> 'Auriculatae'	<i>Schumeria</i> Iljin	<i>K.</i> sect. <i>Schumeria</i>
<i>S.</i> sect. <i>Klasea</i> 'Pinnatifidae', 'Integrifoliae'	<i>S.</i> sect. <i>Klasea</i> 'Coriaceae'	<i>K.</i> sect. <i>Coriaceae</i>
–	<i>S.</i> sect. <i>Demetria</i> Boriss.	<i>K.</i> sect. <i>Demetria</i>
–	<i>S.</i> sect. <i>Klasea</i> 'Centauroides', 'Heterophyllae', 'Nitidae', 'Chartaceae', 'Sogdianae'	<i>K.</i> sect. <i>Klasea</i>
<i>S.</i> sect. <i>Piptochaete</i>	<i>S.</i> sect. <i>Iljinia</i> Boriss.	
	<i>S.</i> sect. <i>Piptochaete</i> Boiss.	

ever, nearly all modern floras included the *Klasea* species in *Serratula*, with the exception of the '*Flora vascular de Andalucía occidental*' (Talavera, 1987). No supraspecific taxa in *Klasea* have hitherto been published.

The aberrant characters of both *K. serratuloides* and *K. leptoclada* have obscured their affinities for a long time. The former has been described independently as *Leuzea serratuloides* DC. and *Phaeopappus freynii* Sint. ex Freyn and, until recently, usually has been recognized as *S. serratuloides* (DC.) Takht. *K. leptoclada* was initially described as *Jurinea leptoclada* Bornm. & Sint. and was later assigned to the monotypic genus *Nikitinia* Iljin. It has been subject to controversial classification in either Carduinae (e.g. Iljin, 1962; Dittrich, 1977) or Centaureinae (Adylov & Zuckerwanik, 1993). Its affinity to *Klasea* has been shown by Susanna *et al.* (2002) and Martins & Hellwig (2005).

MATERIAL AND METHODS

TAXON SAMPLING

An attempt was made to include all *Klasea* species in the molecular phylogenetic analysis. Forty-one accessions distributed in 34 species plus five outgroup taxa were analysed. No suitable material was available for *K. bornmuelleri*, *K. bulgarica*, *K. cardunculus*, *K. gracillima*, *K. hakkiarica*, *K. kurdica*, *K. melanocheila*, *K. suffulta*, and *K. viciifolia*. Furthermore, the two putative hybrids were excluded from the molecular analyses. Taxon names, voucher data, and GenBank accession numbers are given in the Appendix.

DNA ISOLATION, AMPLIFICATION, AND SEQUENCING

Total genomic DNA was extracted from 30–40 mg of silica-dried or herbarium material in cetyltrimethyl-

lammonium bromide (CTAB) buffer following the procedure of Doyle & Doyle (1987) with modifications as described by Hellwig *et al.* (1999). The internal transcribed spacers (ITSs) of nuclear ribosomal DNA were amplified using the primers ITS5 (5'-GGAAGTA AAAGTCGTAACAAGG-3') and P2 (5'-CTCGATGGAA CACGGGATTCTGC-3') for ITS-1 and ITS3 (5'-GCA TCGATGAAGAACGCAGC-3') and ITS4 (5'-TCCTC CGCTTATTGATATGC-3') for ITS-2 [primers ITS5, ITS3, and ITS4 by White *et al.* (1990); primer P2 by Ochsmann (2000)]. Primers 18S-ETS (5'-ACTTACA CATGCATGGCTTAA-3'; Baldwin & Markos, 1998) and ETS-Cen (5'-TTCGCATCGTTTCGGT-3'; modified from ETS-Car-1; Kelch & Baldwin, 2003) were used for the amplification of the 3' portion of the external transcribed spacer (ETS).

Depending on the quality of the extracted DNA, 28–36 cycles of 30 s of denaturation at 95 °C, 60 s of annealing at 48 °C (ITS-1 and ITS-2) or 55 °C (ETS), and 60 s of elongation at 72 °C were run, preceded by an initial denaturation for 180 s and followed by a final elongation for 180 s.

Cycle sequencing was performed using infrared dye-labelled primers and the ThermoSequenase labelled primer cycle sequencing kit (Amersham Pharmacia). Primer sequences were the same as for the polymerase chain reaction (PCR). Sequencing products were resolved on a 6% polyacrylamide gel using an automatic LI-COR DNA sequencer 4000L.

PHYLOGENETIC ANALYSIS

ETS and ITS sequences were edited and aligned manually using the computer program BioEdit version 5.0.9 (Hall, 1999). Of 1045 alignment positions, 173 were phylogenetically informative. The alignment is available from TreeBase. The data set was analysed by Bayesian inference of phylogeny using MrBayes version 3.0B4 (Huelsenbeck & Ronquist, 2001). The

Akaike information criterion (AIC; standard AIC, not using branch lengths as parameters) was calculated on the basis of the log-likelihood scores of 56 models using the computer program Modeltest version 3.5 (Posada & Crandall, 1998) in order to determine the most appropriate DNA substitution model. The GTR + G model (general time reversible and sites assumed to follow a discrete gamma distribution) was selected.

For Bayesian phylogenetic analysis, the GTR + G model was applied without transferring the parameters estimated by Modeltest as priors to MrBayes, estimating specific substitution rates and the gamma shape parameter as part of the analysis. As entrapment in local optima can be avoided through random exchange of parameters between the chains, four Monte Carlo Markov chains (MCMCs) were run for 2 000 000 generations. Markov chains were sampled every 100 generations. The first 2000 trees (corresponding to 200 000 generations) were discarded as burn-in; this is well after reaching stationarity (approximately at 25 000 generations). The analysis resulted in 18 001 sampled trees and parameter estimates. A 50% majority rule tree was calculated. The percentage of a specific branch occurring in the sampled trees represents the posterior probability (pp) that the clade is true under the applied model (Huelsenbeck *et al.*, 2002).

A maximum parsimony analysis was conducted using PAUP* (Swofford, 2000). A heuristic search was performed with ten random addition sequence replicates, tree bisection–reconnection (TBR) branch swapping, and MulTrees option in function. All characters were equally weighted and treated as unordered; gaps were treated as missing data. A strict consensus tree of all most parsimonious trees was calculated. Branch support was evaluated by decay values calculated using Autodecay (Eriksson & Wikström, 1995) and by a bootstrap analysis with 1000 replicates and max. 200 trees saved in each replicate.

In order to determine the affinities of *K. aznavouriana*, for which only the sequencing of ITS-2 was successful, a data matrix of the complete taxon sampling, but ITS-2 only, was generated and analysed by distance analysis (corrected total distance, neighbour-joining algorithm).

MORPHOLOGY AND ANATOMY

The following characters were investigated in all *Klasea* species, except for *K. kurdica* for which no material was available: habit (stem height, branching, leaf arrangement); leaf shape and indument; leaf epidermis cell shape; stomata distribution; shape of involucre; number of series of phyllaries; involucrel

bract size; appendages, coloration, and indument; corolla length, colour, and indument; ratio of corolla lobes and corolla tube to total corolla length; size of filament papillae; anther length; length and shape of basal and apical anther appendages; oxalate crystals in anthers; ratio of the length of free stigmatic lobes to the total length of the stigma; achene size, shape, and colour; ratio of pericarp to testa epidermis thickness; oxalate crystals in the testa and in the pericarp; pappus morphology; teeth and glands on the pappus elements.

For microscopic preparations, small parts of plant tissue were boiled for a short time in water with a drop of dishwashing liquid added. For cross-sections of achenes, these were immersed in a 1 : 1 mixture of Jung embedding medium (Leica Instruments GmbH) and water, heated in a water bath, and incubated for at least 24 h. The achenes were then embedded in embedding medium, frozen at -20°C , cut in 20- μm -thick slices with a Cryocut 1800 microtome (Leica Instruments GmbH), and embedded on microscope slides in Aquatex (Merck).

Depending on the availability of herbarium material, one to seven specimens of each species were investigated. Those characters that were greatly variable within species or more or less constant for all species were disregarded for the discussion of character evolution. As far as possible, only characters which were easy to determine were used to construct a determination key.

BIOGEOGRAPHY

Geographic coordinates were determined using online gazetteers (<http://www.fallingrain.com/world> and <http://www.nga.mil/geonames/GNS>) and atlases, mainly on the basis of locality descriptions given on herbarium specimens and, to a lesser extent, on data given in the literature. Localities were mapped and, for the purpose of readability, localities close to each other were united into one. In order to determine the ancestral areas of the genus and its subgroups, a dispersal vicariance analysis (DIVA) was performed using the computer program DIVA (Ronquist, 1996), assigning a cost of unity to dispersal and extinction events and no cost to speciation events. A phylogenetic tree was generated on the basis of the same data set and with the same parameter settings as above, but, for those species which were sampled more than once, only one operational taxonomic unit (OTU) was retained. As a fully resolved tree is required for DIVA, an 'all compatible' consensus tree also containing weakly supported branches was used. Unit areas were defined by distribution gaps and by minimizing the number of species occurring in more than one area (Fig. 1).

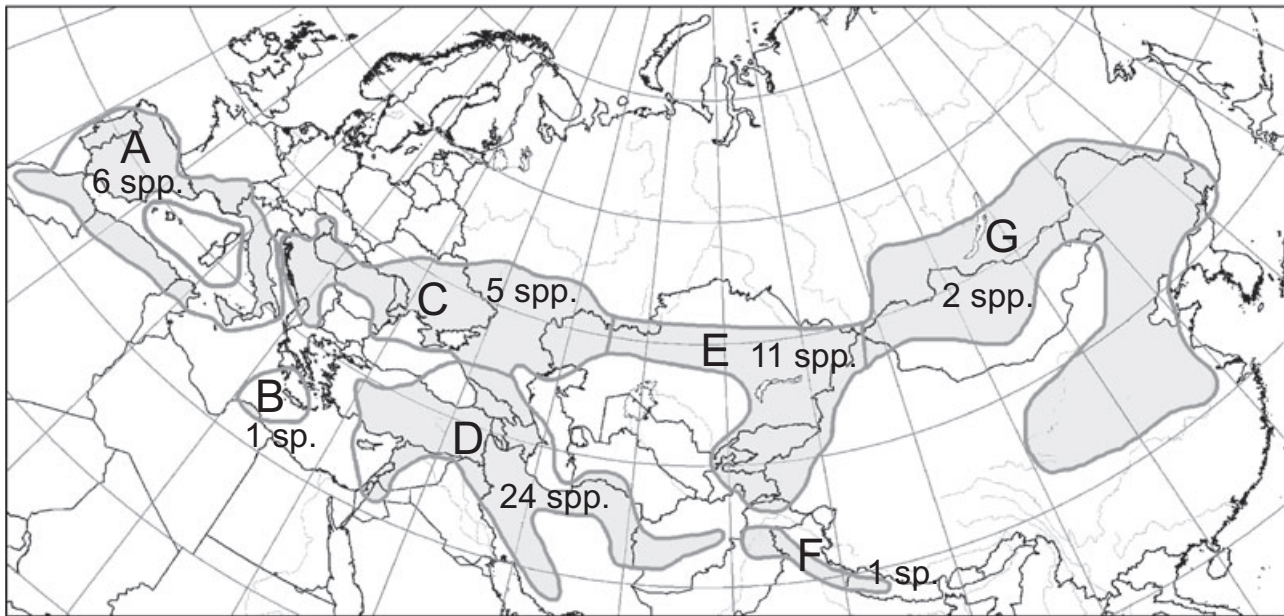


Figure 1. Approximate distribution of *Klasea* and unit areas as used for dispersal vicariance analysis (DIVA). The species numbers also include species not included in DIVA.

RESULTS

PHYLOGENY

The strict consensus tree from the maximum parsimony analysis is congruent with the Bayesian phylogenetic tree shown in Figure 2, with the exception of an additional weakly supported clade uniting *K. lycopifolia* and *K. procumbens* (bootstrap percentage < 50, decay value 1). The 50% majority rule tree from the Bayesian phylogenetic analysis shows a basal polytomy within the ingroup. The largest clade ('*Klasea*'), which is moderately supported by $pp = 0.93$, contains the species classified by Borisova (1963a) in *Serratula* sect. *Iljinia*, sect. *Piptochaete*, and the major part of sect. *Klasea*. All species with a distribution east of 70° of eastern longitude belong to this clade, as well as some more widespread European and west and central Asian species. Within the *Klasea* clade, there are only a few clades with absolute support: one consisting of the two subspecies of *K. centauroides*, another consisting of the two samples of *K. nudicaulis*, and a third uniting *K. aphyllopoda* and *K. chartacea*.

Another clade of the basal polytomy is rather weakly supported ($pp = 0.67$, decay value 2), and therefore its well-supported constituents ('*Demetria*' and '*Quinquefoliae*') would be better regarded separately. The *Quinquefoliae* clade consists of the two samples of *K. quinquefolia* only, whereas the *Demetria* clade unites most of the west Mediterranean species, which form a moderately supported ($pp = 0.91$) clade,

with the west Asian *K. khuzistanica*, *K. oligocephala*, and *K. pusilla*. Within the west Mediterranean group, *K. flavescens* is apart from the other species. The two samples of *K. boetica* and *K. pinnatifida*, respectively, do not group with each other.

The *Schumeria*–*Leuzeopsis* clade is fully resolved with absolute support: *Leuzeopsis* (*K. serratuloides*) is sister to *Schumeria*; within the latter, *K. cerinthifolia* is sister to *K. latifolia* + *K. cretica*. The species of this clade occur in west Asia with outposts in the west (*K. cretica* in Greece and Libya) and in the east (*K. latifolia* in the Kopet Dagh Mountains and in Afghanistan).

The remaining five branches of the basal polytomy are made up of one taxon each (*K. coriacea*, *K. grandifolia*, *K. leptoclada*, *K. kotschyi*, *K. lasiocephala*), which are all distributed in west Asia (*K. leptoclada* in the Kopet Dagh Mountains).

In the distance analysis based on ITS-2 sequences, *K. aznavouriana* and *K. grandifolia* constitute a clade with 86% bootstrap support (tree not shown).

MORPHOLOGY

The trichome types observed in *Klasea* are illustrated in Figure 3. Different types of apical anther appendage shape can be distinguished (Fig. 4). In Table 2, capitula arrangement, leaf indument, corolla colour, and the type of apical anther appendage are listed for all investigated species.

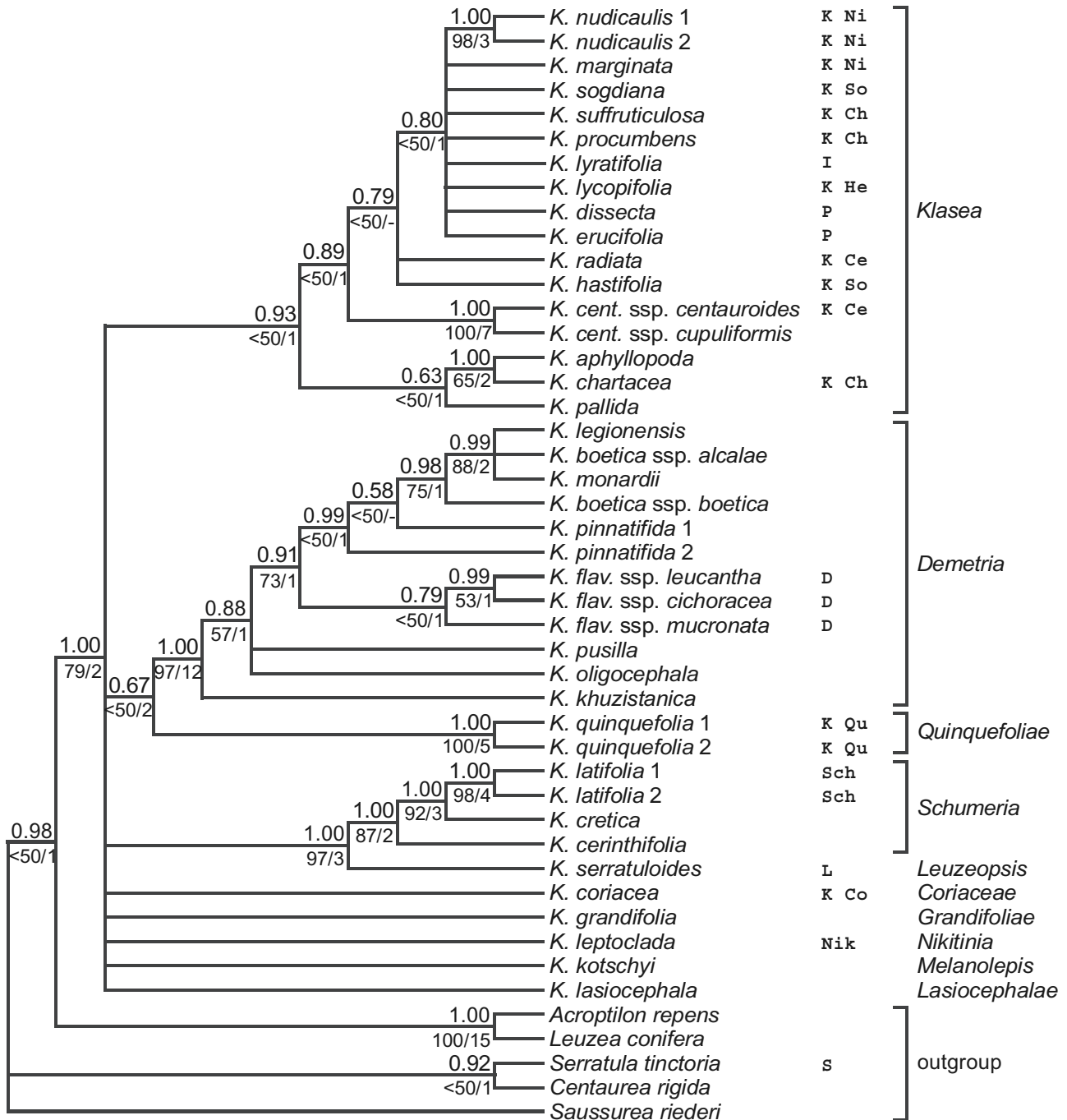


Figure 2. Sixty per cent majority rule consensus tree of 19 001 trees from the Bayesian phylogenetic analysis. Numbers above branches are *a posteriori* probabilities. Numbers below branches are bootstrap percentages and decay values from the maximum parsimony analysis. The classification according to ‘*Flora SSSR*’ (abbreviations; Iljin, 1962; Borisova, 1963a, b) and the classification according to this paper (italicized) are given. Nik, genus *Nikitinia*; Sch, genus *Schumeria*; D, *Serratula* sect. *Demetria*; I, *S.* sect. *Iljinia*; L, *S.* sect. *Leuzeopsis*; K, *S.* sect. *Klasea*; P, *S.* sect. *Piptochaete*; S, *S.* sect. *Serratula*; Ce, ser. ‘*Centauroides*’; Ch, ser. ‘*Chartaceae*’; Co, ser. ‘*Coriaceae*’; He, ser. ‘*Heterophyllae*’; Ni, ser. ‘*Nitidae*’; Qu, ser. ‘*Quinquifoliae*’; So, ser. ‘*sogdianae*’.

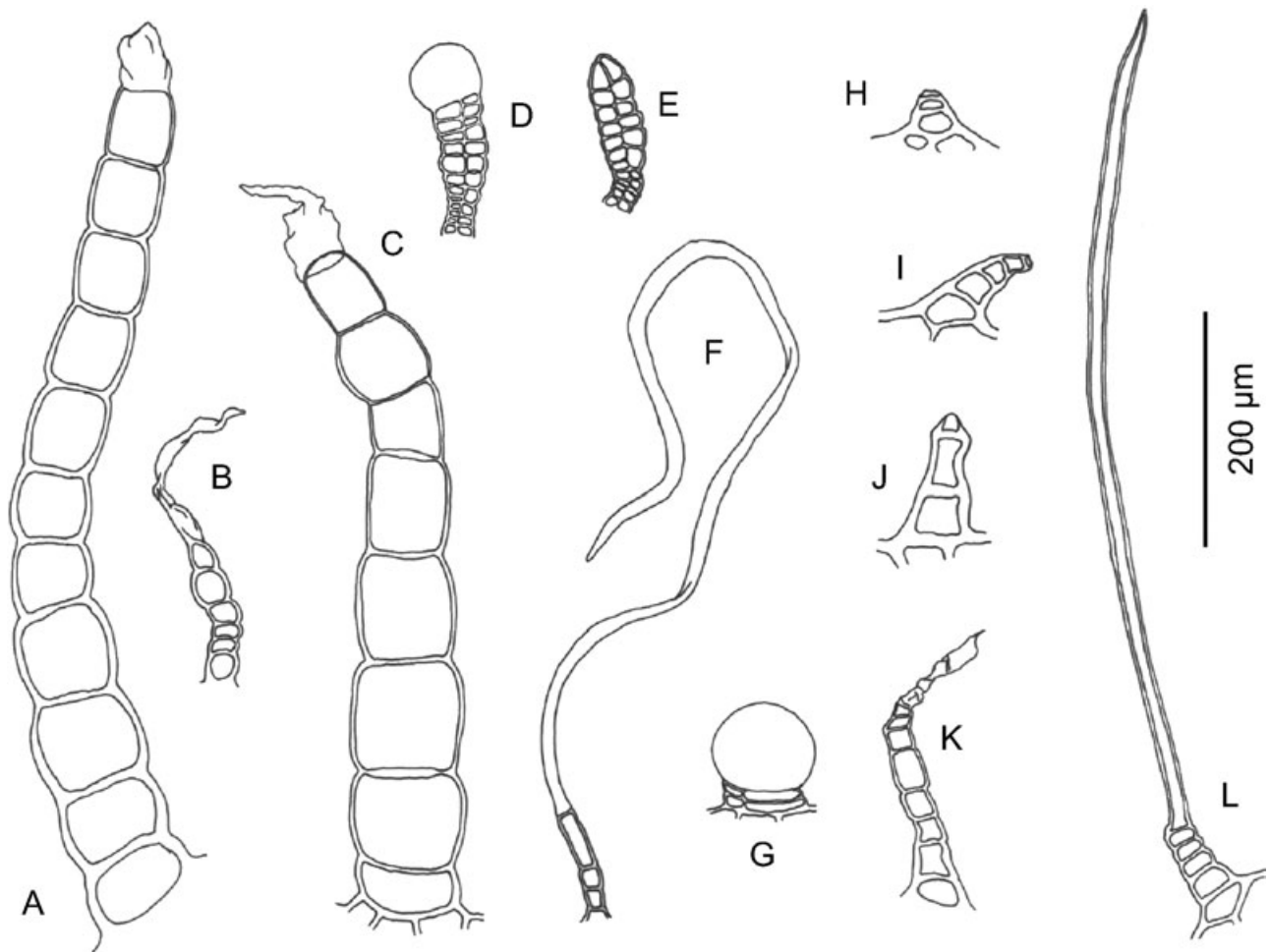


Figure 3. Trichomes in *Klasea*. A, Large multicellular hair (*K. centauroides*, leaf surface). B, Small multicellular hair (*K. centauroides*, leaf surface). C, Multicellular hair (*K. pallida*, leaf surface). D, E, Biseriate clavate hairs (*K. nudicaulis*, corolla). F, Filiform hair (*K. pinnatifida*, leaf vein). G, Gland (*K. erucifolia*, leaf surface). H–K, Multicellular hairs on the leaf margins (H, *K. hakkiarica*; I, *K. nudicaulis*; J, *K. pinnatifida*; K, *K. marginata*); L, Pedestal hair (*K. viciifolia*, leaf margin).

BIOGEOGRAPHY

The localization of the investigated herbarium specimens (black) and the localities given in the literature (grey) are displayed in Figures 5–9. DIVA indicates an origin of the genus, as well as all sections except sect. *Klasea*, in west Asia, whereas sect. *Klasea* is likely to have originated from central Asia (Fig. 10).

DISCUSSION

MORPHOLOGICAL CHARACTERS

Many of the investigated characters, especially the morphometric ones, are of little use in phylogenetics because of the high degree of homoplasy and the difficulty coding them into distinct character states; however, they are useful for the determination of species

and have therefore been used for the key. In addition, several characters are either variable within a species, more or less constant in all species, or obviously homoplastic, and are thus of restricted use for the systematics of the genus. In the following paragraphs, the usefulness of the investigated morphological characters and character complexes will be discussed.

Capitula arrangement: The majority of the species have one or few capitula per plant. The polycephalous taxa (*K. erucifolia*, *K. centauroides* ssp. *polycephala*, *K. quinquefolia*, *K. aznavouriana*, *K. grandifolia*) are distributed throughout the phylogenetic tree, and thus this character is not useful for systematics. The capitula are terminal on stems or branches in all taxa, except for *K. bornmuelleri*, with exclusively axillary capitula, and *K. lasiocephala*, with axillary, scapose or,

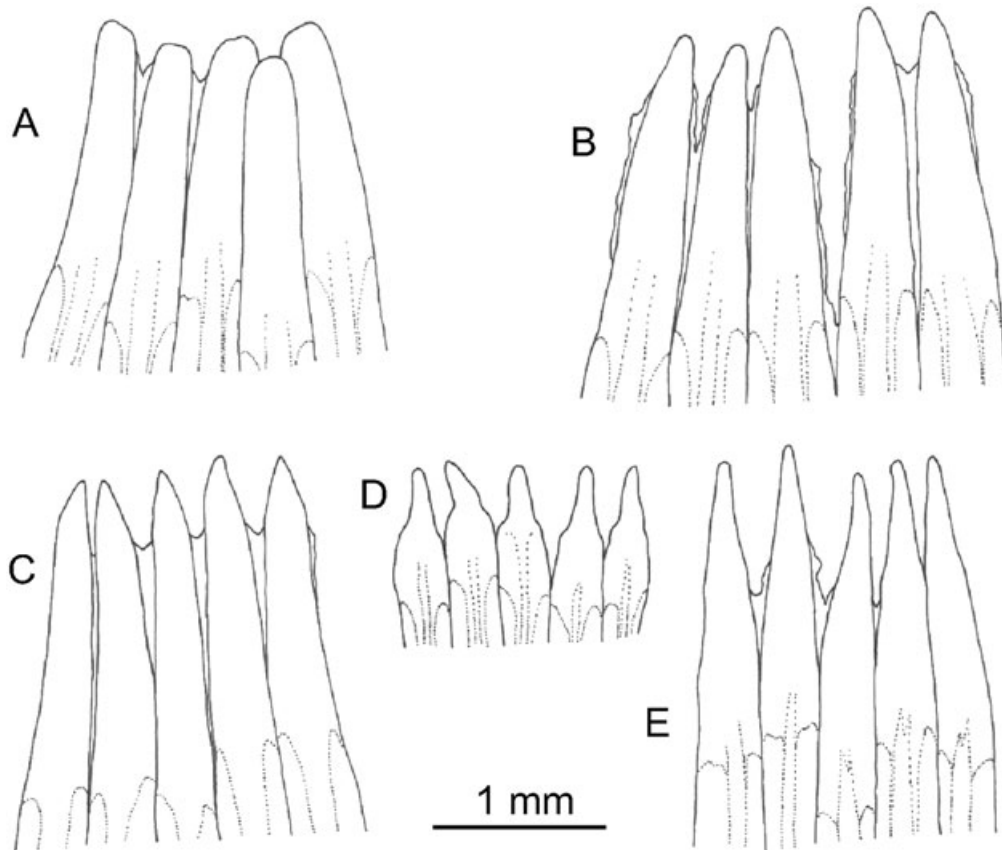


Figure 4. Apical anther appendages. Pollen sacs are marked with dotted lines. A, *Schumeria* type (*K. latifolia*). B, C, Intermediate types (*K. leptoclada*, *K. coriacea*). D, *Lasiocephalae* type (*K. bornmuelleri*). E, *Melanolepis* type (*K. hakkiarica*).

exceptionally, terminal capitula. The presence of axillary capitula is judged as a synapomorphy of *K.* sect. *Lasiocephalae*.

Indument: Four main types of trichome have been observed in *Klasea*: (1) various subtypes of multicellular uniseriate hairs: ‘worm hairs’ (Fig. 3A–C), multicellular hairs on the leaf margins (Fig. 3H–K), and pedestal hairs (Fig. 3L); (2) filiform hairs (Fig. 3F); (3) glands (Fig. 3G); (4) biseriate clavate hairs (Fig. 3D, E) mostly on the adaxial side of median phyllaries, sometimes also on the apex of the inner phyllaries, on the pappus bristles, or on the corolla lobes.

It is necessary to distinguish between the occurrence of multicellular hairs at the leaf margin and those on the leaf blade. Marginal hairs are present in most species, although they are often absent in some individuals. In three species of sect. *Schumeria*, the marginal hairs, if present, have a much elongated narrow terminal cell and therefore are referred to as pedestal hairs (Fig. 3L). Multicellular hairs on the leaf blade are always present in sect. *Quinquifoliae*, but

are not present in all species or in all individuals within a species in the sections *Klasea*, *Demetria*, and *Grandifoliae*. The absence of these hairs is characteristic for the *Nudicaulis* group of sect. *Klasea* and for sect. *Schumeria*. The very polymorphic *K. centauroides* (s.l.) is characterized by the presence of two different types of multicellular hair on the leaf blade (Fig. 3A, B). The presence of filiform hairs is a good character to circumscribe sect. *Demetria*, where they are concentrated on the veins at least on the adaxial side. Glands (Fig. 3G) are present in five species of sect. *Klasea* and in the hybrid *K. × bogdensis*, but only in three species are these always present, and therefore this character is of restricted use. The presence of biseriate clavate hairs (Fig. 3D, E) on the adaxial side of the phyllaries is not a useful character, as they occur in almost all species and, if they are present in other parts (pappus bristles, corolla lobes), they are never present in all individuals within a species.

Involucre: The morphology of the involucre is of major importance in delimiting species, but very few charac-

Table 2. Taxonomically important characters of the investigated *Klasea* species. Indument (see Fig. 3): C, marginal hairs ('cilia'); F, filiform hairs; G, glands; M, multicellular hairs; P, pedestal hairs; lower case letters, only few hairs present or lacking in some specimens; M*, two types of multicellular hair present (Fig. 3A, B). Apical anther appendages (see Fig. 4)

Section	Species	Capitula	Indument	Corolla	Anther appendages
<i>Klasea</i>	<i>K. nudicaulis</i>	Terminal	C - - -	Purple	A
	<i>K. haussknechtii</i>	Terminal	C - - -	Purple	A
	<i>K. marginata</i>	Terminal	C - - -	Purple	A-C
	<i>K. cardunculus</i>	Terminal	C - - -	Purple	A(-C)
	<i>K. ' bogdensis</i>	Terminal	c M - g	Purple	A
	<i>K. erucifolia</i>	Terminal	c M - G	Purple	A
	<i>K. dissecta</i>	Terminal	c M - G	Purple	A
	<i>K. pallida</i>	Terminal	C M - G	Purple	A
	<i>K. suffruticulosa</i>	Terminal	C m - -	Purple	A-B
	<i>K. aphyllopoda</i>	Terminal	c - - -	Purple	A-B
	<i>K. chartacea</i>	Terminal	c - - -	Purple	(A-B)
	<i>K. procumbens</i>	Terminal	C - - -	Purple	A
	<i>K. hastifolia</i>	Terminal	- - - -	Purple	A(-C)
	<i>K. lyratifolia</i>	Terminal	C M f -	Purple	A-B
	<i>K. sogdiana</i>	Terminal	C m - g	Purple	A(-C)
	<i>K. lycopifolia</i>	Terminal	C M - -	Purple	A-B
	<i>K. bulgarica</i>	Terminal	C m - -	Purple	A-B
	<i>K. radiata</i>	Terminal	C M - -	Purple	A(-B)
	<i>K. centauroides</i>	Terminal	C M* - g	Purple	A-B
	<i>Demetria</i>	<i>K. pinnatifida</i>	Terminal	C - F -	Purple
<i>K. boetica</i>		Terminal	C m F -	Purple	A
<i>K. legionensis</i>		Terminal	C - F -	Purple	A(-B)
<i>K. integrifolia</i>		Terminal	C - F -	Purple	A
<i>K. flavescens</i>		Terminal	C m f -	Purple, yellow, cream	A-B
<i>K. khuzistanica</i>		Terminal	C m F -	Yellow	?
<i>K. oligocephala</i>		Terminal	- - F -	Purple	A-C
<i>K. pusilla</i>		Terminal	C m F -	Purple	A-C
Hybrid	<i>K. × mouterdei</i>	Terminal	c - F -	Purple	A(-C)
<i>Schumeria</i>	<i>K. cerinthifolia</i>	Terminal	- - - -	Yellow	A
	<i>K. latifolia</i>	Terminal	p - - -	Yellow	A
	<i>K. suffulta</i>	Terminal	c - - -	Yellow	A
	<i>K. gracillima</i>	Terminal	- - - -	Yellow	A
	<i>K. viciifolia</i>	Terminal	p - - -	Yellow	A
	<i>K. cretica</i>	Terminal	p - - -	Purple	A
<i>Leuzeopsis</i>	<i>K. serratuloides</i>	Terminal	- - f -	Purple	A, C
<i>Nikitinia</i>	<i>K. leptoclada</i>	Terminal	- - - -	Purple	B
<i>Coriaceae</i>	<i>K. coriacea</i>	Terminal	- - - -	Purple	C
<i>Lasiocephalae</i>	<i>K. lasiocephala</i>	Ax./term.	- - P -	Purple	D
	<i>K. bornmuelleri</i>	Axillary	- - - -	Purple	D
<i>Quinquefoliae</i>	<i>K. quinquefolia</i>	Terminal	C M - -	Purple	D-E
<i>Melanolepis</i>	<i>K. kotschyi</i>	Terminal	- - - -	Purple	E
	<i>K. hakkiarica</i>	Terminal	- - - -	Purple	E
	<i>K. melanocheila</i>	Terminal	c - - -	Purple	E

ters have distinct states and therefore systematic conclusions can hardly be drawn. Typically, the outer and median phyllaries are abruptly constricted into a mucro or apical spine, and the inner ones are elongated and chartaceous in their distal part. In the sections *Schumeria* and *Lasiocephalae*, the apical spine is

often missing, and, in *K. bulgarica* and partially in *K. nudicaulis*, the median phyllaries have a scarious appendage instead of an apical spine. The phyllaries are usually coriaceous and imbricately appressed, but in sect. *Demetria* (except for *K. oligocephala*) they are rather loose (not appressed), and in sect. *Lasioceph-*

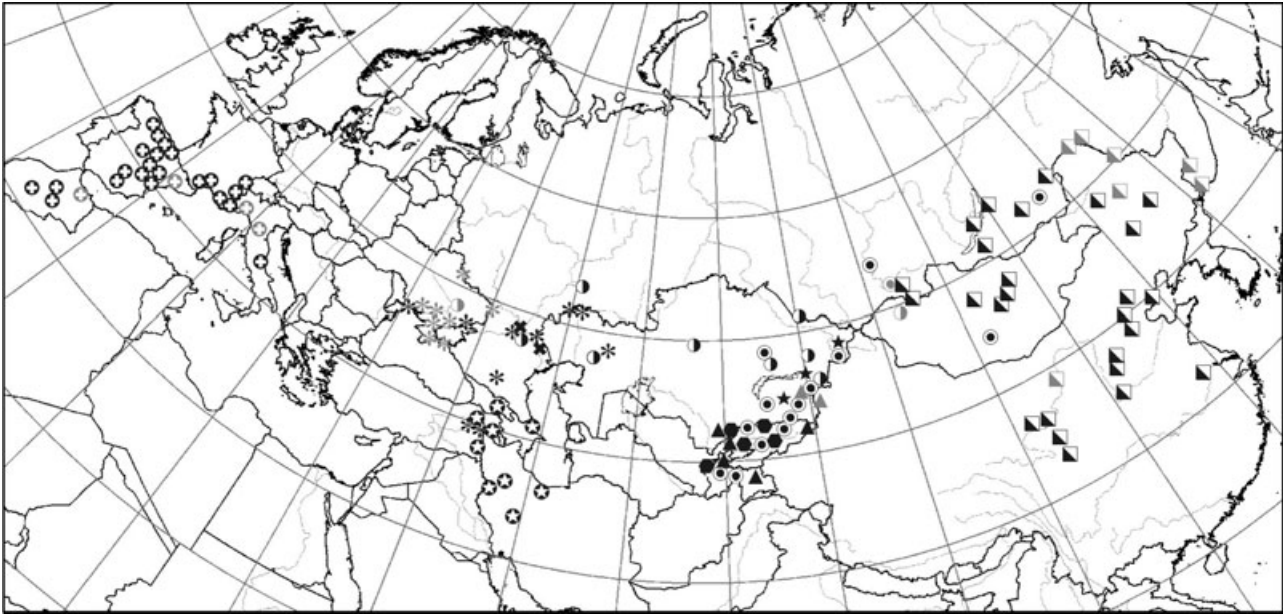


Figure 5. Distribution of *Klasea* sect. *Klasea* p.p. Locality data taken from the literature are indicated by grey symbols. X, *K. x bogdensis*; ◻, *K. cardunculus*; ◻, *K. centauroides*; ★, *K. dissecta*; *, *K. erucifolia*; ◻, *K. haussknechtii*; ▲, *K. lyratifolia*; ◻, *K. marginata*; ◻, *K. nudicaulis*; ●, *K. sogdiana*.

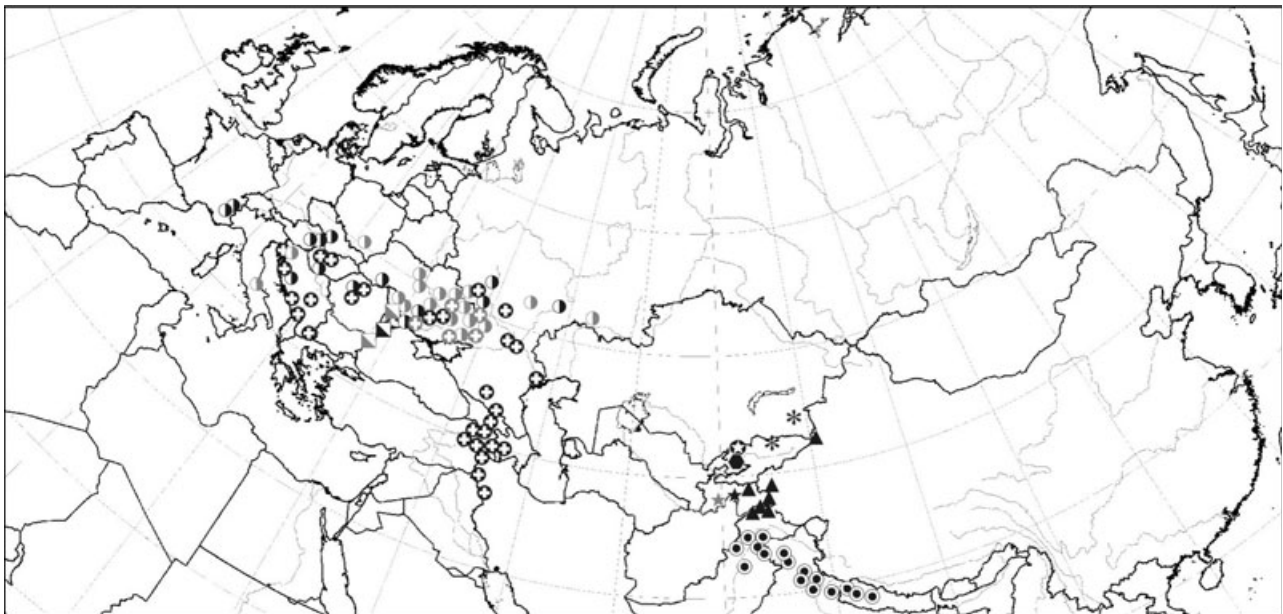


Figure 6. Distribution of *Klasea* sect. *Klasea* p.p. Locality data taken from the literature are indicated by grey symbols. ●, *K. aphyllopoda*; ◻, *K. bulgarica*; ★, *K. chartacea*; ◻, *K. hastifolia*; ◻, *K. lycopifolia*; ◻, *K. pallida*; ▲, *K. procumbens*; ◻, *K. radiata*; *, *K. suffruticulosa*.

alae they are of a herbaceous consistency rather than coriaceous. The colour of the distal part of the phyllaries has been used to distinguish species, especially within the *Nudicaulis* group, but the size and colouring (black or brown) of the dark-coloured portion seems to be of little value. Nevertheless, the presence of dark-coloured portions of the phyllaries is charac-

teristic for the sections *Melanolepis* and *Lasiocephalae* and, partially, for the *Nudicaulis* group of sect. *Klasea*.

Corolla colour: Purple is the predominant corolla colour in *Klasea* and is very likely the plesiomorphic state. Yellow or cream corollas occur in most of the members of sect. *Schumeria* and in a few members of

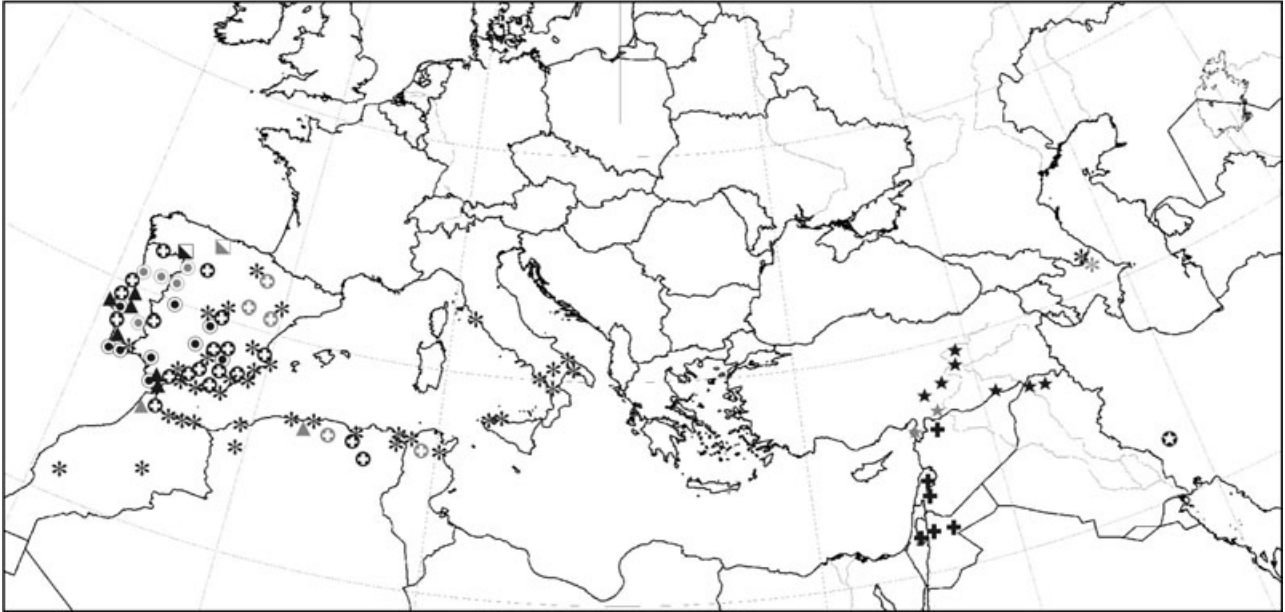


Figure 7. Distribution of *Klasea* sect. *Demetria*. Locality data taken from the literature are indicated by grey symbols. \blacktriangle , *K. boetica*; *, *K. flavescens*; \odot , *K. integrifolia*; \oplus , *K. khuzistanica*; \blacksquare , *K. legionensis*; \star , *K. oligocephala*; \odot , *K. pinnatifida*; \oplus , *K. pusilla*.

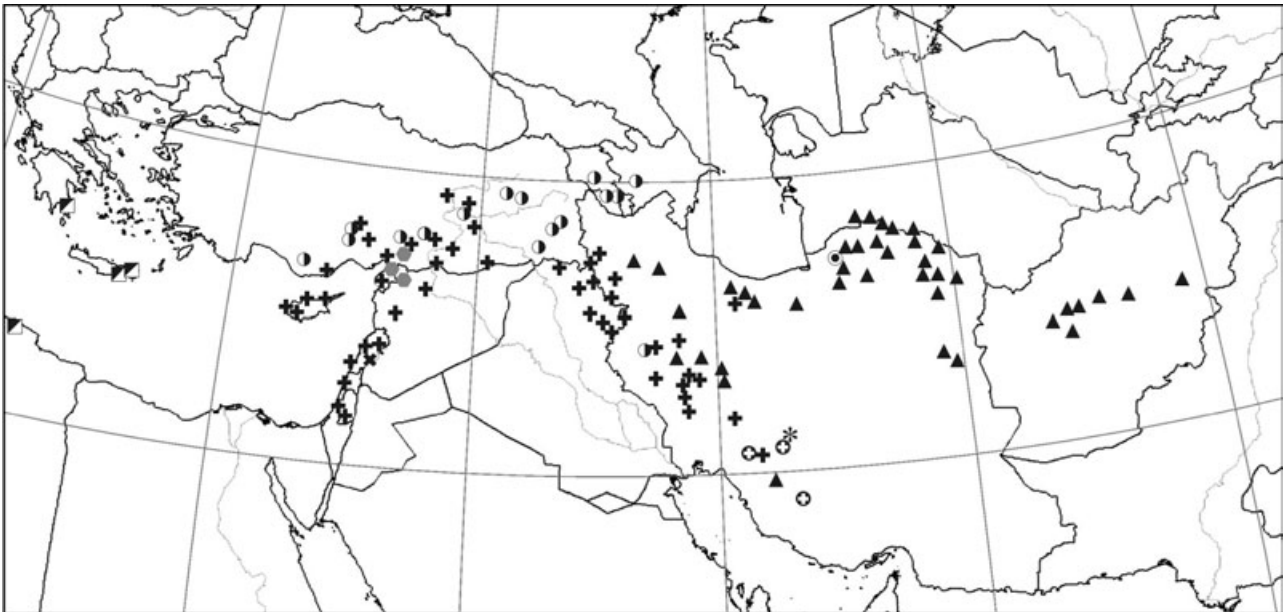


Figure 8. Distribution map of *K. x mouterdei* and sections *Leuzeopsis* and *Schumeria*. Locality data taken from the literature are indicated by grey symbols. Intersectional hybrid: \times , *K. x mouterdei*. *Leuzeopsis*: \blacksquare , *K. serratuloides*. *Schumeria*: \oplus , *K. cerinthifolia*; \blacksquare , *K. cretica*; \odot , *K. gracillima*; \odot , *K. kurdica*; \blacktriangle , *K. latifolia*; *, *K. suffulta*; \odot , *K. viciifolia*.

sect. *Demetria* (*K. flavescens* p.p and *K. khuzistanica*). Surprisingly, the purple-flowered *K. cretica* appears to be nested within the yellow-flowered *K. sect. Schumeria*. Thus, the coloration in *K. cretica* might be a result of a reversal from yellow to purple.

Apical anther appendages: The shape of the apical anther appendages can be assigned to three main types or to intermediate forms: (1) shortly triangular with concave margins (*Lasiocephalae* type; Fig. 4D), which is observed only in the two species of sect.

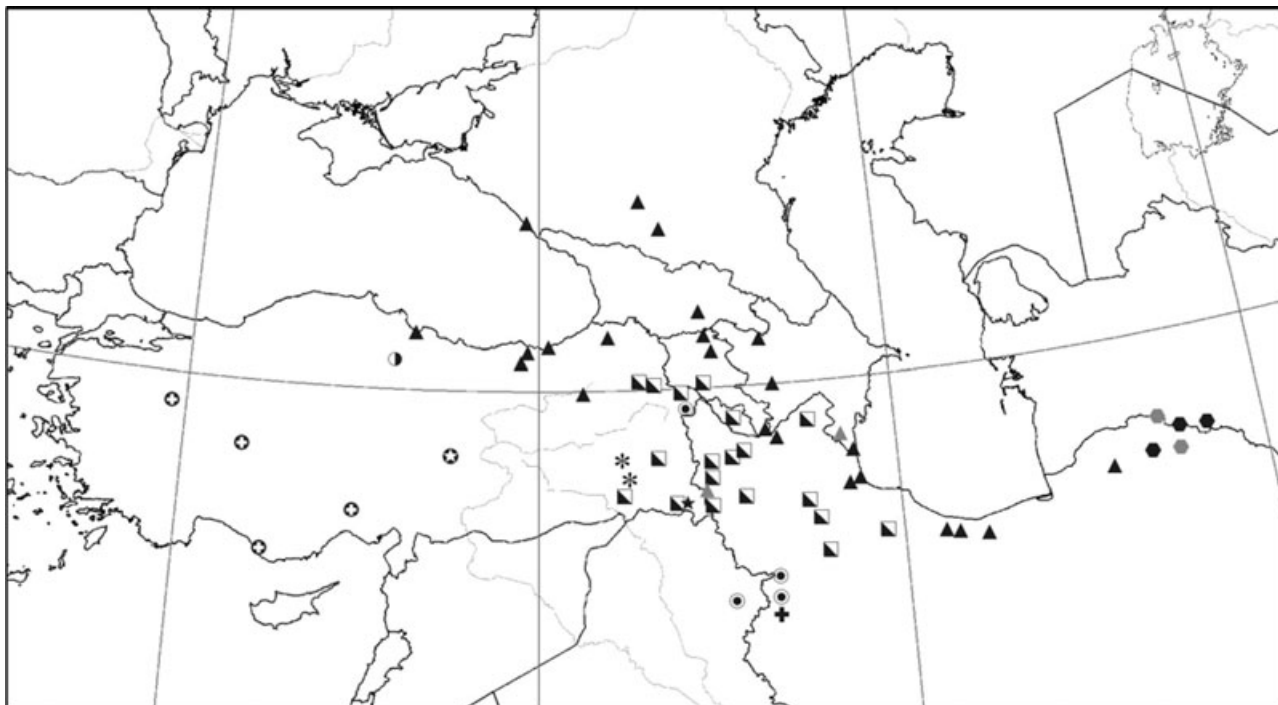


Figure 9. Distribution of *Klasea* sections *Coriaceae*, *Grandifoliae*, *Lasiocephalae*, *Melanolepis*, *Nikitinia*, and *Quinquefoliae*. Locality data taken from the literature are indicated by grey symbols. *Coriaceae*: ◻, *K. coriacea*. *Grandifoliae*: ◐, *K. aznavouriana*; ◑, *K. grandifolia*. *Lasiocephalae*: ⊕, *K. bornmuelleri*; ⊖, *K. lasiocephala*. *Melanolepis*: ★, *K. hakkiarica*; *, *K. kotschyi*; †, *K. melanocheila*. *Nikitinia*: ●, *K. leptoclada*. *Quinquefoliae*: ▲, *K. quinquefolia*.

Lasiocephalae; (2) narrowly triangular (*Melanolepis* type; Fig. 4E) in sect. *Melanolepis*; and (3) broadly rounded to slightly emarginate (*Schumeria* type; Fig. 4A), which is found in the sections *Schumeria* and *Leuzeopsis* and in several members of sect. *Klasea*. An intermediate type approaching the *Melanolepis* type, i.e. acute, but margins clearly convex (Fig. 4C), is found in the sections *Quinquefoliae* and *Coriaceae*. Intermediate forms approaching the *Schumeria* type, i.e. attenuate-obtuse or parabola-shaped (Fig. 4B), are characteristic for sect. *Demetria*, *Grandifoliae*, *Nikitinia*, and part of sect. *Klasea*. *K. serratuloides* is the only species in which a considerable intraspecific variation of the apical anther appendages was observed (*Schumeria* type, slightly emarginate, and an intermediate type). The *Schumeria* type is observed in those groups judged as phylogenetically younger, whereas the presumably older groups have anther appendages of the *Lasiocephalae* type, *Melanolepis* type, or an intermediate form similar to the latter; there might be a tendency towards obtuse appendages in the evolution of the genus.

Achene morphology and anatomy: The achenes of *Klasea* are glabrous; they have resin ducts in the pericarp and oxalate crystals in both the pericarp and the testa. Variable characters are the presence or absence

of ribs, pericarp thickness and colour, and the shape of the apical zone. Because of the lack of mature achenes of several species, only an incomplete picture of the variability and evolution of achene anatomical characters and pappus morphology could be drawn.

Pappus: The pappus of all *Klasea* species is simple, i.e. consisting of several rows of bristles of the same type more or less united at their base. The bristles decrease in length from the centre outwards. The length of the teeth on the bristles is very variable, from about one-fifth of the diameter of the bristle in *K. quinquefolia* to up to 20 times the diameter of the bristle in *K. serratuloides* and *K. suffulta*; however, it is often highly variable within a species and seems to be hardly correlated to systematic groups. In *K. lasiocephala*, the pappus falls off as an entity, whereas, in all other species for which mature achenes are known, the pappus is persistent or deciduous but falling apart.

PHYLOGENY AND SYSTEMATICS

The moderately supported (0.93) *Klasea* clade contains about 50% of all *Klasea* species. Most have been classified in sect. *Klasea* by Borisova (1963a), but it also includes the species previously classified in the

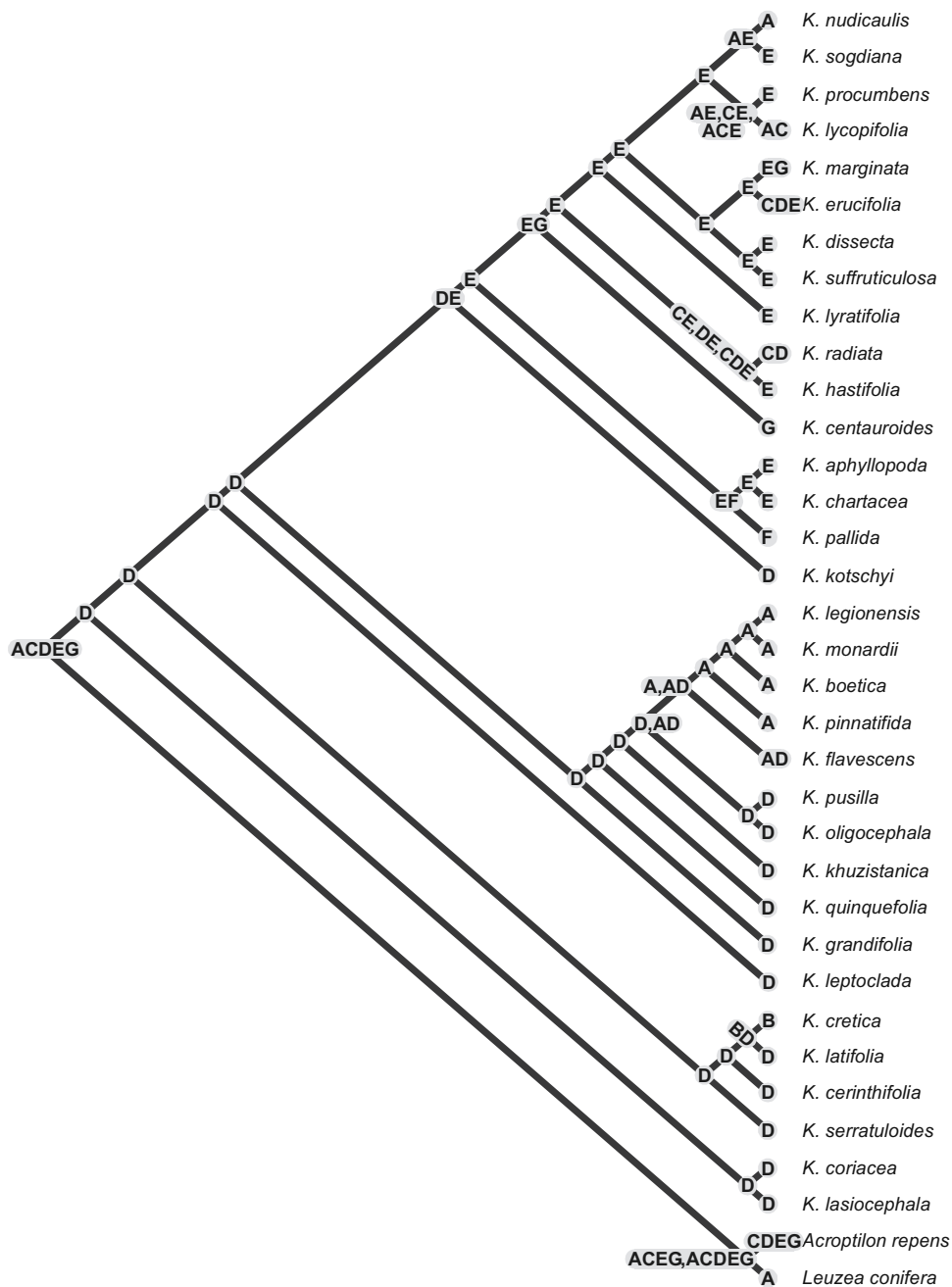


Figure 10. Results of dispersal vicariance analysis showing ancestral areas for each internal node and present areas of terminal nodes. For definition of areas, see Figure 1.

sections *Iljinia* and *Piptochaete*. Sect. *Iljinia* was segregated from sect. *Klasea* on the basis of stem height and leaf shape (Borisova, 1963a), and sect. *Piptochaete* was distinguished from sect. *Klasea* by the caducous pappus consisting of few bristles, which are obviously characters not suitable for sectional delimitation. Two species (*K. quinquefolia* and *K. coriacea*), which were classified in sect. *Klasea* by Borisova (1963a), do not fall into the *Klasea* clade. Within this clade,

K. aphyllopoda and *K. chartacea* form a well-supported group. These two species have been assumed to be very closely related to each other and possibly even to be conspecific by Borisova (1963a). However, on the basis of the investigated herbarium material, these species are well distinguished. Several of the species included here have been recognized as two or more distinct species by previous authors (*K. nudicaulis*, *K. marginata*, *K. sogdiana*, *K. lyratifolia*, *K. dissecta*,

K. radiata, *K. centauroides*), illustrating the taxonomic complexity of the group as a result of ongoing speciation and/or hybridization events (for details, see the synopsis at the end of this paper). There are only few morphological synapomorphies for the *Klasea* clade: it is characterized by apical anther appendages of the *Schumeria* type (Fig. 4A), in many cases tending towards an intermediate type (Table 2). This type is also present in two further sections: in sect. *Schumeria*, from which sect. *Klasea* is distinguished by always purple corollas, usually striate phyllaries, and leaves often with an indument of multicellular hairs (Fig. 3A–C), sometimes additionally of glands (Fig. 3G); and in sect. *Demetria*, from which sect. *Klasea* differs by the absence of filiform hairs (Fig. 3F) and by phyllaries with a distinct appendage (usually a spine or mucro). Borisova's (1963a) informal series 'Chartaceae' is not monophyletic. The two species included in the series 'Heterophyllae', *K. lycopifolia* and *K. bulgarica*, are morphologically very similar to each other and are therefore regarded as sister species. The scarious appendages of the phyllaries in *K. bulgarica* are an autapomorphy of this species. Zahariadi established the section *Lepidocephalae* on the basis of this single character, which seems to have no taxonomic value as it is variable even within a species (*K. nudicaulis*). For the other series, no decision can be made with regard to monophyly on the basis of the present data because of the poor resolution within sect. *Klasea*.

The two species of *K.* sect. *Grandifoliae* are morphologically very close to sect. *Klasea*, and their assignment to a separate section is mainly because of the position of *K. grandifolia* in the molecular phylogenetic tree (Fig. 2). They are characterized by very large lower cauline leaves and polycephalous, dense, corymbose synflorescences, involucre constricted in the upper half, and apical anther appendages of an intermediate type (Fig. 4B), not approaching the *Schumeria* type as in sect. *Klasea*. The analysis of the ITS-2 sequences corroborates the statement of Davis & Kupicha (1975) that *K. aznavouriana* probably is most closely related to *K. grandifolia*.

Klasea hakkiarica has been described on the basis of a specimen previously included in *K. kotschyi* (Davis & Kupicha, 1988), and there is no doubt that both species are very closely related to each other, the difference between them being the number of capitula per stem, the shape of the involucre, and the length of the apical spines of the phyllaries. The placement of *K. melanocheila* in sect. *Melanolepis* is more problematic. As the type specimen at JE was the only material available, neither molecular nor fruit anatomical data could be collected. On the basis of morphological characters (leaf blade completely glabrous, phyllaries black-tipped), no decision can be made about whether

it is closely related to the *Nudicaulis* group of sect. *Klasea*, as proposed by Iljin (1934), or to sect. *Melanolepis*. The main character giving a clue to its affinity to *K. kotschyi* and *K. hakkiarica* is the acutely triangular (not obtuse) shape of the apical anther appendages.

Section *Demetria* is composed of the taxonomically difficult group of west Mediterranean species (Cantó, 1984) and the three rather distinct west Asian species *K. oligocephala*, *K. pusilla*, and *K. khuzistanica*. This group is characterized by the presence of filiform hairs (Fig. 3F) which are concentrated on the leaf veins. Only in *K. flavescens* are these sparse in some specimens. Outside the section, filiform hairs on leaves occur in *K. lyratifolia* and *K. serratuloides*, but, in these species, they are equally dispersed throughout the leaf blade. Except for *K. oligocephala*, the phyllaries are loose rather than imbricately appressed and show a gradual transition into the apical spine, instead of exhibiting a clear distinction between the blade and the appendage. The group of the west Mediterranean species *K. boetica*, *K. legionensis*, *K. integrifolia*, and *K. pinnatifida* has been subject to an extensive study by Cantó (1984). Her concept of species and subspecies delimitation is adopted here, but the species are transferred from *Serratula* to *Klasea*. There is evidence that hybridization is common within this group: polyploidy up to the hexaploid level (Cantó, 1984), frequent polymorphic sequence positions, continuous character distribution, and, resulting from this, problematic species delimitation. For example, *K. integrifolia* ssp. *algarbiensis* is morphologically intermediate between the two other taxa which occur in southern Portugal, *K. integrifolia* ssp. *integrifolia* and *K. boetica* ssp. *lusitanica*, and is therefore suspected to be a hybrid between them. If it is the case that the polyploids are of allopolyploid origin, recombination of divergent paralogues may result in problems in finding the true phylogeny (Buckler, Ippolito & Holtsford, 1997), and this may be the reason why *K. boetica* and *K. pinnatifida* do not appear as monophyletic in the tree (Fig. 2).

For the well-supported monophyletic group comprising the sections *Leuzeopsis* and *Schumeria*, no morphological synapomorphies could be found, and it is therefore regarded as two separate sections.

Section *Leuzeopsis* contains the single species *K. serratuloides*. It is characterized by large capitula, phyllaries with a rather long reflexed aculeate appendix, leaves covered more or less densely with filiform hairs, achenes apically rounded with an inconspicuous apical rim, and a pinnate pappus.

Klasea sect. *Schumeria* is represented by only three species in the molecular phylogenetic analysis, but there is no doubt that *K. gracillima*, *K. kurdica*, *K. suffulta*, and *K. viciifolia* also belong here, as they are distinguished from *K. latifolia* by taxonomically

less important characters, such as the shape of leaves and involucre. All species placed here in sect. *Schumeria* have glabrous leaves (sometimes except for the margins), at least the upper leaves with entire (not denticulate) margins, phyllaries more or less unicoloured (without darker stria or apical darker part), and light brownish-grey achenes. *K. bornmuelleri*, which has been included in *Schumeria* by Iljin (1960), does not belong to this section; this will be discussed later. Surprisingly, the purple-flowered *K. cretica*, which has mostly been regarded as a subspecies of *S. cichoracea* (= *K. flavescens* ssp. *cichoracea*), is nested within the otherwise yellow-flowered *Schumeria*. Moreover, the corolla colour, decurrent leaves, at least the lower ones remotely toothed, and congruencies in the involucre morphology give reason to suppose a close relationship between *K. cretica* and *K. flavescens*. Decurrent leaves are also present in *K. latifolia* of sect. *Schumeria*. The leaf indument gives evidence for the placement of *K. cretica* in sect. *Schumeria*. The leaf blade is completely glabrous as in the other *Schumeria* species, but unlike in sect. *Demetria*, and in some specimens there are pedestal hairs at the leaf margin, which are observed elsewhere only in *K. latifolia* and *K. viciifolia* (Table 2). Solely on morphology it may be impossible to decide whether *K. cretica* belongs to sect. *Demetria* (*K. flavescens*) or sect. *Schumeria*. A hybrid origin of *K. cretica*, which could be supposed on the basis of the intermediate morphological characters, is unlikely because potential parent species have no occurrences nearby. Geographically, it is isolated, being endemic to Crete, southern Peloponnese, and Cyrenaica, where it is the only *Klasea* species, whereas other species of sect. *Schumeria* have their westernmost distribution in Cyprus and the Taurus mountains of southern Anatolia.

The exact placement of sect. *Nikitinia* within the genus is not resolved by the molecular data. Some morphological characters support a closer relationship to sect. *Coriaceae*, which is also part of the basal polytomy in the cladogram (Fig. 2): for example, long thin terminal branches with several reduced, more or less linear leaves, involucre usually with an attenuate base, phyllaries strictly appressed and without or with a very short (< 0.8 mm) mucro, and short corolla lobes (30–40% of the limb; in other sections usually 40–60%). Nevertheless, their treatment in two separate sections is favoured here.

Nikitinia has achenes with a sub-basal detachment area and has therefore often been regarded as a member of *Carduinae*; it is distinguished from all other *Klasea* species by the narrowly cylindrical to obconical involucre.

Klasea quinquefolia is characterized by some unique features within the genus, including hypostomatic leaves (all other amphistomatic), cells of

adaxial leaf epidermis with arcuate (not straight) cell walls, coloured pappus (purple when young, brownish when dry), and long papillae on the filaments (reaching 50% of the width of the filaments, in other species 3–30%).

Section *Lasiocephalae* is made up of two species rather different in appearance. *K. lasiocephala* has petiolate, finely divided, mostly basal leaves, and *K. bornmuelleri* has mostly cauline, large, undivided, sessile to semiamplexicaul leaves. The latter species has been included in *Schumeria* by Iljin (1960) apparently because of the leaf morphology. When taking into account characters of the capitula, it becomes obvious that *K. bornmuelleri* was misplaced in *Schumeria*: *Schumeria* is characterized by terminal, medium-sized capitula with coriaceous, yellowish-green phyllaries and mostly yellow flowers. In contrast, *K. bornmuelleri* has axillary, small capitula with herbaceous, apically dark-coloured phyllaries and purple flowers. In all these characters, as well as the indument of the phyllaries and the shape of the apical anther appendages, it approaches much more the conditions in *K. lasiocephala*. The axillary capitula, herbaceous phyllaries, and apical anther appendages of the *Lasiocephalae* type are unique within the genus, and thus it is appropriate to place both species together in a section.

Mature achenes of *K. bornmuelleri* are not known; those of *K. lasiocephala* are almost black, apically rounded without an apical rim, and the pappus is united in a basal ring and falls off as an entity at maturity.

Hybridization seems to play an important role in the evolution of the genus. In the two cases of *K. × bogdensis* and *K. × mouterdei*, the parental species are rather distantly related to each other and morphologically very different. Thus taxa with intermediate characters and a range restricted to the area in which both putative parental species occur can be clearly identified as hybrids. Within polymorphic species or species complexes (*K. nudicaulis* group, *K. centauroides*, and the complex of *K. pinnatifida*, *K. boetica*, *K. legionensis*, and *K. integrifolia*), there are extreme forms which may deserve specific rank, but intermediate forms exist which may actually be hybrids between them. Diversification is apparently still ongoing in these groups.

BIOGEOGRAPHY

The range of *Klasea* encompasses the meridional and submeridional zones of the Old World from south-west Europe and north Africa to almost the Pacific coast of northern China and the Russian Far East. Representatives of nine of the ten sections are native to a region reaching from central Asia Minor to north-western

Iran, sect. *Nikitinia* occurs in the Kopet Dagh Mountains of north-eastern Iran and southern Turkmenistan, whereas all other parts of the range are occupied by representatives of the sections *Klasea*, *Demetria*, and *Schumeria* only. The west Asian region is depicted as the ancestral area of the genus by DIVA (Fig. 10).

Although section *Klasea* covers most of the range of the genus, many species are restricted to central Asia. East of 70° of eastern longitude there are no species of other sections present (Figs 5–9). The results of DIVA (Fig. 10) indicate that the ancestral area of sect. *Klasea* is in central Asia and, within this region, most probably the Tianshan–Pamir–Alai mountain range because the majority of the species occur there. For the evolutionary history of the genus, it can be concluded that the radiation giving rise to the ancestors of the sections occurred in west Asia. The ancestors of sect. *Klasea* dispersed eastwards to central Asia, and only rather recently a large-scale dispersal took place by members of sect. *Klasea* to colonize east Asia, the Himalayas, large parts of Europe, and to re-migrate to west Asia.

The basal taxa of sect. *Demetria* are distributed in west Asia, and thus a dispersal of the ancestor of the west Mediterranean taxa might have occurred westwards. The history of *K. flavescens* ssp. *caucasica* remains an unresolved problem. Morphologically, it is very close to the west Mediterranean *K. flavescens*, especially to ssp. *cichoracea*, and is therefore assigned to that species here. This relationship could not be investigated by molecular data because of the lack of DNA material. The most likely explanation of the disjunction between *K. flavescens* ssp. *caucasica* and the remaining subspecies is a long-distance dispersal from the western Mediterranean to the Caucasus. An alternative scenario is that the extant disjunct range is the remnant of a wide continuous distribution, which would mean that it became extinct in a huge area covering Greece, Turkey, and Transcaucasia. Similar

disjunctions have been observed in *Rhododendron ponticum* L. (Popova, 1972) and *Astragalus lusitanicus* Lam. (Chater, 1968), but these species are also present in Turkey and Bulgaria and in Greece, respectively.

Evidence for recent radiation, speciation, and hybridization is apparent, especially at the edges of the range in the east (*K. centauroides*), north (*K. × bogdensis*), and west (*K. nudicaulis* and the west Mediterranean group of sect. *Demetria*). In contrast, most of the species inhabiting the ancestral area are rather homogeneous and morphologically rather distinct from each other, and are thus most probably reproductively isolated from each other.

It is remarkable that the Aegean region is inhabited by only one species (*K. cretica*), despite the fact that it is rather close to regions inhabited by several *Klasea* species (central and east Anatolia in the east, Italy, North Africa, and the Iberian Peninsula in the west, south-east and east Europe in the north) and potential habitats occur.

The correlation between pappus characters, dispersal facilities, and the range of a species could be the subject of future investigations; for example, an explanation of the rather restricted range of *K. lasiocephala* could be the poor ability to disperse by wind because of the easily deciduous pappus.

KEY TO THE *KLASEA* SPECIES

The diameter of the involucre must be measured in the middle of a non-compressed capitula during anthesis or, if only compressed capitula are available, it must be estimated how the diameter would be in the fresh state. Involucral bract appendages are ignored for the diameter measurement.

Characters of achenes were not included in the key because mostly flowering plants without mature achenes were collected.

- | | | |
|----|--|------------------------------------|
| 1. | Flowers yellow or cream. | |
| 2. | Outer and median phyllaries without appendage or with mucro 0.1–2 mm long (sect. <i>Schumeria</i> p.p.). | |
| 3. | Basal leaves pinnate or pinnatisect. | |
| 4. | Terminal branches with several (5–20) entire semiamplexicaul leaves, involucre cylindrical..... | 29. <i>K. cerinthifolia</i> |
| 4* | Terminal branches with fewer leaves, involucre ovoid to cup-shaped. | |
| 5. | All leaves pinnate or pinnatisect, stems leafless above..... | 34. <i>K. kurdica</i> |
| 5* | Uppermost leaves undivided, stem foliated almost up to the capitula. | |
| 6. | Leaflets ovate to oblong, 5–15 mm broad, cauline leaves sessile, ±semiamplexicaul..... | 33. <i>K. viciifolia</i> |
| 6* | Leaflets linear to narrowly oblong, 1–4 mm broad, cauline leaves decurrent on the stem | 32. <i>K. gracillima</i> |
| 3* | All leaves undivided. | |
| 7. | Involucres 20–30 mm in diameter, subtended by a leaf, apical spine of phyllaries c. 2 mm long..... | 31. <i>K. suffulta</i> |
| 7* | Involucres (7–)13–18 mm in diameter, not subtended by a leaf, apical spine of phyllaries 0.2–1 mm long | 30. <i>K. latifolia</i> |

- 2*. Outer and median phyllaries with apical spine 3–8 mm long (sect. *Demetria* p.p.).
8. Leaves irregularly pinnatisect with irregularly dentate segments, phyllaries in c. 10 rows..... 25. *K. khuzistanica*
- 8*. Leaves undivided, oblong to narrowly lanceolate, shallowly dentate, phyllaries in c. 7 rows..... 24. *K. flavescens* p.p.
- 1*. Flowers pink or purple, very rarely almost white.
9. Capitula arising from leaf axils of basal or cauline leaves on leafless peduncles, if some capitula terminal on ±foliated peduncles then either corolla 7–11 mm long or larger cauline leaves semiamplexicaul and always bearing a branch or stalked capitulum in the leaf axil.
10. Corolla 12–17 mm long, phyllaries yellowish-green throughout..... 13. *K. hastifolia*
- 10*. Corolla 7–11 mm long, phyllaries black or blackish at apex (sect. *Lasiocephalae*).
11. Leaves entire, semiamplexicaul, mostly cauline 40. *K. bornmuelleri*
- 11*. Leaves pinnate or pinnatisect, mostly basal 39. *K. lasiocephala*
- 9*. All capitula terminal on (sometimes very short) stems or branches, peduncles ±foliated.
12. Leaves broadly elliptical or lyre-shaped, irregularly lobed, involucre 10–23 mm in diameter 26. *K. oligocephala*
- 12*. Leaves undivided, pinnatifid, pinnatisect, or rarely pinnate, margin entire, dentate, or denticulate, or if irregularly lobed then involucre 25–50 mm in diameter.
13. Stems richly branched, bearing 8–8 capitula (rarely fewer in weak individuals).
14. Involucre 3–9(–10) mm in diameter.
15. Abaxial side of the leaf blade with multicellular hairs and minute glands.
16. Synflorescence compact, innermost phyllaries straight at anthesis..... 7. *K. dissecta*
- 16*. Synflorescence loose, appendages of innermost phyllaries ±radiating at anthesis.
17. Capitula fewer than 20, (4–)6–12 mm in diameter..... 5. *K. × bogdensis*
- 17*. Capitula 20–8 in number, 3–6 mm in diameter 6. *K. erucifolia*
- 15*. Leaves glabrous, subglabrous or with few multicellular hairs, not glandular.
18. All leaves much reduced, plants virgately branched 37. *K. leptoclada*
- 18*. At least basal and lower cauline leaves well developed.
19. Capitula very numerous in dense corymbs, basal leaves very large, 10–25 cm wide 45. *K. grandifolia*
- 19*. Capitula fewer than 10, basal leaves 0.5–2.5 cm wide 4. *K. cardunculus*
- 14*. Involucre (9–)10–23 mm in diameter.
20. Lower cauline leaves pinnate or ternate (leaflets sometimes decurrent on the rachis), appendages of innermost phyllaries and pappus with lilac tinge or light brown when dry 41. *K. quinquefolia*
- 20*. All leaves undivided, pinnatifid or pinnatisect, appendages of innermost phyllaries and pappus straw-coloured.
21. Median phyllaries 1.5–2.5 mm wide.
22. Involucre 16–25 mm long, basal and lower cauline leaves with 1–4 pairs of narrow lateral laciniae and a large terminal narrowly elliptic to lanceolate denticulate lobe 15. *K. sogdiana*
- 22*. Involucre 10–16(–19) mm long, basal and lower cauline leaves undivided or pinnatifid to pinnatisect, but terminal lobe neither much larger than lateral lobes nor denticulate.
23. Leaves glabrous (except for the margin), ±glaucous..... 4. *K. cardunculus*
- 23*. Leaves with multicellular hairs and few minute glands..... 5. *K. × bogdensis*
- 21*. Median phyllaries 2.5–5 mm wide.
24. All leaves pinnatisect, lateral segments and terminal lobe linear to narrowly oblong, entire or dentate, terminal segment not conspicuously larger than the lateral segments..... 19. *K. centauroides* ssp. *polycephala*
- 24*. Upper cauline leaves undivided, lower cauline leaves undivided or lyrate to pinnatisect with the terminal lobe much larger than lateral segments.
25. Involucre constricted in upper part, innermost phyllaries geniculate 46. *K. aznavouriana*
- 25*. Involucre not constricted, innermost phyllaries ±straight.
26. Venation of lateral leaf segments of lower cauline leaves with three or more prominent veins arising from the rachis..... 38. *K. coriacea*
- 26*. Lateral leaf segments with only one conspicuous vein 15. *K. sogdiana*
- 13*. Stems simple or poorly branched, bearing 1–5(–7) capitula.
27. Median phyllaries with well-delimited triangular or sickle-shaped black or dark-brown area at apex.
28. Outer and median phyllaries with a scarios appendage..... 17. *K. bulgarica*
- 28*. Outer and median phyllaries with an apical spine or mucro, but without a scarios appendage.
29. Leaves pubescent of multicellular hairs, sometimes sparsely so and sometimes only the lower side of the leaf blade.
30. Upper half of stems leafless, leaves mostly basal, basal leaves larger than cauline leaves..... 8. *K. pallida*

- 30*. Upper half of stems foliated (uppermost leaves sometimes diminished), leaves mostly cauline, basal leaves not conspicuously larger than cauline leaves, sometimes withered at anthesis.
31. Mucro of median phyllaries 1.5–3 mm long, cauline leaves pinnatifid to lyrate-pinnatifid 18. *K. radiata* ssp. *biebersteiniana*
- 31*. Mucro of median phyllaries 0.2–1.2 mm long, cauline leaves pinnatisect or undivided 19. *K. centauroides*
- 29*. Leaves glabrous on both sides, marginal hairs present or not.
32. All leaves completely glabrous (sect. *Melanolepis* p.p.).
33. Stems simple or with sterile branches, capitulum solitary, spine of median phyllaries c. 3–4 mm long 43. *K. hakkiarica*
- 33*. Stems branched, capitula 3–5, spine of median phyllaries 0.5–1.5 mm long 42. *K. kotschyi*
- 32*. At least some (mostly the upper) leaves with marginal multicellular hairs (hairs sometimes only few and short), leaf surfaces glabrous.
34. Leaves prominently reticulate-veined, ovate in outline 11. *K. chartacea*
- 34*. Leaves with prominent midvein, faintly reticulate-veined, narrowly oblong to linear-lanceolate in outline.
35. Median phyllaries shortly acuminate, the mucro 0.2–0.5 mm long 44. *K. melanocheila*
- 35*. Median phyllaries with an apical spine 1–4 mm long 1–4. *K. nudicaulis* group
- 27*. Median phyllaries greenish or yellowish throughout, sometimes with light-brown spot at apex or dark-coloured scarious margin or striate towards apex.
36. Phyllaries 6–11 mm wide.
37. Stems very short (0.5–3 cm), leaves pinnate, leaflets irregularly pinnatisect 27. *K. pusilla*
- 37*. Stems longer (4–50 cm), leaves undivided or lyrate-pinnatisect 36. *K. serratuloides*
- 36*. Phyllaries 1–6 mm wide.
38. Lower cauline leaves pinnatisect with (7–)10–20 pairs of segments 18. *K. radiata*
- 38*. Lower cauline leaves undivided, lyrate-pinnatifid, or pinnatisect with 5–6(–9) pairs of segments.
39. Adaxial side of the leaf blades with scattered multicellular hairs.
40. Stems always simple, short (up to 10 cm long), margin of phyllaries black 14. *K. lyratifolia*
- 40*. Stems simple or branched, >15 cm long, or if shorter then margin of phyllaries pale-coloured.
41. Median phyllaries with a mucro or spine 2–6 mm long.
42. Cauline leaves narrowly lanceolate, often decurrent 24. *K. flavescens*
- 42*. Cauline leaves pinnatifid or lyrate-pinnatifid, not decurrent 18. *K. radiata* ssp. *biebersteiniana*
- 41*. Median phyllaries with a mucro or spine 0.3–1.5 mm long.
43. Peduncles long (stems leafless or with one reduced leaf in the uppermost 15 cm).
44. Petiole of the basal leaves usually longer than the leaf blade, leaf blade of basal leaves undivided, ovate to oblong, transitioning into the pinnatifid or pinnatisect upper cauline leaves, space between segments narrower than segment width 16. *K. lycopifolia*
- 44*. Petiole of the basal leaves shorter or equalling the leaf blade, all leaves similar or, if different, then upper cauline leaves pinnatisect with remote segments (space between segments wider than segments).
45. Achenes pale, margins of the phyllaries not coloured, leaves concentrated near the base of stem, the basal leaves usually conspicuously larger than the cauline leaves 8. *K. pallida*
- 45*. Achenes brown, margins of the phyllaries often reddish-brownish, lower part of the stem ± evenly foliated, the basal leaves not conspicuously larger than the cauline leaves, often withered at anthesis 19. *K. centauroides*
- 43*. Peduncles shorter, uppermost leaf < 10 cm below the capitulum.
46. Leaves coriaceous, undivided to pinnatifid, oblong to lanceolate, acutely dentate, often with narrow whitish cartilaginous margin, phyllaries pale throughout 9. *K. suffruticulosa*
- 46*. Leaves herbaceous, without cartilaginous margin, pinnatifid to pinnatisect, or undivided-lanceolate and then phyllaries with black apex.
47. Involucre 4–10(–12) mm in diameter, margins of phyllaries pale 5. *K. × bogdensis*
- 47*. Involucre (11–)12–25 mm in diameter, margins of phyllaries mostly purplish 19. *K. centauroides*
- 39*. Adaxial side of the leaf blades glabrous or arachnoid or woolly pubescent, but without multicellular hairs.
48. At least one side of the leaf blade with arachnoid or woolly indument confined to or concentrated on the veins (and rhachis).
49. Leaves pinnately divided 28. *K. × mouterdei*
- 49*. Leaves undivided, pinnatifid, or pinnatisect (sect. *Demetria* p.p.).
50. Phyllaries narrowly triangular or linear-lanceolate, apical spine straight 21. *K. boetica*
- 50*. Phyllaries ovate or obovate, apical spine or mucro usually bent outwards.
51. Cauline leaves narrowly lanceolate, decurrent on the stem or sessile 24. *K. flavescens*
- 51*. Cauline leaves pinnatisect, pinnatifid, or undivided and ovate to lanceolate, petiolate.

52. Median cauline leaves deltoid or ovate in outline, densely woolly pubescent along the veins on the adaxial side of the leaf blade 20. *K. pinnatifida*
- 52*. Median cauline leaves lanceolate to oblong in outline, sparsely woolly pubescent along the veins on the adaxial side of the leaf blade.
53. Phyllaries 1.8–2.8 mm wide, stems (10–)30–85 cm long, sparsely woolly pubescent 22. *K. legionensis*
- 53*. Phyllaries 3–6 mm wide or 1.5–3 mm wide and then stems 1–10 cm, stem densely woolly pubescent 23. *K. integrifolia*
- 48*. Leaf blade glabrous on both sides or rarely with crispate pedicel hairs not concentrated along the veins.
54. Stems ±horizontal 12. *K. procumbens*
- 54*. Stems erect.
55. Leaves coriaceous, venation pale, prominently reticulate.
56. Leaves lyrate to pinnatisect, venation of lateral leaf segments of lower cauline leaves with three or more prominent veins arising from the rachis 38. *K. coriacea*
- 56*. Leaves undivided or towards base ±pinnatifid and then lateral segments with one prominent vein.
57. Leaves entire, obtusely dentate to lobate, without conspicuous cartilaginous white margin, stem simple, foliated only near base 10. *K. aphyllopoda*
- 57*. Leaves acutely dentate, usually with conspicuous cartilaginous white margin, stems usually branched, foliated throughout 9. *K. suffruticulosa*
- 55*. Leaves herbaceous, reticulating veins not prominent, concolorous with the interspace.
58. Upper cauline leaves decurrent, mucro of median phyllaries 1.2–2.5 mm long 35. *K. cretica*
- 58*. Upper cauline leaves not decurrent or decurrent and then apical spine of median phyllaries 3–7 mm long.
59. Upper cauline leaves ±glaucous, undivided or pinnatifid to largely toothed, margin entire 1–4. *K. nudicaulis* group
- 59*. Leaves not glaucous, margin of lower cauline leaves dentate, upper cauline leaves undivided and with denticulate margin or lyrate to pinnatisect.
60. Phyllaries strictly appressed, involucre 11–15 mm in diameter, stems (2–)4–8-cephalous 15. *K. sogdiana*
- 60*. Phyllaries somewhat spreading, involucre 15–35 mm in diameter, stems 1–3-cephalous 24. *K. flavescens*

SYNOPSIS OF *KLASEA*

Klasea Cass., Dict. Sci. Nat. 35: 173; 41: 321 (1825), *Rhaponticum* subgen. *Klasea* (Cass.) Less., Synops. Gen. Comp.: 6 (1832), *Serratula* sect. *Klasea* (Cass.) DC., Prodr. 6: 668 (1838).

Nikitinia Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 356 (1960), *Schumeria* Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 363 (1960), *Microlophopsis* Czerep., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. SR 20: 488 (1960)

× *Centauseratula* Arènes, Notul. Syst. Herb. Paris 14: 188 (1952).

Typus generis: *Klasea centauroides* (L.) Cass. ex Kitag.

Perennial unarmed herbs, capitula homogamous, bisexual, phyllaries in 4–10 series, outer and median ones usually with a short soft spine or mucro, inner phyllaries linear, protruding, apically abaxially densely covered with short bristles, clinanthium densely covered with long smooth bristles, filaments papillose, stigma shortly bilobate, achenes glabrous, containing needle-like oxalate crystals in the testa and plate-like oxalate crystals in the pericarp, pappus simple, consisting of several series of rough, barbellate or shortly pinnate pappus elements.

Klasea Cass. sect. *Klasea*

Leaves often with multicellular hairs, sometimes additionally with glands, corolla pink or purple, apical anther appendages more or less rounded.

1–4. *Klasea nudicaulis* group (*Serratula* sect. *Klasea* ser. *Nitidae* Boriss. nom. inval., ICBN art. 36.1 (Greuter et al., 2000))

This is a taxonomically difficult complex of closely related taxa which needs to be studied in more detail. Four of the taxa may be recognized as species, which are well isolated geographically, except for an overlap of *K. cardunculus* and *K. marginata* (see Fig. 5): (1) *K. nudicaulis* in southern Europe and Morocco; (2) *K. haussknechtii* in the Caucasus, Transcaucasia, Iran, and Anatolia; (3) *K. marginata* in the mountains in central Asia and adjacent Russia, Mongolia, and China; and (4) *K. cardunculus* in the lowland steppes of Russia, Ukraine, Kazakhstan, China, and Mongolia. The assignment to one of these species solely on morphological characters may be difficult for some specimens, in particular the distinction between *K. nudicaulis* and *K. haussknechtii* is often impossible. The *K. nudicaulis* group is characterized by glaucous glabrous leaves with marginal multicellular hairs and achenes with a dark thin pericarp (one-eighth to one-third as thick as the testa epidermis;

only in *K. cardunculus* up to two-thirds as thick as the testa epidermis) and a truncate apex without an apical rim.

A. Stems (1–)2–5(–9)-cephalous, involucre 7–13(–17) mm in diameter 4. ***K. cardunculus***

A*. Stems usually simple, rarely 2–3-cephalous and then involucre 12–20 mm in diameter.

B. Median phyllaries black or dark brown in their distal part (mucro and margin often brighter) 3. ***K. marginata***

B*. Median phyllaries light brown or greenish in their distal part.

C. Phyllaries ± abruptly constricted into a spine or with scarious appendage, apex usually conspicuously darker than the rest 1. ***K. nudicaulis***

C*. Phyllaries gradually attenuate into a short spine, greenish throughout 2. ***K. haussknechtii***

1. ***Klasea nudicaulis*** (L.) Fourr., Ann. Soc. Linn. Lyon, n.s. 17: 98 (1869), *Centaurea nudicaulis* L., Sp. Pl. 2: 1300 (1763), *Serratula nudicaulis* (L.) DC. in Lam. & DC., Fl. Fr., éd. 3, 4: 86 (1815).

Serratula ibrahimii Iljin, Repert. Spec. Nov. Regni Veg. 35: 355 (1934), *Klasea ibrahimii* (Iljin) Holub, Folia Geobot. Phytotax. 12: 427 (1977).

Serratula nudicaulis ssp. *demissa* Iljin, Repert. Spec. Nov. Regni Veg. 35: 356–357 (1934).

Serratula nudicaulis var. *subinermis* Coss. ex Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 173 (1865).

Serratula nudicaulis ssp. *subinermis* (Coss. ex Willk.) Malagarriga, Las Subsp. y Variac. Geogr. 16 (1973).

Serratula albarracinensis Pau, Not. Bot. Fl. Españ. 2: 30 (1888), *Serratula nudicaulis* ssp. *albarracinensis* (Pau) Malagarriga, Sinopsis Fl. Iber. 1253 (1979).

Serratula eliasii Sennen, Bol. Soc. Iber. Ci. Nat. 1929, 28: 107 (1930).

Distribution: France, Italy, Morocco, Spain (Fig. 5).

2. ***Klasea haussknechtii*** (Boiss.) Holub, Folia Geobot. Phytotax. 12: 427 (1977), *Serratula haussknechtii* Boiss., Fl. Orient. 3: 589 (1875), *Serratula nudicaulis* ssp. *haussknechtii* (Boiss.) Bornm., Vestn. Tiflissk. Bot. Sada 32: 2 (1914).

Serratula nudicaulis var. *gilanica* Bornm., Vestn. Tiflissk. Bot. Sada 32: 3 (1914).

Serratula nudicaulis var. *transcaucasica* Bornm., Vestn. Tiflissk. Bot. Sada 32: 2 (1914), *Serratula transcaucasica* (Bornm.) Sosn. ex Grossh., Fl. Kavkaza 4: 194 (1934).

Distribution: Armenia, Azerbaijan, Georgia, Iran, Turkey (Fig. 5).

3. ***Klasea marginata*** (Tausch) Kitag., J. Jap. Bot. 40: 137 (1965), *Serratula marginata* Tausch, Flora 11: 484 (1828).

Serratula glauca Ledeb., Mém. Acad. Imp. Sci. St.-Pétersbourg 5: 560 (1812) non L. (1753), *Serratula nitida* var. *glauca* (Ledeb.) Trautv., Bull. Soc. Imp. Naturalistes Moscou 39: 379 (1866), *Serratula nudicaulis* var. *glauca* (Ledeb.) Pau, Bull. Acad. Int. Geogr. Bot. 77 (1906), *Klasea glauca* (Ledeb.) Kitag., J. Jap. Bot. 21: 139 (1947).

Serratula laxmannii Fisch. ex DC., Prodr. 6: 669 (1838), *Klasea laxmannii* (Fisch. ex DC.) Kitag., J. Jap. Bot. 25: 40 (1950).

Serratula dshungarica Iljin, Repert. Spec. Nov. Regni Veg. 35: 357–358 (1934).

Serratula algida Iljin, Repert. Spec. Nov. Regni Veg. 35: 357 (1934), *Klasea algida* (Iljin) Hidalgo, Ann. Bot. (Oxford) 97: 714 (2006).

Distribution: China, Kazakhstan, Kyrgyzstan, Mongolia, Russia, Tajikistan (Fig. 5).

Serratula kirghisorum Iljin, Repert. Spec. Nov. Regni Veg. 35: 358 (1934), is a variant of *K. marginata* or possibly a hybrid of *K. cardunculus* and *K. marginata*.

4. ***Klasea cardunculus*** (Pall.) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Centaurea cardunculus* Pall., Reise Russ. Reich. 1: 500 (1771), *Serratula cardunculus* (Pall.) Schischk. in Krylov, Fl. Sibir. Occ., ed. 2, 11: 2937 (1949).

Serratula nitida Fisch. ex Spreng., Syst. Veg. 3: 390 (1826).

Distribution: China, Kazakhstan, Mongolia, Russia, Ukraine (Fig. 5).

5. ***Klasea × bogdensis*** L. Martins **nothosp. nov.** (*K. cardunculus* × *K. erucifolia*).

Holotypus: Russia, obl. Volgograd, lower Volga, Volgograd (Zarizyn): steppe on a north-exposed slope near the western periphery of the city (Beketovka district), c. 11 km SE Gor'kovskii, c. 6 km SW Gornaya Polyana, 6.vi.1998, *K.-F. Günther & M. Schnittler 20322* (JE) (Fig. 11).

Planta inter parentes intermedia, a *K. erucifolia* capitulis paucioribus (numero 2–20) et latioribus (diametro (4–)6–12 mm) et a *K. cardunculo* foliis pinatifidis, indumento pilis multicellularibus et glandibus quasi sessilibus necnon caulibus sparse crispate lanatis differt.

The epithet refers to Malyi Bogdo and Bol'shoi Bogdo hills (Russia, Astrakhanskaya obl.) and has been used by Iljin (1936) for an informal variety of *Serratula nitida* (= *K. cardunculus*) which is most probably identical to this hybrid.

Distribution: Russia (Fig. 5).

6. ***Klasea erucifolia*** (L.) Greuter & Wagenitz, Willdenowia 33: 58 (2003), *Xeranthemum erucifolium* L.,



Figure 11. *Klasea x bogdensis*, holotype.

Sp. Pl. 858 (1753), *Serratula erucifolia* (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 3: 424 (1914).

Serratula xeranthemoides M. Bieb., Fl. Taur.-Caucas. 2: 265 (1808).

Distribution: Armenia, Georgia(?), Kazakhstan, Moldavia(?), Russia, Turkey, Ukraine (Fig. 5).

7. *Klasea dissecta* (Ledeb.) L. Martins **comb. nov.**, basionym: *Serratula dissecta* Ledeb., Fl. Alt. 4: 40 (1833).

Serratula angulata Kar. & Kir., Bull. Soc. Imp. Naturalistes Moscou 14: 453 (1841).

Distribution: China, Kazakhstan (Fig. 5).

8. *Klasea pallida* (DC.) Holub, Preslia 70: 106 (1998), *Serratula pallida* DC., Prodr. 6: 670 (1838).

Distribution: India, Nepal, Pakistan (Fig. 6).

9. *Klasea suffruticulosa* (Schrenk) L. Martins, Taxon 54: 636 (2005), *Serratula suffruticulosa* Schrenk, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 3: 110 (1845).

Serratula suffruticulosa auct.

Distribution: China, Kazakhstan, Kyrgyzstan (Fig. 6).

10. *Klasea aphyllopoda* (Iljin) Holub, Folia Geobot. Phytotax. 12: 427 (1977), *Serratula aphyllopoda* Iljin, Repert. Spec. Nov. Regni Veg. 35: 359–360 (1934).

Distribution: Kyrgyzstan, Uzbekistan (Fig. 6).

11. *Klasea chartacea* (C. Winkl.) L. Martins, Taxon 54: 636 (2005), *Serratula chartacea* C. Winkl., Trudy Imp. S.-Peterburgsk. Bot. Sada 9: 524 (1886).

Distribution: Tajikistan (Fig. 6).

12. *Klasea procumbens* (Regel) Holub, Folia Geobot. Phytotax. 12: 427 (1977), *Serratula procumbens* Regel, Bull. Soc. Imp. Naturalistes Moscou 40: 165 (1867).

Distribution: Afghanistan, China, Pakistan, Tajikistan (Fig. 6).

13. *Klasea hastifolia* (Korovin & Kult. ex Iljin) L. Martins, Taxon 54: 636 (2005), *Serratula hastifolia* Korov. & Kult. ex Iljin, Repert. Spec. Nov. Regni Veg. 35: 360 (1934).

Distribution: Kyrgyzstan (Fig. 6).

14. *Klasea lyratifolia* (Schrenk) L. Martins, Taxon 54: 636 (2005), *Serratula lyratifolia* Schrenk in Fischer & Meyer, Enum. Pl. Nov. 1: 45 (1841).

Serratula tianschanica Saposhn. & Nikitina, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 6: 31 (1926).

Serratula modestii Boriss., Fl. URSS 28: 606 (1963).

Distribution: China, Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan(?) (Fig. 5).

Klasea rugosa (Iljin) Kitag., J. Jap. Bot. 25: 40 (1950), *Serratula rugosa* Iljin, Izv. Glavn. Bot. Sada S.S.S.R. 27: 87 (1928).

K. rugosa is probably conspecific with *K. lyratifolia*. It is said to differ from it by rugose achenes (Iljin, 1928).

15. *Klasea sogdiana* (Bunge) L. Martins **comb. nov.**, basionym: *Serratula sogdiana* Bunge, Beitr. Fl. Russl. 191 (1852).

Serratula alata C. A. Mey. ex Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 7, 14(4): 56 (1869).

Serratula trautvetteriana Regel & Schmalh., Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 321 (1879).

Distribution: China, Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan (Fig. 5).

Serratula lancifolia Zak., Fl. Uzbekistan. 6: 388, 515 (1962) is probably conspecific with *K. sogdiana*. It is said to differ from the latter by undivided, in the distal part entire leaves, very short spines of the phyllaries and smaller capitula (Borisova, 1963a).

16. *Klasea lycopifolia* (Vill.) A. Löve & D. Löve, Bot. Not. 114: 43 (1961), *Carduus lycopifolius* Vill., Prosp. Hist. Pl. Dauphiné: 30 (1779), *Serratula lycopifolia* (Vill.) A. Kern., Oesterr. Bot. Z. 22: 13 (1872).

Serratula heterophylla auct. non (L.) Desf.

Distribution: Austria, Bosnia and Hercegovina, Czech Republic, France, Croatia, Hungary, Italy, Moldavia, Poland, Romania, Russia, Slovakia, Slovenia, Ukraine (Fig. 6).

17. *Klasea bulgarica* (Acht. & Stoj.) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Serratula bulgarica* Acht. & Stoj., Bull. Soc. Bot. Bulgar. 5: 111–112 (1932). *Serratula caput-najae* Zahar., Bull. Sect. Sci. Acad. Roumaine 28: 318 (1946).

Distribution: Bulgaria, Moldavia, Romania (Fig. 6).

18. *Klasea radiata* (Waldst. & Kit.) A. Löve & D. Löve, Bot. Not. 114: 43 (1961), *Carduus radiatus* Waldst. & Kit., Descr. Icon. Pl. Hung. 1: 9, tab. 11 (1802), *Serratula radiata* (Waldst. & Kit.) M. Bieb., Fl. Taur.-Caucas. 3: 545 (1819).

Distribution: Albania, Armenia, Austria, Azerbaijan, Bosnia and Hercegovina, Bulgaria(?), Croatia, Georgia, Hungary, Iran, Macedonia, Moldavia, Romania, Russia, Serbia and Montenegro, Slovenia, Turkey, Ukraine (Fig. 6).

A. Stem ± evenly foliated throughout, hairy, usually branched.

- B. Lower cauline leaves pinnatisect with (8–)10–15 pairs of segments, mucro of median involucre bracts 1–1.5 mm long a ***K. radiata* ssp. *radiata***
- B*. Cauline leaves pinnatisect with up to 7 pairs of segments to lyrate with a pinnatifid distal part and few basal segments, mucro of median phyllaries 1.5–3 mm long b ***K. radiata* ssp. *biebersteiniana***
- A*. Stem foliated in its basal part only (rarely few diminished leaves in the upper part of the stem), hairy or glabrous, usually simple (only ssp. *cetinjensis* rarely branched).
- C. Innermost phyllaries longer than (> 1.2 times) diameter of involucre, mucro of median phyllaries 0.3–0.8(–1.2) mm long, leaf segments linear c ***K. radiata* ssp. *cetinjensis***
- C*. Innermost phyllaries shorter than or about as long as the diameter of the involucre, mucro of median phyllaries 1–5 mm long, or mucro shorter and then leaf segments oblong to narrowly triangular, but not linear.
- D. Segments of basal and lower cauline leaves triangular or oblong, mucro 0.5–1 mm e ***K. radiata* ssp. *gmelinii***
- D*. Segments of all leaves narrowly linear, mucro of median phyllaries 1.5–5 mm long.
- E. Mucro 1.5–2 mm long, stem glabrous f ***K. radiata* ssp. *tanaitica***
- E*. Mucro 2–5 mm long, stem hairy to subglabrous .. d ***K. radiata* ssp. *donetzica***
- 18a. ***Klasea radiata* ssp. *radiata***
- 18b. ***Klasea radiata* ssp. *biebersteiniana*** (Grossh.) Greuter, Willdenowia 35: 236 (2005), *Serratula radiata* ssp. *biebersteiniana* Grossh., Fl. Kavk. 4: 194 (1934), *Serratula biebersteiniana* (Grossh.) Takht. in Takhtajan & Fedorov, Atlas Fl. Erevana: 323 (1945), *Klasea biebersteiniana* (Grossh.) Hidalgo, Ann. Bot. (Oxford) 97: 714 (2006).
- 18c. ***Klasea radiata* ssp. *cetinjensis*** (Rohlena) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Serratula radiata* var. *cetinjensis* Rohlena, Magyar Bot. Lapok 3: 321 (1904), *Serratula cetinjensis* (Rohlena) Teyber, Oesterr. Bot. Z. 62: 65 (1912), *Klasea cetinjensis* (Rohlena) Holub, Folia Geobot. Phytotax. 12: 305 (1977).
- 18d. ***Klasea radiata* ssp. *donetzica*** (Dubovik) L. Martins **comb. nov.**, basionym: *Serratula donetzica* Dubovik, Fl. RSS Ucr. 12: 560 (1965), *Klasea donetzica* (Dubovik) Holub, Preslia 70: 106 (1998).
- 18e. ***Klasea radiata* ssp. *gmelinii*** (Tausch) L. Martins **comb. nov.**, basionym: *Serratula gmelinii* Tausch, Flora 11: 485 (1828), *Klasea gmelinii* (Tausch) Holub, Folia Geobot. Phytotax. 12: 305 (1977). *Serratula isophylla* Claus, Beitr. Pflanzenk. Russ. Reiches 8: 118, 301 (1851).
- 18f. ***Klasea radiata* ssp. *tanaitica*** (P. Smirn.) L. Martins **comb. nov.**, basionym: *Serratula tanaitica* P. Smirn., Byull. Moskovsk. Obshch. Isp. Prir. Otd. Biol., n. s. 49: 92 (1940), *Klasea tanaitica* (P. Smirn.) Holub, Preslia 70: 106 (1998).
19. ***Klasea centauroides*** (L.) Cass. ex Kitag., Neo-Lineam. Fl. Manshur. 654 (1979), *Serratula centauroides* L., Sp. Pl. 820 (1753).
- Klasea ortholepis* (Kitag.) Kitag., J. Jap. Bot. 21: 139 (1947), *Serratula ortholepis* Kitag.
- Serratula hayatae* Nakai, Bot. Mag. (Tokyo) 25: 56 (1911), *Klasea hayatae* (Nakai) Kitag., J. Jap. Bot. 21: 140 (1947).
- Distribution*: China, North Korea, Mongolia, Russia (Fig. 5).
- A. Capitula 10–50, involucre 8–11 mm in diameter d ***K. centauroides* ssp. *polycephala***
- A*. Stem bearing 1–4(–12) capitula, but plant sometimes many-stemmed, involucre 11–25 mm in diameter.
- B. All leaves undivided e ***K. centauroides* ssp. *cupuliformis***
- B*. At least middle cauline leaves pinnatifid to pinnatisect.
- C. Involucre obconical, inner phyllaries straight, without clear distinction between basal part and scarious appendage, median phyllaries ±concolorous straw-coloured to light green c ***K. centauroides* ssp. *chanetii***
- C*. Involucre semiglobular to ovoid, inner phyllaries mostly geniculate between basal part and appendage, median phyllaries with dark tip and/or violet-pinkish scarious margins.
- D. Stem ±foliated throughout a ***K. centauroides* ssp. *centauroides***
- D*. Stem ±leafless in upper part.
- E. Leaves ±equal in shape, median phyllaries 1.5–2.2 mm wide b ***K. centauroides* ssp. *komarovii***
- E*. Basal leaves ±undivided, cauline leaves pinnatifid, median phyllaries 2.5–4 mm wide f ***K. centauroides* ssp. *strangulata***
- 19a. ***Klasea centauroides*** (L.) Cass. ex Kitag. **ssp. *centauroides***.
- Klasea mongolicola* (Kitag.) Kitag., J. Jap. Bot. 21: 139 (1947), *Serratula mongolicola* Kitag., Bot. Mag. (Tokyo) 48: 913 (1934), *Serratula yamatsutana* var. *mongolicola* (Kitag.) Kitag., Lineam. Fl. Mansh. 471 (1939).
- Klasea centauroides* var. *albiflora* Y. B. Chang, Bull. Bot. Res. North-East. Forest. Inst. 3(2): 158 (1983). *Serratula yamatsutana* Kitag., Bot. Mag. (Tokyo) 48: 911 (1934), *Klasea centauroides* var. *yamatsutana* (Kitag.) Kitag., Neo-Lineam. Fl. Manshur. 654 (1979).

Serratula pectinata Turcz. ex Herder, Bull. Soc. Imp. Naturalistes Moscou 43: 94 (1870).

Serratula hsinganensis Kitag., Bot. Mag. (Tokyo) 48: 916 (1934).

19b. *Klasea centauroides* ssp. *komarovii* (Iljin) L. Martins **comb. nov.**, basionym: *Serratula komarovii* Iljin, Izv. Glavn. Bot. Sada S.S.S.R. 27: 89 (1928), *Klasea komarovii* (Iljin) Kitag., J. Jap. Bot. 21: 139 (1947).

Serratula nishimurana Kitag., Bot. Mag. (Tokyo) 48: 913 (1934), *Klasea nishimurana* ('*nishimurae*') (Kitag.) Kitag., Neo-Lineam. Fl. Manshur. 655 (1979). *Serratula charbinensis* A. I. Baranov & Skvortsov, Quart. J. Taiwan Mus. 19: 164 (1966).

19c. *Klasea centauroides* ssp. *chanetii* (H. Lév.) L. Martins **comb. nov.**, basionym: *Serratula chanetii* H. Lév., Repert. Spec. Nov. Regni Veg. 10: 351 (1912).

Serratula potaninii Iljin, Izv. Glavn. Bot. Sada S.S.S.R. 27: 88 (1928), *Klasea potaninii* (Iljin) Kitag., J. Jap. Bot. 25: 40 (1950).

19d. *Klasea centauroides* ssp. *polycephala* (Iljin) L. Martins **comb. nov.**, basionym: *Serratula polycephala* Iljin, Izv. Glavn. Bot. Sada S.S.S.R. 27: 90 (1928), *Klasea polycephala* (Iljin) Kitag., J. Jap. Bot. 21: 140 (1947).

Serratula polycephala var. *leucantha* Kitag., Rep. First Sci. Exped. Manch. sect. 4, 4: 57, 97 (1936), *Klasea polycephala* f. *leucantha* (Kitag.) Kitag., J. Jap. Bot. 21: 140 (1947).

19e. *Klasea centauroides* ssp. *cupuliformis* (Nakai & Kitag.) L. Martins **comb. nov.**, basionym: *Serratula cupuliformis* Nakai & Kitag., Rep. Exped. Manchoukuo Sect. IV, Pt. 1, Pl. Nov. Jehol. 66 (1934), *Klasea cupuliformis* (Nakai & Kitag.) Kitag., J. Jap. Bot. 21: 139 (1947).

19f. *Klasea centauroides* ssp. *strangulata* (Iljin) L. Martins **comb. nov.**, basionym: *Serratula strangulata* Iljin, Izv. Glavn. Bot. Sada S.S.S.R. 27: 89 (1928), *Klasea strangulata* (Iljin) Kitag., J. Jap. Bot. 25: 40 (1950).

Klasea* sect. *Demetria (Boriss.) L. Martins **comb. nov.**, basionym: *Serratula* sect. *Demetria* Boriss., Fl. URSS 28: 607 (1963)

Typus sectionis: *Serratula caucasica* Boiss. (= *Klasea flavescens* ssp. *caucasica* (Boiss.) L. Martins).

Stems usually simple or sparingly branched, leaves with more or less conspicuous woolly indumentum along the veins, phyllaries usually not appressed, corolla usually purple or pink, sometimes yellow or cream.

20. *Klasea pinnatifida* (Cav.) Cass. ex Talavera in Valdés *et al.* Fl. Vascular de Andalucía Occ. 3: 164 (1987), *Carduus pinnatifidus* Cav., Icon. Descr. 1: 58, t.

83 (1791), *Serratula pinnatifida* (Cav.) Poir. in Lamarck, Encycl. Méth. Bot. 6: 561 (1805).

Serratula mairei Iljin, Repert. Spec. Nov. Regni Veg. 35: 354–355 (1934).

Centaurea barrelieri Dufour, Ann. gén. Sc. Phys. 7: 301–302 (1820), *Serratula barrelieri* (Dufour) Dufour, Ann. Sc. Nat. Ser. I. 23: 156 (1831), *Serratula pinnatifida* var. *barrelieri* (Dufour) Font Quer, In Memoriam do Professor D. A. X. Pereira Coutinho 2: 157 (1941).

Distribution: Algeria, Spain, Morocco, Portugal, Tunisia (Fig. 7).

21. *Klasea boetica* ('*boetica*') (Boiss. ex DC.) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Serratula boetica* Boiss. ex DC., Prodr. 7: 306 (1838).

Distribution: Algeria, Spain, Morocco, Portugal (Fig. 7).

A. Basal leaves lanceolate in outline, spine of median phyllaries 6–14 mm long.....

..... c *K. boetica* ssp. *lusitanica*
A*. Basal leaves elliptic, ovate or ovate-lanceolate in outline, spine of median phyllaries 3–7(–9) mm long.

B. Leaves elliptic, ovate or ovate-lanceolate, undivided, ±entire a *K. boetica* ssp. *boetica*

B*. Leaves ovate-lanceolate in outline, pinnatisect b *K. boetica* ssp. *alcalae*

21a. *Klasea boetica* ssp. *boetica*.

21b. *Klasea boetica* ssp. *alcalae* (Coss.) Cantó & Rivas Mart., Lazaroa 5: 319 (1983), *Serratula alcalae* Coss., Notes Pl. Crit. 2: 40 (1849), *Serratula boetica* ssp. *alcalae* (Coss.) Rouy, Ill. Pl. Eur. Rar. 5: 39, t. 119 (1896), *Klasea alcalae* (Coss.) Holub, Folia Geobot. Phytotax. 12: 305 (1977).

21c. *Klasea boetica* ssp. *lusitanica* (Cantó) Cantó & Rivas Mart., Lazaroa 5: 319 (1983), *Serratula boetica* ssp. *lusitanica* Cantó, Lazaroa 3: 385 (1981), *Klasea lusitanica* (Cantó) Holub, Preslia 70: 106 (1998).

Serratula boetica f. *sampaiana* Cantó, Lazaroa 6: 52 (1984), *Serratula boetica* var. *sampaiana* (Cantó) Cantó, Lagasalia 15 (Extra): 380 (1988).

22. *Klasea legionensis* (Lacaita) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Serratula legionensis* Lacaita, Cavanillesia 3: 37 (1930).

Distribution: Spain (Fig. 7).

23. *Klasea integrifolia* (Vahl) Greuter, Willdenowia 35: 235 (2005), *Cynara integrifolia* Vahl, Symb. Bot. 1: 68 (1790).

Serratula monardii Dufour, Ann. Sci. Nat. (Paris) 23: 155 (1831), *Jurinea monardii* (Dufour) DC., Prodr. 6: 677 (1838), *Klasea monardii* (Dufour) Holub, Folia Geobot. Phytotax. 18: 204 (1983).

Distribution: Spain, Portugal (Fig. 7).

A. Median phyllaries ovate or obovate, 3–6 mm wide
.....a ***K. integrifolia* ssp. *integrifolia***

A*. Median phyllaries narrowly triangular to ovate-triangular, 1.2–3 mm wide
.....
.....b ***K. integrifolia* ssp. *algarbiensis***

23a. ***Klasea integrifolia* ssp. *integrifolia***.

Serratula pauana ('*paueana*') Iljin, Repert. Spec. Nov. Regni Veg. 35: 354 (1934), *Klasea pauana* (Iljin) Holub, Folia Geobot. Phytotax. 12: 305 (1977).

Serratula abulensis Pau, Bol. Soc. Espan. Hist. Nat. 21: 150 (1921), *Klasea abulensis* (Pau) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Serratula monardii* f. *abulensis* (Pau) Cantó, Lazaroa 6: 56 (1984).

Serratula pinnatifida var. *glabrata* Pérez Lara, Anal. Real Soc. Esp. Hist. Nat. 16: 342 (1887).

23b. ***Klasea integrifolia* ssp. *algarbiensis*** (Cantó) Greuter, Willdenowia 35: 235 (2005), *Serratula monardii* var. *algarbiensis* Cantó, Lazaroa 6: 60 (1984), *Klasea monardii* ssp. *algarbiensis* (Cantó) Greuter & Wagenitz, Willdenowia 33: 59 (2003).

Klasea integrifolia ssp. *algarbiensis* is morphologically intermediate between *K. boetica* ssp. *lusitanica* and *K. integrifolia* ssp. *integrifolia* and occurs in southern Portugal where their ranges overlap. It is therefore likely to be a hybrid between these two taxa.

24. ***Klasea flavescens*** (L.) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Carduus flavescens* L., Sp. Pl. 825 (1753), *Serratula flavescens* (L.) Poir. in Lam., Encyc. Méth. Bot. 6: 562 (1805).

Distribution: Algeria, Azerbaijan, Spain, Italy, Morocco, Portugal, Russia, Tunisia (Fig. 7).

A. Flowers yellow or cream.

B. Median phyllaries gradually tapering into apical spine, spine straight or patent
.....a ***K. flavescens* ssp. *flavescens***

B*. Median phyllaries abruptly constricted into apical spine, spine \pm deflexed
.....
.....b ***K. flavescens* ssp. *leucantha***

A*. Flowers pink to purple.

C. Leaf bases not or very slightly decurrent
.....c ***K. flavescens* ssp. *mucronata***

C*. Leaf bases clearly decurrent.

D. Median phyllaries 1.8–3 mm wide, their apical spine 4–7(–8) mm long
.....d ***K. flavescens* ssp. *cichoracea***

D*. Median phyllaries 3–4 mm wide, their apical spine 7–10 mm long
.....e ***K. flavescens* ssp. *caucasica***

24a. ***Klasea flavescens* ssp. *flavescens***.

24b. ***Klasea flavescens* ssp. *leucantha*** (Cav.) Cantó & Rivas Mart., Lazaroa 5: 319 (1983), *Carduus leucanthus* Cav., Icon. Descr. 2: 52, t. 165 (1793), *Serratula leucantha* (Cav.) DC., Prodr. 6: 670 (1838), *Klasea leucantha* (Cav.) Holub, Folia Geobot. Phytotax. 12:

305 (1977), *Serratula flavescens* ssp. *leucantha* (Cav.) Cantó & Costa, Lazaroa 3: 193 (1981).

Serratula neglecta Iljin, Repert. Spec. Nov. Regni Veg. 35: 353 (1934), *Klasea flavescens* var. *neglecta* (Iljin) Cantó & Rivas Mart., Lazaroa 5: 319 (1983), *Serratula flavescens* var. *neglecta* (Iljin) Cantó, Lazaroa 6: 73 (1984), *Klasea flavescens* ssp. *neglecta* (Iljin) Greuter & Wagenitz, Willdenowia 33: 59 (2003).

24c. ***Klasea flavescens* ssp. *mucronata*** (Desf.) Cantó & Rivas Mart., Lazaroa 5: 319 (1983), *Serratula mucronata* Desf., Fl. Atlant. 2: 243, t. 219 (1800), *Klasea mucronata* (Desf.) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Serratula flavescens* ssp. *mucronata* (Desf.) Cantó, Lazaroa 3: 193 (1984).

24d. ***Klasea flavescens* ssp. *cichoracea*** (L.) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Centaurea cichoracea* L., Sp. Pl. 2: 1299 (1763), *Klasea cichoracea* (L.) Webb, Iter Hisp. 34 (1838).

24e. ***Klasea flavescens* ssp. *caucasica*** (Boiss.) L. Martins **comb. nov.**, basionym: *Serratula caucasica* Boiss., Fl. Orient. 3: 590 (1875), *Klasea caucasica* (Boiss.) Greuter, Willdenowia 35: 235 (2005).

25. ***Klasea khuzistanica*** (Mozaff.) Mozaff., Ann. Bot. (Oxford) 97: 714 (2006), *Centaurea khuzistanica* Mozaff., Iranian J. Bot. 5(2): 84 (1992), *Serratula khuzistanica* (Mozaff.) Mozaff., Bot. J. Linnean Soc. 128: 420 (1998).

Distribution: Iran (Fig. 7).

26. ***Klasea oligocephala*** (DC.) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Serratula oligocephala* DC., Prodr. 6: 669 (1838).

Distribution: Iraq, Iran, Turkey (Fig. 7).

27. ***Klasea pusilla*** (Labill.) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Cynara pusilla* Labill., Icon. Pl. Syr. 3: 11, pl. 7 (1809), *Leuzea pusilla* (Labill.) Spreng., Syst. Veg., ed. 16, 3: 382 (1826), *Rhaponticum pusillum* (Labill.) Boiss., Fl. Orient. 3: 592 (1875), *Serratula pusilla* (Labill.) Dittrich, Candollea 36: 350 (1981).

Rhaponticum pygmaeum DC., Prodr. 6: 665 (1838), *Centaurea pygmaea* (DC.) Benth. in Bentham & Hooker, Gen. Pl. 2: 482 (1873).

Distribution: Israel and Palestinian territories, Jordan, Lebanon, Syria (Fig. 7).

Intersectional hybrid

28. ***Klasea* \times *mouterdei*** (Arènes) Greuter & Wagenitz, Willdenowia 33: 59 (2003) (*K. pusilla* \times *K. cerinthifolia*), \times *Centaurea serratula mouterdei* Arènes, Notul. Syst. Herb. Paris 14: 188 (1952), *Serratula mouterdei* (Arènes) Dittrich, Candollea 36: 359 (1981).

Centaurea serratula mouterdei was described as an intergeneric hybrid between *Serratula cerinthifolia* (= *K. cerinthifolia*) and *Centaurea pygmaea* (= *K. pusilla*). Dittrich (1981) was not able to either confirm or reject the hypothesis of a hybrid origin of this species based on morphological and anatomical characters.

Distribution: Lebanon (Fig. 8).

Klasea* sect. *Schumeria (Iljin) L. Martins **comb. et stat. nov.**, basionym: *Schumeria* Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 363 (1960)

Microlophopsis Czerep., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 488 (1960)

Typus sectionis: *Klasea cerinthifolia* (Sm.) Greuter & Wagenitz.

Leaves or leaflets usually entire, upper cauline leaves decurrent or amplexicaul, corolla usually yellow, rarely pink, narrow part of corolla tube usually longer than half the total corolla length, apical anther appendages rounded.

29. ***Klasea cerinthifolia*** (Sm.) Greuter & Wagenitz, Willdenowia 33: 58 (2003), *Centaurea cerinthifolia* Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 2: 197 (1813), *Serratula cerinthifolia* (Sm.) Boiss., Fl. Orient. 3: 585 (1875), *Schumeria cerinthifolia* (Sm.) Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 363 (1960) comb. inval.

Serratula cordata Cass., Dict. Sci. Nat. 50: 468 (1827).

Distribution: Cyprus, Israel and Palestinian territories, Iraq, Iran, Lebanon, Syria, Turkey (Fig. 8).

30. ***Klasea latifolia*** (Boiss.) L. Martins, Taxon 54: 636 (2005), *Serratula latifolia* Boiss., Diagn. Pl. Orient., ser. 1, 10: 96 (1849), *Schumeria latifolia* (Boiss.) Iljin, Not. Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 364 (1960) comb. inval.

Serratula litwinowii Iljin, Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 5: 112 (1924), *Schumeria litwinowii* (Iljin) Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 364 (1960) comb. inval.

Centaurea plumosa Aitch. & Hemsl., Trans. Linn. Soc. Ser. 2, 3: 81 (1888) non A. Kern., *Microlophopsis plumosa* (Aitch. & Hemsl.) Czerep., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 488 (1960).

Distribution: Afghanistan, Iran, Turkmenistan (Fig. 8).

31. ***Klasea suffulta*** (Rech. f.) L. Martins **comb. nov.**, basionym: *Serratula suffulta* Rech. f., Fl. Iran. 139b: 292 (1980).

Distribution: Iran (Fig. 8).

32. ***Klasea gracillima*** (Rech. f.) L. Martins **comb. nov.**, basionym: *Serratula gracillima* Rech. f., Fl. Iran. 139b: 291 (1980).

Distribution: Iran (Fig. 8).

33. ***Klasea viciifolia*** (Boiss. & Hausskn.) L. Martins **comb. nov.**, basionym: *Serratula viciifolia* ('*viciaefolia*') Boiss. & Hausskn. in Boissier, Fl. Orient. 3: 586 (1875), *Schumeria viciifolia* (Boiss. & Hausskn.) Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 364 (1960) comb. inval.

Distribution: Iran (Fig. 8).

34. ***Klasea kurdica*** (Post) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Serratula kurdica* Post, Pl. Post. 4: 8 (1892).

Distribution: Syria, Turkey (Fig. 8).

35. ***Klasea cretica*** (Turrill) Holub, Folia Geobot. Phytotax. 12: 305 (1977), *Serratula cichoracea* (L.) DC. ssp. *cretica* Turrill, Kew Bull. 12: 391 (1958), *Klasea flavescens* ssp. *cretica* (Turrill) Greuter & Wagenitz, Willdenowia 33: 59 (2003).

Distribution: Greece, Libya (Fig. 8).

Klasea* sect. *Leuzeopsis (Boriss.) L. Martins **comb. nov.**, basionym: *Serratula* sect. *Leuzeopsis* Boriss., Fl. URSS 28: 607 (1963)

Typus sectionis: *Klasea serratuloides* (DC.) Greuter & Wagenitz.

Stems usually short, simple, leaves coriaceous, capitula large (3–4 cm in diameter), phyllaries with a long bent-down mucro, apical anther appendages rounded or slightly emarginate.

36. ***Klasea serratuloides*** (DC.) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Leuzea serratuloides* DC., Prodr. 6: 666 (1838), *Serratula serratuloides* (DC.) Takht., Trudy Armyansk. Fil. Akad. Nauk S.S.S.R., Ser. Biol. 2: 90 (1937).

Phaeopappus freynii Sint. ex Freyn, Oesterr. Bot. Z. 42: 235 (1892).

Distribution: Armenia, Azerbaijan, Iran, Turkey (Fig. 8).

Klasea* sect. *Nikitinia (Iljin) L. Martins **comb. et stat. nov.**, basionym: *Nikitinia* Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 356 (1960)

Typus sectionis: *Klasea leptoclada* (Bornm. & Sint.) L. Martins.

Stems virgately branched, leaves small, linear, involucre narrowly cylindrical to funnel-shaped, detachment area of achenes basal or sub-basal.

37. *Klasea leptoclada* (Bornm. & Sint.) L. Martins, Taxon 54: 636 (2005), *Jurinea leptoclada* Bornm. & Sint. Russk. Bot Zhurn. 1911: 5 (1911), *Nikitinia leptoclada* (Bornm. & Sint.) Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 356 (1960). *Distribution*: Iran, Turkmenistan (Fig. 9).

***Klasea* sect. *Coriaceae* L. Martins sect. nov.**
(= *Serratula* ser. *Coriaceae* Boriss., nom. inval., ICBN art. 36.1 (Greuter et al., 2000)).

Caulis superne virgato-ramosus, folia inferiora magna, pinnatisecta, folia superiora valde diminuta, linearia, folia omnia glabra. Involucris basi attenuati, involucris phylla mucronulata mucrone brevi ad 1 mm longa aut sine mucrone. Antherarum appendices apicales ensiformes.

Typus sectionis: *Klasea coriacea* (Fisch. & C. A. Mey. ex DC.) Holub.

Stems branched in upper part, leaves glabrous, lower cauline leaves large, pinnatisect, lateral leaf segments with three prominent veins arising from the rhachis, upper cauline leaves much diminished, linear, involucre attenuate at base, apical anther appendages sword-shaped.

38. *Klasea coriacea* (Fisch. & C. A. Mey. ex DC.) Holub, Folia Geobot. Phytotax. 12: 427 (1977), *Serratula coriacea* Fisch. & C. A. Mey. ex DC., Prodr. 6: 668 (1838).

Distribution: Armenia, Azerbaijan, Iran, Turkey (Fig. 9).

***Klasea* sect. *Lasiocephalae* L. Martins sect. nov.**
Herbae humiles vel subcaules, pedunculi aphylli vel subaphylli, axillaria aut basalia, involucris phylla lanata, apicem vs. brunnea-atrata, corolla brevis (ad 11 mm longa), antherarum tubus brevis (ad 4 mm longus), antherarum appendicibus triangularibus vel acuminatis.

Typus sectionis: *Klasea lasiocephala* (Bornm.) Greuter & Wagenitz.

Stems short, peduncles usually leafless, emerging from leaf axils of basal or cauline leaves, phyllaries rather soft, dark at apex, covered with soft long hairs, in 4–5 series, corolla short (7–11 mm), filaments covered with very short papillae (3–5% of the width of the filaments).

39. *Klasea lasiocephala* (Bornm.) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Serratula lasiocephala* Bornm., Repert. Spec. Nov. Regni Veg. 5: 167 (1908).

Distribution: Turkey (Fig. 9).

40. *Klasea bornmuelleri* (Azn.) Greuter & Wagenitz, Willdenowia 33: 58 (2003), *Serratula bornmuelleri*

Azn., Repert. Spec. Nov. Regni Veg. 11: 397 (1912), *Schumeria bornmuelleri* (Azn.) Iljin, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 364 (1960) comb. inval.

Distribution: Turkey (Fig. 9).

***Klasea* sect. *Quinquefoliae* L. Martins sect. nov.**
(= *Serratula* ser. *Quinquefoliae* Boriss. nom. inval., ICBN art. 36.1 (Greuter et al., 2000))

Caulis ramosus, folia praeter superiores pinnata aut ternata, hypostomatica. Involucris phylla interiora purpurea. Filamenta papillosa papillis usque ad dimidium latitudinis filamentorum longis. Antherarum appendices apicales acutae.

Typus sectionis: *Klasea quinquefolia* (M. Bieb. ex Willd.) Cass. ex Greuter & Wagenitz.

Stems branched in upper part, leaves compound 3- or 5-foliolate, hypostomatic, inner phyllaries and pappus bristles tinged with purple in fresh condition, filaments covered with long papillae (reaching half the width of the filaments), apical anther appendages acute.

41. *Klasea quinquefolia* (M. Bieb. ex Willd.) Cass. ex Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Serratula quinquefolia* M. Bieb. ex Willd., Sp. Pl. 3: 1639 (1803).

Distribution: Armenia, Azerbaijan, Georgia, Iran, Russia, Turkey (Fig. 9).

***Klasea* sect. *Melanolepis* L. Martins sect. nov.**
Herbae mono- vel oligocephalae. Folia glabra aut solum margine breviter ciliata. Involucris phylla exteriora et media apice atrata. Antherarum appendices apicales anguste-triangularares.

Typus sectionis: *Klasea kotschyi* (Boiss.) Greuter & Wagenitz.

Stems simple or sparingly branched, leaves glabrous, phyllaries black at apex, apical anther appendages narrowly triangular.

42. *Klasea kotschyi* (Boiss.) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Serratula kotschyi* Boiss., Fl. Orient. 3: 590 (1875).

Distribution: Turkey (Fig. 9).

43. *Klasea hakkiarica* (P. H. Davis) Greuter & Wagenitz, Willdenowia 33: 59 (2003), *Serratula hakkiarica* P. H. Davis, Fl. Turkey 10: 235 (1988).

Distribution: Turkey (Fig. 9).

44. *Klasea melanocheila* (Boiss. & Hausskn.) Holub, Folia Geobot. Phytotax. 12: 427 (1977), *Serratula melanocheila* Boiss. & Hausskn. in Boissier, Fl. Orient. 3: 589 (1875).

Distribution: Iran (Fig. 9).

***Klasea* sect. *Grandifoliae* L. Martins sect. nov.**
Herbae superne ramosissimae polycephalae, involu-
cra ovoidea vel campanulata, antherarum appendices
apicales attenuatae obtusiusculae.

Typus sectionis: Klasea grandifolia (P. H. Davis)
Greuter & Wagenitz.

Lower cauline leaves very large (= 10 × 20 cm),
stems richly branched above, capitula in dense
corymbs, involucre ovoid to campanulate.

45. ***Klasea grandifolia*** (P. H. Davis) Greuter &
Wagenitz, *Willdenowia* 33: 59 (2003), *Serratula gran-*
difolia P. H. Davis, *Notes Roy. Bot. Gard. Edinburgh*,
33: 293 (1974).

Distribution: Iraq, Turkey (Fig. 9).

46. ***Klasea aznavouriana*** (Bornm.) Greuter &
Wagenitz, *Willdenowia* 33: 58 (2003), *Serratula*
aznavouriana Bornm., *Bull. Herb. Boissier*, ser. 2, 6:
233–234 (1906).

Distribution: Turkey (Fig. 9).

Species excludendae

Klasea chinensis (S. Moore) Kitag. = ***Rhaponticum***
chinense (S. Moore) L. Martins & Hidalgo, **comb.**
nov., basionym: *Serratula chinensis* S. Moore, *J. Bot.*
13: 228 (1875).

Klasea insularis (Iljin) Holub = *Serratula coronata*
L. var. *insularis* (Iljin) Kitam.

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APPENDIX

VOUCHER DATA AND GENBANK ACCESSION NUMBERS OF THE TAXA INCLUDED IN THE MOLECULAR PHYLOGENETIC ANALYSIS

- Klasea aphyllopoda* (Ijlin) Holub, Kyrgyzstan: Dzhahalal-Abad oblast, 1 km E Tash-Kömür, 13.vii.2003, L. Martins 874 (JE), AJ868003, AJ868004, AJ868005.
- Klasea aznavouriana* (Bornm.) Greuter & Wagenitz, Turkey: prov. Amasya, Merzifon 1905, *Manissadjan s.n.* (G), AM117916.
- Klasea boetica* ssp. *alcalae* (Coss.) Cantó & Rivas Mart., Spain: prov. Cádiz, Los Barrios, Monte de Bolafuegos, 7.v.1980, P. Cantó & P. Cubas s.n. (JE), AJ868006, AJ868007, AJ868008.
- Klasea boetica* (Boiss. ex DC.) Holub ssp. *boetica*, Spain: prov. Málaga: Carratraca, 19.vi.1981, P. Cantó & S. Laorga s.n. (JE), AM117845, AM117846, AM117847.
- Klasea centauroides* (L.) Cass. ex Kitag. ssp. *centauroides*, China: Inner Mongolia, Argun river, 2.ix.1935, G. Fochler-Hauke s.n. (M), AJ868009, AJ868010, AJ868011.
- Klasea centauroides* ssp. *cupuliformis* (Nakai & Kitag.) L. Martins, cult. in Bot. Garden Göteborg, *H. Smith II.151* (W), AJ868018, AJ868019, AJ868020.

Klasea cerinthifolia (Sm.) Greuter & Wagenitz, Turkey: prov. Tunceli, 3 km S Tunceli, 20.vii.1973, *F. Holtz et al.* 735 (GOET), AJ868012, AJ868013, AJ868014.

Klasea chartacea (C. Winkl.) L. Martins, Tajikistan: Badakhshan, valley of Vanch river, Bukai ravine, 13.vii.1962, *S. S. Ikonikov* 13698 (LE), AJ868015, AJ868016, AJ868017.

Klasea coriacea (Fisch. & C. A. Mey. ex DC.) Holub, Turkey: prov. Kars, between Kagizman and Akcay, 19.vii.1966, *P. H. Davis* 46851 (E), AM117881, AM117882, AM117883.

Klasea cretica (Turrill) Holub, Greece: Crete, Ep. Sitia, above Mirsini, 29.x.1966, *W. Greuter* 7814 (W), AM117902, AM117903, AM117904.

Klasea dissecta (Ledeb.) L. Martins, Kazakhstan: Eastern Balkhash area, Arkharly mountains, 28.v.1976, *V. P. Bochantsev & V. V. Bochantsev* 979 (LE), AM117875, AM117876, AM117877.

Klasea erucifolia (L.) Greuter & Wagenitz, Turkey: prov. Erzurum, Ağrı – Horasan, 1.viii.1984, *M. Nydegger* 19548 (FR), AJ920388, AJ920389, AJ920390.

Klasea flavescens ssp. *cichoracea* (L.) Greuter & Wagenitz, Italy: Toscana, Monte Argentario, 18.vi.1987, *J. Grau & E. Beyer s.n.* (M), AJ868024, AJ868025, AJ868026.

Klasea flavescens ssp. *leucantha* (Cav.) Cantó & Rivas Mart., Spain: Sierra de Mijas, *E. Rothe* 1618 (JE), AM117839, AM117840, AM117841.

Klasea flavescens ssp. *mucronata* (Desf.) Cantó & Rivas Mart., Spain: prov. Murcia, Pena de Aguilar, 2–3 km E Portman, 20.v.1983, *E. Bayer, J. Grau & G. Lopez s.n.* (M), AM117851, AM117852, AM117853.

Klasea grandifolia (P. H. Davis) Greuter & Wagenitz, Turkey: C3/4 Konya, Seydisehir – Gölyüzü, Koyü arası, 29.vi.1981, *H. Ocakverdi* 648 (E), AM117896, AM117897, AM117898.

Klasea hastifolia (Korovin & Kult. ex Iljin) L. Martins, Kyrgyzstan: Talas oblast, Kara-Koyun valley, 17.vii.2003, *G. Laz'kov & N. Kenzhebaeva s.n.* (JE), AM117911, AM117912, AM117913.

Klasea integrifolia (Vahl) Greuter ssp. *integrifolia*, Spain: prov. Huelva, Hinojos, 18.vi.1980, *P. Cantó & C. Navarro s.n.* (JE), AM117848, AM117849, AM117850.

Klasea khuzistanica (Mozaff.) Mozaff., Iran: Khuzistan, Dezful to Shahion, after Bishebozan, Bazargah, 19.iv.1990, *V. Mozaffarian* 70181 (IRAN), AM117860, AM117861, AM117862.

Klasea kotschyi (Boiss.) Greuter & Wagenitz, Turkey: prov. Bitlis, Karz Dag above Kamer, 24.viii.1954, *P. H. Davis & O. Polunin* 24563 (E), AM117899, AM117900, AM117901.

Klasea lasiocephala (Bornm.) Greuter & Wagenitz, Turkey: prov. Antalya, Gazipaşa, Çayır yakası yaylasi, 23.vi.1984, *Sümbül* 3055 (E), AM117914, AM117915.

Klasea latifolia (Boiss.) L. Martins, Turkmenistan: Ashkhabad, 30 km S Kaachka, Archin'yan ravine, 4.v.1963, *I. A. Gubanov* 173 (LE), AJ868027, AJ868028, AJ868029.

Klasea latifolia (Boiss.) L. Martins ('*Schumeria litwinowii*'), Turkmenistan: Central Kopet Dag, Prokhladnoe, 21.vi.1953, *T. Nadkina s.n.* (LE), AM117905, AM117906, AM117907.

Klasea legionensis (Lacaita) Holub, Spain: prov. Zamora, Valle de Samabria, Ribadelago, 10.viii.1979, *Cantó et al. s.n.* (JE), AM117842, AM117843, AM117844.

Klasea leptoclada (Bornm. & Sint.) L. Martins, Turkmenistan: Ashkhabad, Suluklü (Saratovka), vii.1900, *P. Sintenis* 694 (JE), AJ868030, AJ868031, AJ868032.

Klasea lycopifolia (Vill.) A. Löve & D. Löve, Slovenia: Istria, above Rakitovec, 9.vii.1951, *E. Mayer s.n.* (M), AM117890, AM117891, AM117892.

Klasea lyratifolia (Schrenk) L. Martins, Kyrgyzstan: Ysyk-Köl oblast, Chon-Ak-Suu valley, 25.vii.2003, *L. Martins* 979 (JE), AJ868033, AJ868034, AJ868035.

Klasea marginata (Tausch) Kitag., Kyrgyzstan: Ysyk-Köl oblast, Chon-Ak-Suu valley, 25.vii.2003, *L. Martins* 983 (JE), AM117872, AM117873, AM117874.

Klasea nudicaulis (L.) Fourr. [1], France: Hautes-Alpes, Pic de Gleize, 27.vii.1990, *J. Müller* 5799 (JE), AM117866, AM117867, AM117868.

Klasea nudicaulis (L.) Fourr. [2], Spain: prov. Granada, Sierra de Baza, *E. Rothe* 1647 (JE), AJ868036, AJ868037, AJ868038.

Klasea oligocephala (DC.) Greuter & Wagenitz, Turkey: prov. Tunceli, Munzur dag, above Ovacik, 16.vii.1957, *P. H. Davis & I. C. Hedge* 3116 7 (GOET), AM117887, AM117888, AM117889.

Klasea pallida (DC.) Holub, Pakistan: W-Himalaya, below Shogran, 12.v.1990, *U. Schickhoff* 290 (GOET), AM117893, AM117894, AM117895.

Klasea pinnatifida (Cav.) Cass. ex Talavera [1], Spain: prov. Toledo, between Ocana and Manzenares, 5 km N La Guardia, 4.vi.1973, *D. Podlech & Lippert* 2496 8 (M), AM117857, AM117858, AM117859.

Klasea pinnatifida (Cav.) Cass. ex Talavera [2], Spain: Valle de Abol, *E. Rothe* 1624 (JE), AM117854, AM117855, AM117856.

Klasea procumbens (Regel) Holub, China: Xinjiang, between Pirali and Taxkorgan, 20.vii.1991, *G. Miede & S. Miede* 5224 (GOET), AM117878, AM117879, AM117880.

Klasea pusilla (Labill.) Greuter & Wagenitz, Israel: Judean mountains, 14.iv.1987, *C. Holzappel s.n.* (GOET), AM117884, AM117885, AM117886.

Klasea quinquefolia (M. Bieb. ex Willd.) Cass. ex Greuter & Wagenitz [1], Iran: prov. Mazandaran,

Haraz valley, near Karehsang, 26.ix.1974, *Hedge et al.* 14714 (E), AM117863, AM117864, AM117865.

Klasea quinquefolia (M. Bieb. ex Willd.) Cass. ex Greuter & Wagenitz [2], cult. in Botanical Garden Monaco, 9.viii.1888, *Kreuzpointner* 22282 (M), AJ868042, AJ868043, AJ868044.

Klasea radiata (Waldst. & Kit.) A. Löve & D. Löve ssp. *radiata*, cult. in Botanical Garden Jena 2002, *L. Martins* 1029 (JE), AM117869, AM117870, AM117871.

Klasea serratuloides (DC.) Greuter & Wagenitz, Armenia (?): 4.viii.1954, *S. Tamamshyan & Denisova s.n.* (LE), AJ920391, AJ920392, AJ920393.

Klasea sogdiana (Bunge) L. Martins, Kyrgyzstan, Talas oblast, Kara-Koyun valley, 17.vii.2003, *L. Martins* 911 (JE), AM117908, AM117909, AM117910.

Klasea suffruticulosa (Schrenk) L. Martins, Kyrgyzstan: Chui oblast/Ysyk-Köl oblast, Chu valley (Boom ravine) between Kemin and Balykchy,

19.vii.2003, *L. Martins* 931 (JE), AJ868048, AJ868049, AJ868050.

Outgroup

Acroptilon repens (L.) DC., Kyrgyzstan: Dzhahalal-Abad oblast, valley of Beke-Chal river, 12.vii.2003, *L. Martins* 870 (JE), AJ867982, AJ867983, AJ867984.

Centaurea rigida Banks & Sol., Turkey: prov. Mardin, 50 km W Cizre, 28.v.1983, *F. Sorger* 83-10-2 (W), AJ867988, AJ867989, AJ867990.

Leuzea conifera (L.) DC., France: Alpes-Maritimes, Le Castel Gineste N Utelle, 6.vi.1999, *C. Renker & A. Beyer* 348 (JE), AJ868051, AJ868052, AJ868053.

Saussurea riederi Herder, cult. in Botanical Garden Göttingen ex sem. BG Uppsala: Japan, Hokkaido, AJ868069, AJ868070, AJ868071.

Serratula tinctoria L. ssp. *tinctoria*, Spain: prov. Cantabria, Armuero, 6.viii.1981, *O. Sánchez-Mata s.n.* (JE), AJ868084, AJ868085, AJ868086.