

Microsatellite variation, sexual reproduction and taxonomic revision of *Taraxacum* sect. *Dioszegia*: relationships at a large spatial scale

Mikrosatelitová variabilita, pohlavní rozmnožování a taxonomie *Taraxacum* sect. *Dioszegia*: vztahy na velké prostorové škále

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The coexistence of agamospermy and sexuality characterizes most of the ~60 sections of the genus *Taraxacum*. Section *Dioszegia*, comprising *T. serotinum* and its allies, are an exception because only sexuals are reported for all the members of this group. On the basis of the analysis of microsatellite (SSRs) variation, distribution and morphology, we addressed problems related to their mode of reproduction, among-population relationships, taxonomy and within-population variation, using samples from populations in an area extending from southern France to the European part of southern Russia and Iran. We found strong isolation by distance and deep spatio-temporal structure among populations. As a rule, outcrossing was the dominant mode of reproduction, with one notable exception: *T. serotinum* subsp. *tomentosum* (\equiv *T. pyrropappum*) was autogamous and not heterozygous. This subspecies is understood as a relic of a continental migration of *T. serotinum* in the late glacial/early post-glacial period, which became autogamous. *Taraxacum haussknechtii* is relatively highly heterozygous with a high degree of connectivity among populations, whereas populations of *T. serotinum* subsp. *serotinum* show high level of inter-population variability. A taxonomic revision of sect. *Dioszegia* recognizes *T. serotinum* subsp. *serotinum* (including an aberrant taxon, newly described as var. *iranicum*), *T. serotinum* subsp. *tomentosum* and *T. haussknechtii*. Full synonymy was compiled and lectotypes designated for six names. A list of the herbarium material studied is given for the latter three taxa, and a distribution map is provided for *T. haussknechtii*.

Key words: autogamy, Europe, Iran, isolation by distance, microsatellites, population variation, reproduction, *Taraxacum*, taxonomy

Introduction

The genus *Taraxacum* (*Asteraceae-Cichorieae-Crepidinae*), with about 60 sections and about 2,800 species, is generally considered to be a complicated example of a genus with coexisting agamospermy and sexuality, as summarized by Kirschner et al. (2003) and Štěpánek & Kirschner (2012). The problematic features are (i) mutual structural similarity, (ii) agamospermy and common coexistence of agamosperms with sexuals, (iii) hybridity and (iv) polyploidy (except for three tetraploid sexual species in the sect. *Piesis*, all known polyploid taxa are agamospermous). In particular, the repeated ancient or recent hybridization events are common in the evolutionary history of the majority of taxa.

While there are about 10 sections for which sexuality is not recorded, in the majority of the sections both agamospermy and sexuality are recorded, with common geographical parthenogenesis (Hörandl 2006). If we disregard monotypic sections with a single sexual species, such as sect. *Antarctica* (*T. gilliesii*), sect. *Biennia* (*T. nutans*) and sect. *Glacialia* (*T. glaciale*), there are only four sections in which all the members reproduce sexually: the Southern Hemisphere sect. *Australasica* and the three Northern Hemisphere sections, sects. *Primigenia*, *Dioszegia* and *Piesis* (Kirschner et al. 1994, Kirschner & Štěpánek 1998).

Plants belonging to the section *Dioszegia* (Heuffel) Heuffel are characteristically diploid and sexual (Doll 1975, Krahulcová 1993). They are perennial hemicryptophytes growing in well drained deep soils. Morphologically, this section is characterized by linear-lanceolate, imbricate (and apically arcuate) outer bracts, large subturbinate achenes very gradually narrowing into a subcylindrical to cylindrical cone, subcoriaceous leaves with hairs often growing on small ridges on the leaf surface and summer or late summer flowering. There are three geographical groups of populations usually recognized as separate species, sometimes subspecies, under the names *T. serotinum* (Waldst. et Kit.) Fischer, *T. pyrrhopappum* Boiss. et Reuter and *T. haussknechtii* Uechtr. While populations called *T. pyrrhopappum* and *T. haussknechtii* are restricted to relatively small areas, the former in southern France, Spain and northernmost Morocco, the latter in the Republic of Macedonia and adjacent regions in Albania, Greece and Bulgaria, *T. serotinum* has one of the largest distribution ranges in the genus, extending from the Czech Republic and Austria in the west through southern Ukraine and southern Russia to northern Kazakhstan and the westernmost part of Siberia (cf. Tzvelev 1989) in the north-west, and through Anatolia and Caucasus to Afghanistan in the south and south-east. The taxonomic positions of plants from Afghanistan remain to be determined. Its distribution overlaps that of *T. haussknechtii* (while it is allopatric with *T. pyrrhopappum*).

Gustafsson (1932) was the first to experimentally investigate sexuality in *T. serotinum* by castrating about 30 inflorescence at the bud stage and studying chromosome pairing during meiosis. His results were added to the text during proof reading in the form of the following footnote, which clearly documents sexuality in this species: “Nachdem Vorstehendes geschrieben war, habe ich Gelegenheit gehabt, Kastrationen in großem Massstabe (ungefähr 30 Körbe) von der obenerwähnten diploiden Art *T. serotinum* auszuführen, und es hat sich herausgestellt, dass sie wie erwartet sexuell war; auch waren bei der heterotypischen Metaphase 8 Doppelchromosomen zu sehen.”

Sexual reproduction and the diploid chromosome number of $2n = 16$ were confirmed by a study of new material by Poddubnaja-Arnoldi & Dianowa (1934). As for the possibility of the occurrence of spontaneous hybrids between *T. serotinum* and other diploids of different sections, sterile hybrids between *T. koksaghyz* and *T. serotinum* are recorded (Poddubnaja-Arnoldi 1939). These geographical entities share a diploid chromosome number ($2n = 16$, recently confirmed, e.g. by Krahulcová (1993) for *T. serotinum* and *T. haussknechtii*, and by Galán de Mera (2010) for *T. pyrrhopappum*), regular sized pollen grains, which is an important indicator of sexuality in *Taraxacum* (Nijs et al. 1990) and the failure to produce progeny when the flower heads are emasculated and absence of matrocliny, i.e. their progeny vary and differ considerably from the maternal plant (in agamospermous *Taraxacum*, the offspring are very similar morphologically whereas those produced by sexual reproduction a very different).

Data and material collected for the section *Dioszegia* is to be used for a more detailed revision. In particular, the extent of the genetic differentiation among its members, the reproduction as a basis for the differentiation and variation across large areas occupied by this section are to be evaluated. A nomenclatural and taxonomic survey of the section logically follows the biosystematical analyses.

The following aspects of the intrasectional variation are dealt with in the present paper: (i) modes of reproduction recorded for this section (autogamy versus allogamy); (ii) the extent and character of the variation in populations and groups of populations; (iii) macrogeographical dimension of the genetic variation in *T. serotinum* subsp. *serotinum*; (iv) interspecific relationships within sect. *Dioszegia* based on microsatellite (SSRs) population data compared with the traditional classification; and (v) taxonomic revision of the section, typification of names and detailed morphological descriptions of all intraspecific taxa. Another aspect, not dealt with in the present paper, is the role of sect. *Dioszegia* as a parental group for the derived hybridogenous sections with agamosperous reproduction. This role is documented for sect. *Borysthenica* (Kirschner & Štěpánek 2004), but currently is not supported by molecular evidence.

Material and methods

Plant material

We sampled the whole section aiming at a reasonable geographical coverage and including all the morphological variants of all taxonomic entities. Altogether, 115 plants from 20 localities were included in the analysis of SSRs, and each taxon (except *T. serotinum* var. *iranicum*) is represented by at least one sample bigger than six plants (the largest sample is 26 plants; see Table 1 for the samples used in the SSRs analysis). The geographical locations of where the samples were collected is displayed in Fig. 1. The samples, except the largest sample of 26 plants of *T. serotinum*, collected in the field, are the progenies of random field samples of achenes grown in cultivation at Experimental Garden of the Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic (49°59'41" N, 14°34'01" E, 318 m a.s.l.). Specimens used for morphological comparison are listed in the Appendix 1.

Documentation and sources of information

Voucher specimens are deposited in the herbarium PRA, Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic. It is the largest collection of extra-European dandelions in the world, a result of expeditions to many regions of the Mediterranean, Europe and Middle and central Asia, cultivation of plants grown from seeds obtained from other botanists, seeds collected during expeditions and from cultivation of roots. Details of the cultivation methods are given in Kirschner & Štěpánek (1993). This study was supplemented by the examination of numerous herbarium collections. Those most relevant to the present study are BM, E, G, K, LE, PRC, PR, S, W (abbreviation according to Index Herbariorum at <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>). Most of our revision labels are numbered and refer to the specimen to which they are attached (as 'no. det.', not necessarily to the duplicates).

Table 1. – Samples of four taxa of *Taraxacum* sect. *Dioszegia*. Pop.: population abbreviation. Abbreviations of taxon names (Sp.) are as follows: TST: *T. serotinum* subsp. *tomentosum* from France, TH: *T. haussknechtii* from the Republic of Macedonia, TS-C: *T. serotinum* subsp. *serotinum* from central Europe (Czech Republic and Austria), TS-S: *T. serotinum* subsp. *serotinum* from southern Europe (Bulgaria), TS-E: *T. serotinum* subsp. *serotinum* from eastern Europe (Ukraine and Russia) and TSI: *T. serotinum* var. *iranicum* from Iran. No.: number of individuals. Cult. no.: cultivation number of collections and cultivations of first three authors. No. det.: Determination number of PRA herbarium. Some samples do not have determination number (NA).

Pop.	Sp.	No.	Country	Region	Municipality	WGS 84 N	WGS 84 E	Cult. no.	No. det.
Fe	TST	6	France	Languedoc-Roussillon, Aude	Feuilla	42°55'	2°54'	9198	NA
He	TH	13	Macedonia	Bitola	Heraklea Lyncestis	41°06'	21°20'	8288	27396
Oh	TH	17	Macedonia	Ohrid	Ohrid	41°08'	20°48'	8291	27399
Pr	TH	2	Macedonia	Prilep	Prilep	41°20'	21°33'	8292	27400
Ne	TH	6	Macedonia	Negotino	Negotino	41°29'	22°4'	8293	27401
Sk	TH	9	Macedonia	Skopje	Skopje	41°55'	21°31'	8290	27398
Ma	TH	1	Macedonia	Saraj	Matka	41°57'	21°17'	8289	27397
So	TH	1	Macedonia	Skopje	Skopje	41°58'	21°22'	JŠ VODNO	27395
Ce	TS-C	26	Czech Republic	southern Moravia, Hodonín district	Čejč	48°56'14.6"	16°58'59.4"	Ser1Cejc	NA
Uv	TS-C	1	Czech Republic	southern Moravia, Břeclav district	Úvaly (near Valtice)	48°44'34.3"	16°42'24.8"	Ser2Uvaly	NA
Se	TS-C	3	Czech Republic	southern Moravia, Břeclav district	Sedlec	48°47'50.6"	16°41'58.4"	Ser3Sedlec	NA
Ba	TS-C	3	Czech Republic	southern Moravia, Břeclav district	Bavory	48°50'16.7"	16°37'56.8"	Ser4Bavory	NA
Ha	TS-C	6	Austria	Burgenland	Hainburg an der Donau	48°07'30"	16°57'	5171	27388
Ch	TS-S	3	Bulgaria	Smolyan	Chvojna	41°52'	24°41'	3130	25351
Cp	TS-S	3	Bulgaria	Smolyan	Čepelare	41°51'	24°37'	6800	27393
Mi	TS-E	1	Ukraine	Mykolaivs'ka oblast', Pervomais'k	Between Migija and Semenivka	48°00'	30°59'	3486	27385
Do	TS-E	2	Ukraine	Mykolaivs'ka oblast', 15 km SE of Voznesens'k	Doroshivka	48°28'	31°28'	3527	27387
Po	TS-E	6	Russia	Volgogradskaya oblast', Kumylzhenskiy region, Stantsia Kumylzhenskaya, Potapovskiy Khutor	Potapovskaya Dubrava	49°57'	42°43'	5321	27389
Ka	TSI	2	Iran	Golestan	Kalaleh	37°19'	55°53'30"	11917	26456
Kl	TSI	4	Iran	Golestan	Kalaleh	37°22'30"	55°56'	12296	26458

The nomenclature adopted in the present paper

Sectional nomenclature follows the previous nomenclatural and taxonomic accounts (Kirschner & Štěpánek 1997), see also Kirschner & Štěpánek (1987, 2004). Plant names are in accordance with ICN (McNeill et al. 2012). In order to avoid confusion, we use the name *T. serotinum* subsp. *tomentosum* Lange consistently in what follows, instead of the homotypic *T. pyrrhopappum*.

Methods used in the taxonomic revision of the section and identification of the mode of reproduction

Principles used in the taxonomic evaluation of dandelions are summarized by Trávníček et al. (2010) and Ge et al. (2011) and are followed in the present paper. Identification of the reproduction system in *Taraxacum* is described in detail in Kirschner et al. (2006) and Gustafsson (1932).

Laboratory and statistical analyses

For microsatellite (SSRs) genotyping we used 14 published microsatellite primers MSTA145, MSTA131, MSTA101, MSTA105, MSTA143, MSTA102, MSTA93, MSTA133 and MSTA103 from Vašut et al. (2004) and primers MSTA44B, MSTA53, MSTA61, MSTA73, MSTA78 and MSTA85 from Falque et al. (1998). Primers were originally developed for *T. officinale* agg. (sect. *Taraxacum*) and *T. laevigatum*, respectively. We isolated genomic DNA from leaf material stored in silica gel or herbarium specimens using Qiagen DNeasy Plant Mini Kit (Qiagen, Venlo, Netherlands) following the manufacturer's instructions. Some samples were taken from plants grown in the experimental garden of the Institute of Botany, The Czech Academy of Sciences, Czech Republic in Průhonice. PCR was performed in a volume of 20 μ l (multiplex of up to 9 primers) using Qiagen Multiplex PCR kit (Qiagen, Venlo, Netherlands) following the manufacturer's instructions, with 10 μ M of each primer. PCR conditions were: 95 °C for 15 min (hot start PCR polymerase) and then 30 cycles of 95 °C for 1 min, 54.5 °C for 1 min and 72 °C for 1 min and finally 72 °C for 4 min and a 10 °C hold. Alleles were scored and visualized in GeneMarker 2.4 (SoftGenetics LLC, State College, PA, USA) and rewritten into the data matrix.

Most of the computations were performed in R 3.0 (R Core Team 2013). We used packages ade4 (Dray & Dufour 2007), adegenet (Jombart 2008), ape (Paradis et al. 2004), pegas (Paradis 2010), PopGenKit (Paquette 2012), rworldmap (South 2011), sp (Pebesma & Bivand 2005) and spdep (Bivand 2013). We calculated the basic population statistics, i.e. observed and expected heterozygosity, F-statistics (Weir & Cockerham 1984), allelic richness (Paquette 2012), departure from Hardy-Weinberg equilibrium (HWE; Jombart 2008); only for populations with at least 6 individuals, and number of private alleles. We calculated Mantel test (Mantel 1967, Dray & Dufour 2007), Moran's I (Bivand 2013), principal coordinate analysis (PCoA, Dray & Dufour 2007) and neighbour-joining tree (Saitou & Nei 1987, Paradis et al. 2004, Popescu et al. 2012) of populations (tested by 10,000 permutations). For distance-based analysis we used Neil's chord distance (Nei et al. 1983). Values of departure from HWE and for Moran's I were tested using 100,000 bootstraps. Significance of Mantel's test was tested using 1,000,000 permutations and F-statistics using 1000 permutations.

Spatially explicit Bayesian clustering of populations was computed in BAPS 6.0 (Corander et al. 2008, Cheng et al. 2013). We used K ranging from 2 to 30, 20 times each. Bayesian clustering of individuals was performed in STRUCTURE 2.3.4 (Pritchard et al. 2000, Falush et al. 2003, 2007, Evano et al. 2005, Nordborg et al. 2005, Hubisz et al. 2009). We used K ranging from 1 to 30, 20 times each. Length of burn-in was set to 1,000,000 and number of steps to 100,000,000. This analysis was performed at Biportal of University of Oslo, Norway (Kumar et al. 2009). Outputs of independent runs were sorted using Structure.sum R script (Ehrich 2006) and CLUMPP 1.1.2 (Jakobsson &

Rosenberg 2007) and visualized using *distruct* 1.1 (Rosenberg et al. 2002). Details about R work-flow, software settings etc. are available from first author upon request.

Results

Microsatellite analysis

We genotyped 115 individuals of *Taraxacum* sect. *Dioszegia* using 14 microsatellite (SSRs) primers. PCR product size ranged between 114 and 439 bp. Number of alleles ranged from 3 to 39 per locus and from 1 to 21 per locus per population. In total, we detected 243 alleles, of which 159 were private for species and/or a population (see Table 2 for population statistics). We detected 7 private alleles for *T. serotinum* subsp. *tomentosum*, 47 for *T. haussknechtii* and 105 for *T. serotinum* subsp. *serotinum* (incl. var. *iranicum*), respectively. All multi locus genotypes (MLGs) were unique for respective populations and not shared among species or populations. Basic diversity indices for populations with at least six individuals are given in Table 2. Number of alleles and heterozygosity varied considerably among loci and populations. For example, the 26 individuals of population Ce (*T. serotinum* subsp. *serotinum*) were very polymorphic, but monomorphic at locus *msta102*, which is polymorphic in other smaller populations. Most of the populations are highly heterozygous for most of the loci. Deviations from HWE usually were not statistically significant. Global F_{ST} value was high for *T. serotinum* subsp. *serotinum* (0.26) and low for *T. haussknechtii* (0.14).

Relationships among species and populations

Bayesian spatial clustering of populations in BAPS revealed 14 clusters (Fig. 1). Most populations formed separate clusters, with only some geographically very close populations in the same clusters (for example some Czech populations of *T. serotinum* subsp. *serotinum*, or some populations of *T. haussknechtii*). Bayesian clustering performed in STRUCTURE (see Fig. 2 and Electronic Appendix 1) did not reveal a single most likely clustering pattern. Runs for respective K had a relatively low similarity coefficient and the $\ln P(D)$ curve revealed several possible more probable Ks. As the most probable we selected two results: 5 and 16 clusters (Fig. 2, Electronic Appendix 1). Pattern of 16 clusters revealed by STRUCTURE (Electronic Appendix 1) is very similar to results of spatial clustering of populations from BAPS (Fig. 1). STRUCTURE clearly separated species into their own clusters with a very restricted extent of the among-species “introgression” (in the sense according to Corander et al. 2008), see Fig. 2. The “introgression” was mainly observed between *T. haussknechtii* and *T. serotinum* subsp. *serotinum*. STRUCTURE clustering for K = 16 is in accordance with output of BAPS. In the STRUCTURE result for K = 5 (Fig. 2) in 9 runs of 20, the clusters were formed by *T. serotinum* subsp. *tomentosum*, *T. haussknechtii*, *T. serotinum* var. *iranicum* and two clusters of *T. serotinum* subsp. *serotinum*: central Europe and southern together with eastern Europe. Seven runs differed from the previous pattern in that *T. haussknechtii* formed two clusters (one for population He and the second for the other populations) and populations of *T. serotinum* subsp. *serotinum* from southern and eastern Europe formed a cluster together with *T. serotinum* subsp. *iranicum*. Remaining four runs resulted in a slightly

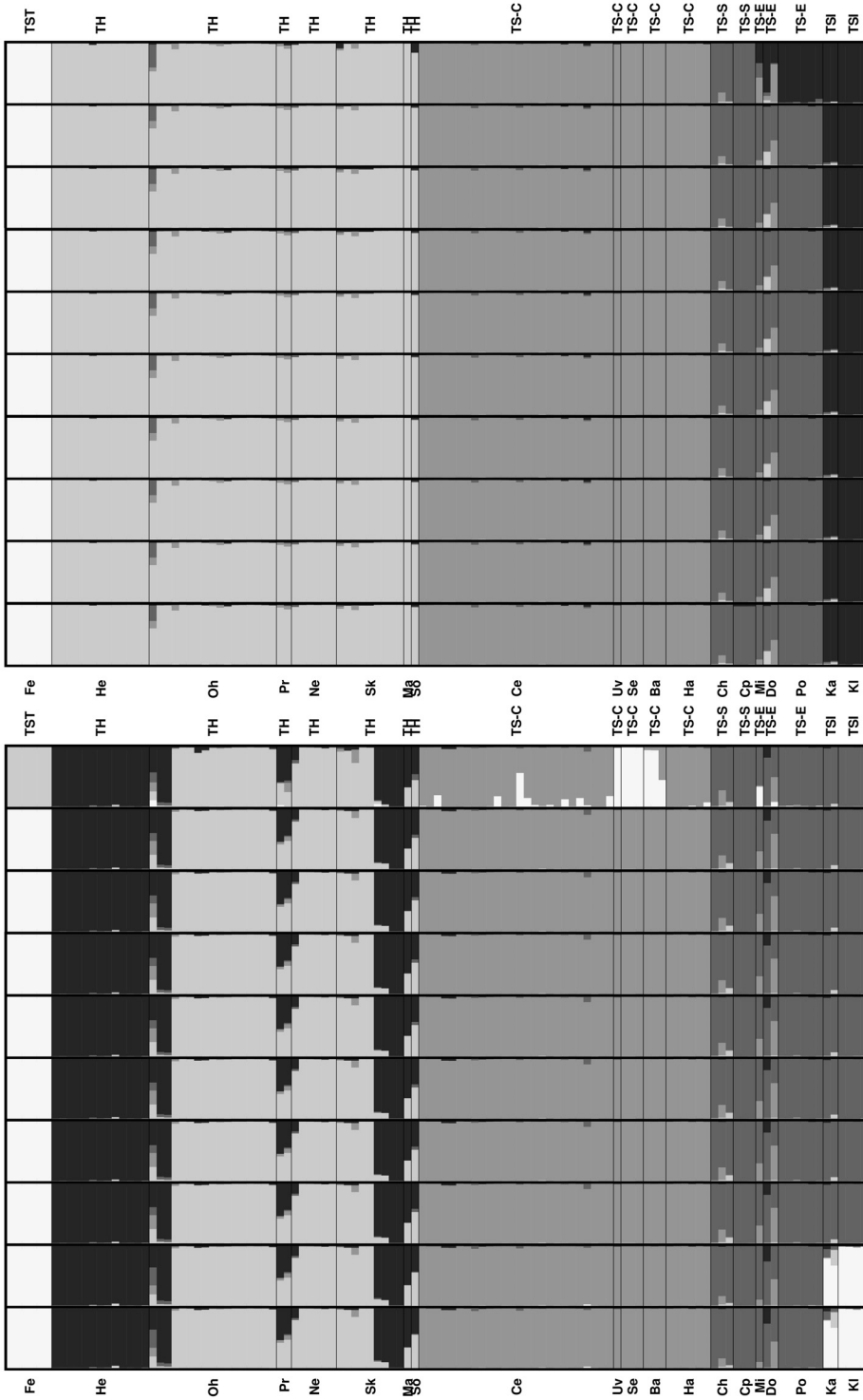


Fig. 2. – Results of STRUCTURE analysis for K = 5 (20 independent runs). *Taraxacum serotinum* subsp. *tomentosum* (TST: Fe) forms a well separated cluster, *T. haussknechtii* (TH: He, Oh, Pr, Ne, Sk, Ma and So) forms one or two clusters (depending on run) and shows a very limited introgression of *T. serotinum* subsp. *serotinum*. Remaining clusters are formed by *T. serotinum* subsp. *serotinum* (TS) from central (TS-C: Ce, Uv, Se, Ba and Ha), southern (TS-S: Ch and Cp) and eastern Europe (TS-E: Mi, Do and Po), respectively. Last cluster is formed by *T. serotinum* var. *iranicum* from Iran (TSI: Ka and KI). Populations of *T. serotinum* var. *iranicum* seem relatively distinctly related to the other populations of that species.

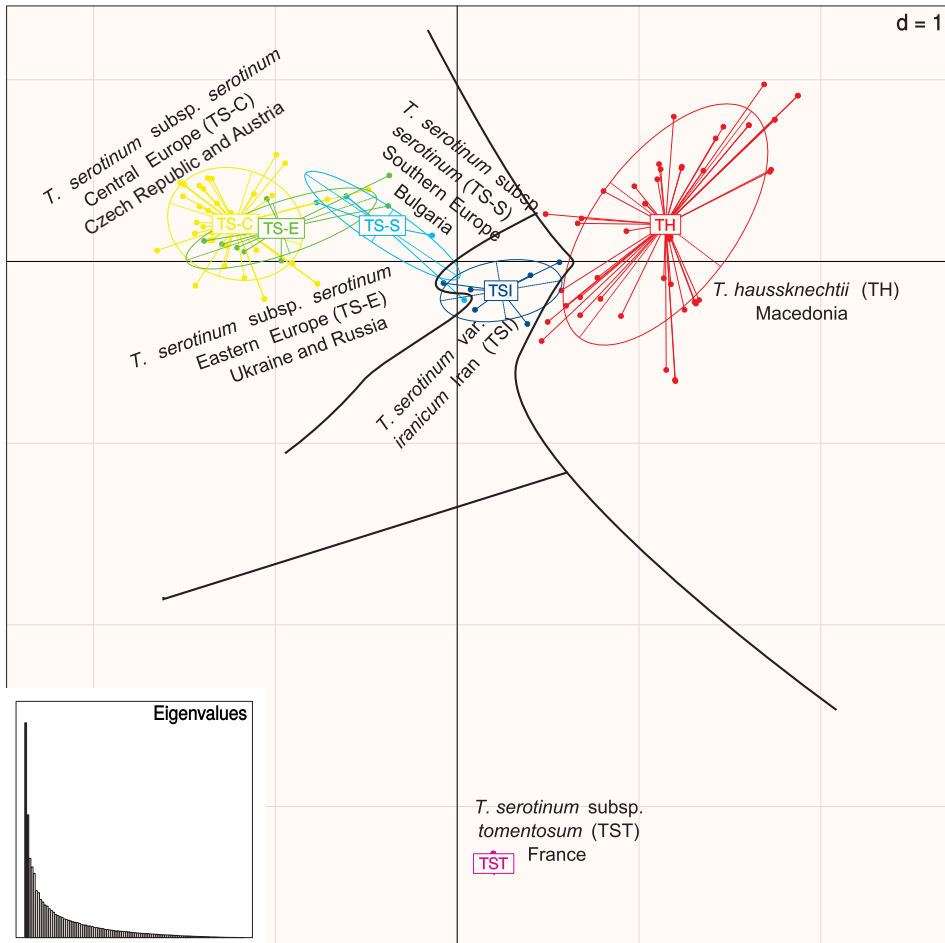


Fig. 3. – PCoA of *Taraxacum* sect. *Dioszegia* indicating that *T. serotinum* subsp. *tomentosum* is distantly related to the other taxa. Populations of *T. haussknechtii* form a well separated cluster. Remaining clusters are formed by populations of *T. serotinum* var. *iranicum* (most closely related to *T. haussknechtii*) and *T. serotinum* subsp. *serotinum* from southern, central and eastern Europe, respectively.

different pattern, although generally similar to the two described. STRUCTURE for $K = 16$ (Electronic Appendix 1) resulted in a generally similar pattern for all runs: most of the populations retain their own “main” clusters and there is extensive introgression (its level is the only difference among the runs) among populations within taxa – for *T. haussknechtii* (practically without population He) and *T. serotinum* subsp. *serotinum*, respectively.

PCoA analysis of all taxa (Fig. 3) shows *T. serotinum* subsp. *tomentosum* as distant from the other taxa, another cluster is formed by *T. haussknechtii* and there is a cluster of groups of *T. serotinum* subsp. *serotinum* and *T. serotinum* var. *iranicum* (i.e. populations from Iran, marginal to *T. serotinum* subsp. *serotinum* and adjacent to *T. haussknechtii*), with distinct sub-clusters of populations from southern Europe and central and eastern Europe, respectively.

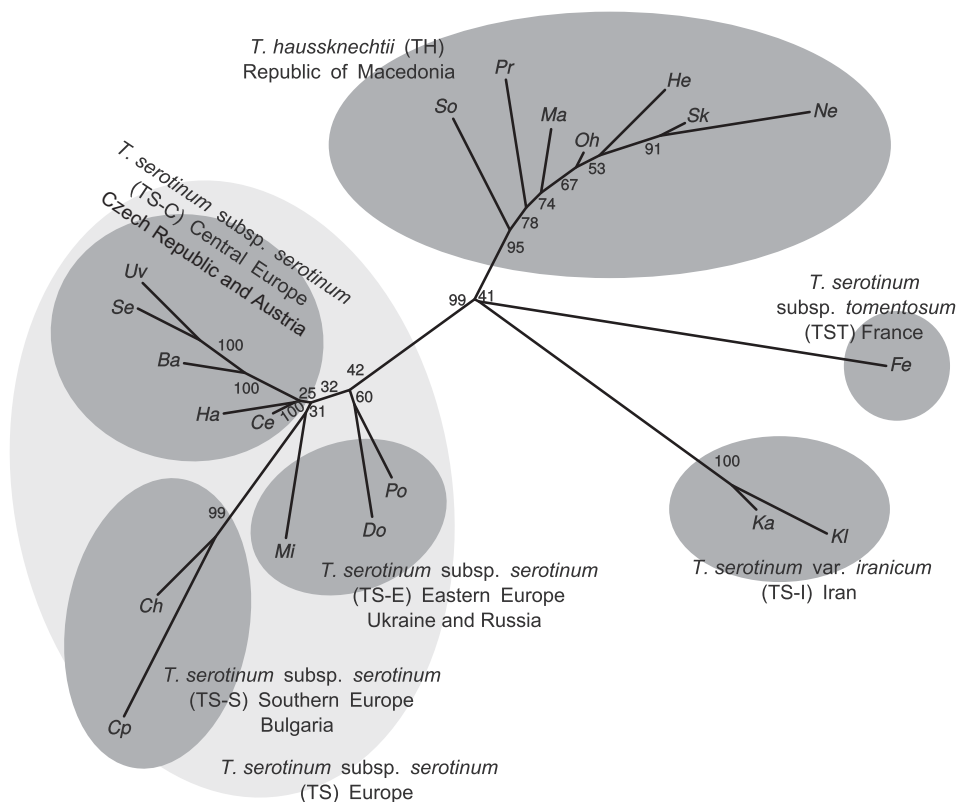


Fig. 4. – Unrooted neighbour-joining tree of populations of *Taraxacum* sect. *Dioszegia*. All taxa form distinct branches. Numbers show bootstrap support.

Mantel test shows a clear isolation by distance pattern (Table 3) for *T. haussknechtii* and *T. serotinum* subsp. *serotinum* (including var. *iranicum*). The value of Moran's I is positive and significant (i.e. the isolation by distance pattern) only for *T. serotinum* subsp. *serotinum* (including var. *iranicum*) and not significant for *T. haussknechtii* (not shown).

Neighbour-joining tree of all populations points to a very clear pattern (Fig. 4): the main branches of the unrooted tree are formed by respective taxa. Exact position of the root is unclear as branches leading to *T. serotinum* var. *iranicum* from Iran (and to *T. serotinum* subsp. *serotinum*), *T. serotinum* subsp. *tomentosum* and *T. haussknechtii* branch very rapidly.

Morphology and the mode of reproduction

Results of the morphological examination of the whole material are summarized in the taxonomic treatment below (Appendix 1, see also Table 4 for comparison of diagnostic characters). We recognize *T. serotinum* subsp. *serotinum*, *T. s.* var. *iranicum*, *T. s.* subsp. *tomentosum* (*T. pyrhopappum*) and *T. haussknechtii*. The separate specific status of

Table 2. – Basic population statistics for populations of at least six individuals. Sp: species, Pop: populations (see Table 1 for detailed information about species and populations), No. of alleles: total number of different alleles detected within population, H_O : observed heterozygosity (average per all loci per population), H_E : expected heterozygosity (average per all loci per population), Allelic richness, No. of private alleles: number of alleles unique for respective population, P-value of departure from HWE: significance of departure from HWE. Abbreviations of names: TST: *T. serotinum* subsp. *tomentosum*, TH: *T. haussknechtii*, TS-C: *T. serotinum* subsp. *serotinum* from central Europe and TS-E: *T. serotinum* subsp. *serotinum* from eastern Europe.

Sp.	Pop.	No. of alleles	H_O	H_E	Allelic richness	No. of private alleles	P-value of departure from HWE
TST	Fe	15	0	0.031	1.00	7	0.005
TH	He	46	0.555	0.481	1.55	1	0.143
TH	Oh	95	0.605	0.707	1.61	12	0.122
TH	Ne	53	0.628	0.554	1.58	3	0.245
TH	Sk	74	0.544	0.679	1.54	4	0.289
TS-C	Ce	118	0.515	0.648	1.48	26	0.234
TS-C	Ha	44	0.528	0.464	1.45	0	0.419
TS-E	Po	38	0.515	0.426	1.40	5	0.291

Table 3. – Mantel tests for *Taraxacum haussknechtii* and *T. serotinum* subsp. *serotinum* (including var. *iranicum*). Observed values are significantly greater than expected values based on 1,000,000 permutations, which indicates significant isolation by distance.

Species	Observation	P-value	Std. Obs	Expectation	Variance
<i>T. haussknechtii</i>	0.57741	0.000001	9.101255	-0.000003	0.004025
<i>T. serotinum</i> subsp. <i>serotinum</i> (incl. var. <i>iranicum</i>)	0.33983	0.000001	8.244719	-0.000001	0.001699

T. haussknechtii is retained on the basis of morphological distinctiveness, geographical endemism and molecular analyses. Within *T. serotinum* subsp. *serotinum*, a similar magnitude of distinctiveness is found in the Iranian plants; we treat them as a newly described variety, var. *iranicum*. The limited number of Iranian specimens and extensive morphological variation of Iranian plants does not make it possible to draw safe conclusions about their taxonomic status and relationships. The allopatric *T. serotinum* subsp. *tomentosum* shows a very low level of morphological differentiation. The features characterizing subsp. *tomentosum* include non-specific attributes, such as short, non-elongated scapes, permanently closed or nearly closed capitula or often a well-developed petiole; it is therefore difficult to draw a line between subsp. *tomentosum* and subsp. *serotinum*. The former two characters point to the fact revealed by the analysis of microsatellite data, the total homozygosity associated with dominant autogamy (see also Hughes & Richards 1988, 1989, and below). The statistical analysis of molecular data shows a more separate position of subsp. *tomentosum* than expected from its morphology; the explanation of this discrepancy is presented in the Discussion.

The analyses of microsatellite data reveal high variation and heterozygosity in *T. serotinum* subsp. *serotinum* and *T. haussknechtii*, pointing to their outcrossing sexuality. For instance, the largest population of *T. serotinum* subsp. *serotinum* studied (Ce, 26 individuals) has both a high mean heterozygosity and genotype diversity, a safe indicator of outcrossing.

Table 4. – Characters distinguishing the taxa in *Taraxacum* section *Dioszegia*.

Character	<i>T. serotinum</i> subsp. <i>serotinum</i> (excluding Iran)	<i>T. serotinum</i> var. <i>iranicum</i> (Iran)	<i>T. serotinum</i> subsp. <i>tomentosum</i> (= <i>T. pyrhopappum</i>)	<i>T. haussknechtii</i>
Leaf posture	usually appressed to the ground	usually erect-patent	usually appressed to the ground	mostly erect-patent
Leaf shape	relatively broad, most often not divided (then having the shape of leaves of <i>Hypochaeris maculata</i> L.), if divided then lateral segments broad, ± obtuse	variable, relatively narrow, divided or undivided (segments similar to those of <i>T. serotinum</i>)	relatively broad, often not divided, not rarely divided (to pinnatisect) with ± broad rounded lateral segments (the shape similar to that of <i>T. obovatum</i>)	conspicuously narrow, almost always pinnatisect to pinnatisect, lateral segments usually acute
Size of leaves	usually 12–20 × 2.5–5.5 cm	10–15 × 2–2.5 (–4) cm	usually 6–11 × 2.5–4 cm	usually 6–12 × 0.5–2 cm
Petiole length	1 (–2) cm	1.5–2.5 cm	1–4 cm	1.5–2 cm
Scape length in full blossom / in fruit	usually longer than leaves, 10–20 cm / to 35 cm	longer than leaves, 12–20 cm / to 25 cm	usually conspicuously shorter than leaves, often only 2–4 cm / usually shorter than leaves, rarely reaching 10–15 cm in fruit	variable, usually 3–12 cm / equalling to clearly overtopping leaves, often over 20 cm
Shape and size of capitulum	small to medium-sized, ~3 cm in diam., ± flat, light to bright yellow	usually small (more material needed)	medium sized but remaining semi-closed, therefore only 1.5–2.5 cm in diam., ± light yellow	small to medium-sized, 1.5–2.5 (–3) cm in diam., ± flat, golden yellow to light yellow, rarely pale ochraceous-yellow
Outer phyllary number	30–46	26–35	26–38	(15–) 18–34
Outer phyllary margin indumentum	usually ± evenly densely ciliate	not available	relatively sparsely ciliate, usually only near phyllary apex	not ciliate or sparsely ciliate, if so, then more densely towards the apex
Rostrum length	(5–) 7–9 (–10.5) mm	9.5–11 (–13) mm	4–8 mm	(4–) 6–9 (–10.5) mm
Pappus length	6–8 (–10) mm	5.5–6 (–7) mm	4.5–7 mm	(5–) 6–8 mm
Pappus colour	variable, dirty whitish, dirty yellowish, pale brownish	pale brownish	invariably pale brownish with ± pinkish tinge (similar to <i>T. bessarabicum</i>)	pale yellowish-brownish, dirty brownish white, greyish-brownish or pale brownish with pinkish tinge

Discussion

Sexuality and reproduction

The section *Dioszegia* was thought to be quite exceptional in the genus *Taraxacum* because all its members are exclusively sexual. The sexuality was tested previously by several authors (see Introduction) and confirmed on the basis of studies on geographically and taxonomically representative samples and the molecular analyses in the present paper. Only another two sexual diploid *Taraxacum* species were studied from the viewpoint of their population genetic differentiation. *Taraxacum bessarabicum* (sect. *Piesis*) is almost completely autogamous and homozygous throughout its large geographical range and almost homogenous genetically in the western part of its range (Kirschner et al. 1994, Kirschner & Štěpánek 2008). *Taraxacum koksaghyz* (sect. *Ceratoidea*, see Kirschner & Štěpánek 2008, Dijk et al. 2010, Kirschner et al. 2013) occupies a medium-sized geographical range in south-eastern Kazakhstan, comparable in size to that of *T. haussknechtii*. It is an obligate out crosser with the absolute predominance of within-population genetic variation (Kirschner et al. 2013). Thus, the sexual taxa in *Taraxacum* exhibit contrasting patterns of genetic variation. Within section *Dioszegia*, with the probable exception of the autogamous *T. serotinum* subsp. *tomentosum* (due to the limited sampling), there is remarkable among-population variation.

Taraxacum serotinum subsp. *tomentosum* exhibits an almost complete homozygosity, which indicates autogamy (also supported by structural adaptation of capitula, which remains partly closed during anthesis; and as a rule scapes do not elongate after anthesis). This view is also supported by its scattered distribution in small populations across southern France, northern Spain and (probably introduced) in northern Morocco. Our results corroborate the idea of self-compatibility introduced by Hughes & Richards (1988, 1989) who studied four plants of *T. serotinum* subsp. *tomentosum* (under the name “*T. pyropappum*”) and 14 plants of their progeny using 15 isozyme loci and did not find any heterozygosity. We therefore tentatively treat this subspecies as an autogamous taxon on the basis of two independent investigations covering two distribution centres of this taxon, France and Spain.

The biggest population of *T. serotinum* subsp. *serotinum* (Čejč, Czech Republic, code: Ce) shows a high level of heterozygosity, but for eight of 14 loci also shows significant departures from HW. A similar pattern is recorded in other populations of this subspecies (see Table 2), which is expected for a sexual species with small populations and limited dispersal ability. Most samples came from random progenies from seeds collected in nature, therefore representing the potential variation of the parental populations. We therefore treat the widely distributed subspecies, in accordance with the literature (Gustafsson 1932, Poddubnaja-Arnoldi & Dianowa 1934), as a sexual outcrossing taxa.

Similarly, all the molecular and morphological results for *T. haussknechtii*, which was relatively densely sampled over an area covering a substantial part of its geographical range, support outcrossing sexuality.

Population analysis of widespread diploid outcrossing sexual species

A comparison of the population genetic parameters of *T. serotinum* subsp. *serotinum* and *T. haussknechtii* reveal that they both correspond to the isolation by distance model (highly significant results of the Mantel test). Global F_{ST} for *T. serotinum* (including var.

iranicum) is as expected high, 0.26; the global F_{ST} value for *T. haussknechtii* (0.14) also points to a strong population substructure. The greater values for global F_{ST} for these two species indicate a high microevolutionary potential, particularly for marginal populations (such as var. *iranicum*). On the other hand, departure from HWE was usually not statistically significant. This can be caused by small sample sizes, despite the isolation of the populations indicated by high number of private alleles and high uniqueness of the MLGs. Most of the case studies of similar situations compare the population genetic diversities of a widespread/rare species pair, which is not meaningful in the case of the isolated *T. serotinum* subsp. *tomentosum* characterized by a shift to autogamy. A heuristic search of genetic differentiation within widespread outcrossing sexual species reported in the literature shows that taxa with limited seed dispersal and entomogamy with specialised pollinators and large, sometimes discontinuous geographical ranges tend to develop a substantial population substructuring (e.g. Gitzendanner & Soltis 2000, He et al. 2000, Twyford et al. 2014), while many of the widespread anemogamous trees or plants that are efficiently pollinated by insects (diverse widespread pollinators, e.g. Gonela et al. 2013) are characterized by the absence of geographical population structure (Gitzendanner & Soltis 2000, García-Gil et al. 2003, Kado et al. 2003, Palmé et al. 2003, Neale & Savolainen 2004, Bloomfield et al. 2011). It should be added, however, that there are many departures from this rule (e.g. Ingvarsson 2005) and the examples listed above usually do not cite other circumstances important for evaluating population genetic diversity, such as (paleo)polyploidy, migration history or possible introgression.

New assessment of the taxonomy and relationships in Taraxacum sect. Dioszegia

In spite of the relatively extensive genetic diversification, all the taxa recognized in the section *Dioszegia* are very similar to one another in terms of the important morphological characters (achenes, outer phyllaries). The lowest level of morphological differentiation is found between the isolated *T. serotinum* subsp. *tomentosum* and *T. s.* subsp. *serotinum* (see Table 4). The main microevolutionary event, the shift from allogamy to autogamy is accompanied by rather inconspicuous structural morphological changes, mainly abbreviated scapes, incompletely opening capitula and usually a well-developed petiole in *T. serotinum* subsp. *tomentosum*, although the difference in the reproduction system, high homozygosity and the genetic make-up of the population studied might support its specific status, the morphological similarity with *T. s.* subsp. *serotinum* points to a lower rank.

The analysis of molecular data indicates that the main qualitative difference between subsp. *tomentosum* and subsp. *serotinum* is the missing alleles in the former. The mean number of alleles per locus in subsp. *tomentosum* is 1.071 while that of the other populations varies from 2.714 to 8.429. Populations are small and autogamous and the events of fixation of rare or new alleles may be quite frequent, which accounts for the other aspect of the molecular differentiation between the two subspecies. The lack of substantial structural morphological divergence between the two subspecies and the nature of the above molecular differences are the main arguments in favour of the subspecific treatment of this autogamous taxon within *T. serotinum*.

Another isolated, morphologically aberrant group of populations is confined to the northern part of Iran, which is genetically rather remote from subsp. *serotinum*, requires further study (some *T. serotinum* plants in Iran do not seem to belong to the same phenetic

group, but that is based on a relatively limited amount of material). The plant specimens listed are so distinctive that we recognize them as a separate variety, var. *iranicum*, which is confined to north-central Iran and is relatively isolated from the nearest regions where *T. serotinum* subsp. *serotinum* occurs (the north and south Caucasus or Anatolia). Plants from Iran were known to be aberrant morphologically (the general habit deviating from the most common pattern of *T. serotinum* in other areas, see e.g. van Soest (1977), who mentions that “the oriental forms ... are mostly similar to *T. haussknechtii* by smaller size, smaller flower heads, more divided leaves”). The degree of differentiation between var. *iranicum* and var. *serotinum* is not easy to evaluate because of the relatively limited material available and, more importantly, because the characters diagnostic of var. *iranicum* are not equally clearly developed in all the Iranian specimens studied. Pending further population research and depending mostly on the basis of the results of the SSRs analyses we treat the Iranian plants as a variety.

Last, the specific status allotted to *T. haussknechtii* requires comment. The material analyzed genetically and the specimens seen are fully representative of this taxon, which has a small geographical range centred in the Republic of Macedonia, Greek Macedonia and adjacent regions of neighbouring countries (Bulgaria, Albania, Serbia). In the north-east, it is parapatric with *T. serotinum* subsp. *serotinum*. Although we have seen much rich Bulgarian material of both taxa, there is no trace of hybridization or morphological transition between them. The isolating mechanisms are not known and may involve a different habitat and a shift in phenology (*T. haussknechtii* flowers earlier). Moreover, *T. haussknechtii* has several features making it possible to draw a line between it and the rest of the section (narrow leaves up to 2 cm wide, leaf lateral segments acute, outer phyllaries only distally sparsely ciliate or subglabrous, quite narrow, usually 0.6–1.2 mm wide).

Microevolution through shifts from allogamy to autogamy: Taraxacum serotinum subsp. tomentosum is a special case

If we disregard hybridization and polyploidy, there are three main evolutionary situations in which a homoploid shift from self-incompatibility or prevailing allogamy towards autogamy may be associated with instant advantages:

First, is a founder situation often followed by adaptive radiation, documented recently, for instance, for Hawaiian species of *Schiedea* Cham. et Schltldl. (Sakai et al. 2006), with three independent origins of obligate autogamy during island colonizations.

The second situation involves cases of sympatric evolution with the development of reproductive barriers through a shift to autogamy; a habitat shift is often also involved. A classic example is the evolution of *Stephanomeria malheurensis* Gottlieb, a descendant of the widespread *Stephanomeria exigua* subsp. *coronaria* (Greene) Gottlieb, which near its northern limit is confined to volcanic hilly sites (Gottlieb 1973, 2003). While the progenitor species has a sporophytic multiallelic self-incompatibility, the descendant species is almost completely autogamous. Another couple of similar cases are those of *Epipactis helleborine* subsp. *neerlandica* (Verm.) Buttler as an allogamous progenitor and the local autogamous derivative described as *E. renzii* Robatsch (Pedersen & Ehlers 2000) or *Aquilegia vulgaris* L. and *A. paui* Font-Quer as a progenitor-derivative pair (Martinell et al. 2011).

The last situation is more complicated: it includes cases of (repeated) migrations and retreats of a widespread outcrossing species during late glacial and early post-glacial periods, often leaving “witness” populations in the formerly colonized areas. As the time available for possible microevolutionary changes was relatively limited, most of these isolated populations of continental migrants are not recognized as separate taxa. As examples, we can cite *Taraxacum bessarabicum* (Hornem.) Hand.-Mazz. (with an enormous continental distribution ranging from northern China and southern Siberia to eastern Austria and south-eastern Czech Republic, and an isolated locality in Auvergne, south-western France) or *Krascheninnikovia ceratoides* (L.) Gueldenst. (occupying a gigantic continental range from China and Mongolia to Austria and south-eastern Moravia (Czech Republic), with isolated sites in Spain and Morocco). At isolated sites, these migratory species may have undergone speciation processes associated with genetic drift, which might have included the shift to autogamy.

The present case of *Taraxacum serotinum* subsp. *tomentosum* involves both continental migration, isolated “witness” populations and a shift towards autogamy. In terms of morphology, the degree of divergence between subsp. *tomentosum* and subsp. *serotinum* is relatively small. At the SSRs level, however, the differentiation is more remarkable (see Fig. 4).

See www.preslia.cz for Electronic Appendix 1

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Souhrn

Soužití agamospermie a pohlavního rozmnožování je charakteristické pro většinu z asi 60 sekcí pampelišek (rod *Taraxacum*). Sekce *Dioszegia*, obsahující p. pozdní (*T. serotinum*), vyskytuje se od jižní Moravy přes jižní a východní Evropu, Malou Asii a Írán až po Afghánistán) a příbuzné druhy představuje výjimečnou sekci, protože pro její členy bylo doposud známo pouze pohlavní rozmnožování. Na základě analýzy mikrosatelitových (SSRs) markerů, rozšíření a morfologie jsme řešili otázky týkající se způsobu rozmnožování, vztahů mezi populacemi, taxonomie a genetické variability v rámci populací, a to za pomoci vzorků sesbíraných od jižní Francie po jižní část evropského Ruska a Írán. Zjistili jsme, že populace jsou silně geneticky izolované a vcelku vykazují velkou strukturovanost. Mnoho populací v řadě lokusů vykazovalo nemalou odchylku od Hardy-Weinbergovy rovnováhy, která ale většinou (kvůli relativně malým populacím) nebyla statisticky průkazná. Cizosprašnost se vyskytuje u všech taxonů v rámci sekce s výjimkou *T. serotinum* subsp. *tomentosum* (známé i pod jménem *T. pyrrhopappum*), které je autogamní a plně homozygotní. Zdá se, že jde o reliktní kontinentální migrace *T. serotinum* v pozdním glaciálu či raném postglaciálu z východu na západ, kdy malé izolované populace v jižní Francii a Španělsku ztratily spojení se zbytkem areálu dále na východě a postupně se u nich vyvinulo samo-sprašení a klesala genetická diverzita. Taxonomická revize sekce *Dioszegia* rozlišila *T. serotinum* subsp. *serotinum* (včetně mírně odlišných populací z Íránu, zde popsáných jako var. *iranicum*), *T. serotinum* subsp. *tomentosum* (\equiv *T. pyrrhopappum*), a *T. haussknechtii* (vyskytuje se v Makedonii a přilehlých oblastech). *Taraxacum haussknechtii* vykazuje relativně vysokou heterozygositu a populace vykazují menší izolovanost, než u *T. serotinum* s.l., což souvisí s tím, že tento druh je rozšířen v menším prostoru, kde jsou (oproti *T. serotinum*) malé

vzdálenosti mezi populacemi umožňující genetickou výměnu. Uvádíme úplnou synonymiku a lektotypy pro šest jmen. K tomu kresby *T. serotinum* subsp. *serotinum* a subsp. *tomentosum* a *T. haussknechtii*. Pro studované druhy (kromě *T. serotinum* subsp. *serotinum*, v tomto případě je dostupný na vyžádání) je uveden soupis revídovaného herbářového materiálu a pro *T. haussknechtii* i mapa rozšíření.

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Appendix 1. – Taxonomic treatment: a revision of *Taraxacum* sect. *Dioszegia*.

Taraxacum* sect. *Dioszegia (Heuffel) Heuffel, Verh. K. K. Zool.-Bot. Ges. Wien 8: 148 (1858). – *Dioszegia* Heuffel, Z. Natur-Heilk. Ungarn 1854: 177 (1854). – Type: *D. crispa* Heuffel (≡ *T. crispum* (Heuffel) Heuffel); holotype: BP 186654, no. det. 3633 (= *T. serotinum*).

≡ *Taraxacum* sect. *Rhodotricha* Hand.-Mazz., Monogr. *Taraxacum*: [XI] (1907), nom. illeg. (Art. 52.1, 52.2). – Type: *T. crispum* (Heuffel) Heuffel (≡ *Dioszegia crispa* Heuffel). [Explicit inclusion of the type of *T.* sect. *Dioszegia* in the protologue of the sect. *Rhodotricha* causes illegitimacy of the latter, see also Kirschner & Štěpánek (1987).]

= *Taraxacum* sect. *Serotina* Soest, Collect. Bot. (Barcelona) 4: 1 (1954). – Type (orig.): *T. serotinum* (Waldst. et Kit.) Fisch. (≡ *Leontodon serotinus* Waldst. et Kit.).

For details of the sectional nomenclature and comments see Kirschner & Štěpánek (1987, 1996, 1997).

Description: Rosulate hemicryptophytes. Flowers and leaves develop simultaneously. Main flowering season: summer to early autumn. Main habitat: secondary dry, semi-steppe sites or xeric grasslands. Plants medium-sized to robust, plant base densely brownish hairy. Leaves subcoriaceous, usually densely hairy, at least beneath, swollen at hair base (often forming low protuberances or ridges), rarely ± flat, shallowly to deeply lobed, lobation pattern usually uncomplicated, lobes usually subpatent to recurved, leaves usually flat, midrib without striatulate pattern, leaf blade unspotted, petioles winged or broadly winged. Scapes erect during flowering, unbranched, growing from the centre of leaf rosette, densely aranose. Involucre with ± rounded base, usually of medium width. Flowers yellow, florets usually very numerous, ligules flat to canalliculate. Interior involucre phyllaries usually callose to corniculate at the apex. Exterior bracts 15–46, relatively regularly arranged, usually imbricate, ± appressed at base, often arcuate to arcuate-recurved at the apex, narrowly linear-lanceolate, usually 5–8 mm long, pale greenish, often suffused red or pinkish, usually faintly bordered or with narrow paler or reddish margins, ciliate or sparsely ciliate to glabrous. Pollen always present, stigma pure yellow. Receptacle glabrous. Achenes subturbinate, usually 4.5–7 mm long, usually 0.8–1.1 mm thick, very gradually narrowing into the cone, achene body usually pale greyish straw brown, sparsely spinulose above, cone subcylindrical to cylindrical (length difficult to measure because of the indistinct transition between achene body and cone), usually 0.8–1.5 mm long. Rostrum thin, usually 6.0–8.0 (–12) mm long, pappus usually 6.5–8.5 mm long, whitish-yellowish to brownish-pinkish, not deciduous. Reproduction: Sexual (diploid).

Diagnostic notes: A group of four taxa, here accepted as species, subspecies and a variety. Characteristic features include linear-lanceolate, imbricate (and apically arcuate) outer bracts, large achenes very gradually narrowing into the cone, subcoriaceous leaves with hairs often growing on small ridges on the leaf surface, and summer or late summer flowering. See Table 4 for comparison of morphological characters among all four taxa.

Comments on habitats: In contrary to the sites occupied by the sect. *Piesis*, *Dioszegia* typically occurs in areas of dry, semisteppe to steppe, often naturally disturbed places.

Distribution: Mainly distributed in SC and SE Europe and from Turkey to Afghanistan and NW Kazakhstan, isolated occurrence in SW Europe; formerly introduced into Morocco.

1. *Taraxacum serotinum* (W. et K.) Fischer, Catal. Jard. Gorenki, p. 34 (1812).

≡ *Leontodon serotinus* W. et K., Descr. Icon. Pl. Hung. 2: 119 (1802). – Type: “Gesammelt b[e]y Wedröd in Hungarn in Gesellschaft meines Freundes Gf. Waldstein 1802” PR 376398/3238 (lectotype, fide Kirschner & Štěpánek 1997, see also Chrtek & Škočdoplová 1982: 219).

a. *Taraxacum serotinum* subsp. *serotinum*

= *Dioszegia crispa* Heuffel, Z. Natur-Heilk. Ungarn 1854: 177 (1854).

≡ *Taraxacum crispum* (Heuffel) Heuffel, Verh. Zool.-Bot. Ges. Wien 8: 148 (1858). – Type: “In collibus arenosis ad Guboráy ... Illyrico-Banatica.”, VII. 1835, Heuffel ut ?*Taraxacum crispum* Heuff. nov. sp., *Dioszegia crispa* Heuff. (holotype: BP 186645, no. det. 3633).

= *Taraxacum libanoticum* DC., Prodr. Syst. Natur. 7: 149 (1838), ut “*Libanoticum*”. – Type indication: “in monte Libano legit cl. Aucher pl. exs. n. 3459! (v. s. comm. à cl. inv.)”. – **Lectotypus, hic designatus:** “3459 Leont. Libanus. m. Aucher Eloy 1837.”, [the date is probably that of accession in DC’s herbarium], Aucher Eloy 3459 (G-DC, no. det. 18921); isolectotype: (G-BOIS, no. det. 18827; P 691557, photo! – only upper left plant).

= *Leontodon lanatus* Ledeb., Mém. Acad. Imp. Sci. St. Pétersbourg Hist. Acad. 5: 554 1815, nom. illeg., non L. 1755. ≡ *Taraxacum serotinum* var. *lanatum* [Ledeb.] Ledeb., Fl. Ross. 2(2): 815 (1844). ≡ *T. serotinum* f. *lanatum* (Ledeb.) Beck, Fl. Nieder-Österreich 2/2: 1314 (1893) ≡ *Taraxacum serotinum* var. *arachnoideo-lanatum* Schur, Enum. Pl. Transsilv. 366 (1866) sine localitate, in syn. cit.: *Leontodon lanatus* Ledeb. [non

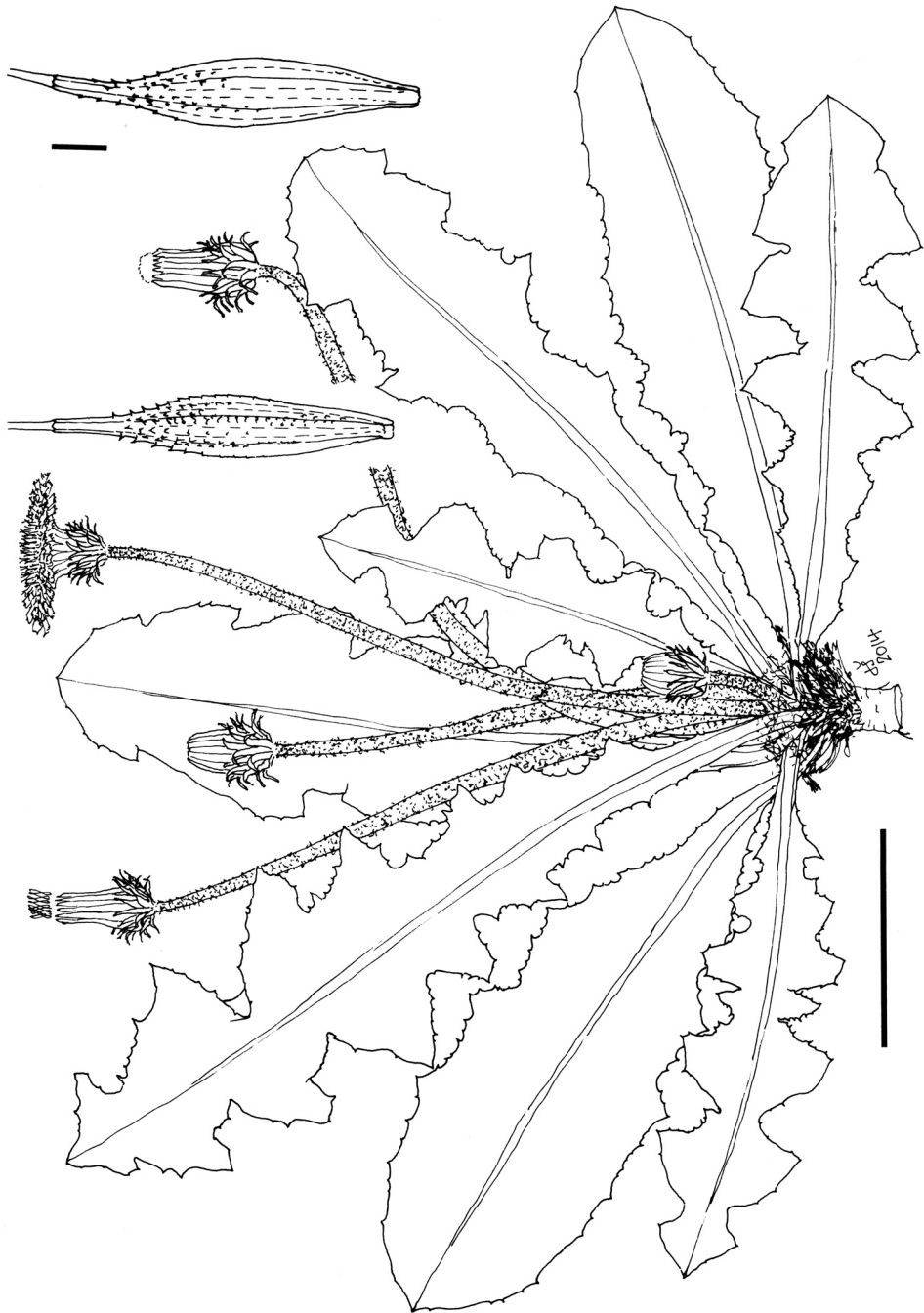


Fig. 5. – *Taraxacum serotinum* subsp. *serotinum*. Habit (A), scale bar = 5 cm, and achenes (B), scale bar = 1 mm. Drawn by J. Štěpánek.

L.] var. β fl. Ross. 2, 812. – Type: “E Sibiria dd [dedit] am. Tilesius” [Tilesius] herb. Ledebour ut *Leontodon lanatus* mihi. *Taraxacum serotinum* f. *lanatus* m. – **Lectotypus, hic designatus**: LE, no. det. 6026 [there may be a mistake in the localization; *T. serotinum* is only recently reported to occur in Siberia and the record may refer to north-westernmost Kazakhstan].

- = *Taraxacum voronovii* Schischkin, Fl. SSSR 29: 536 & 764 (1964). – Type: [Georgia] Yu. N. Voronov et S. V. Yuzepchuk, Poezdka v Yugo-Ossetiyu 1923, no. 870. Circa Čreba (Tskhinvali) [Cchinvali], ad vias, 1. 9. 1923, S. V. Yuzepchuk (**lectotypus, hic designatus**: LE, no. det. 6019, plant A in the middle of the sheet). Icon.: Fig. 5.

Note: The type herbarium sheet of *T. voronovii* consists of numerous smaller plants on the lower half of the sheet, and a bigger specimen in the upper right corner of the sheet, most of them might belong to *T. serotinum*; the only plantlet (A) safely determinable as *T. serotinum* is selected as the lectotype. There is a bigger plant on the same sheet that probably belongs to a taxon close to *T. stenolepium* Hand.-Mazz. The original description combines the characters of both taxa but the achene description is closer to *T. serotinum*.

Description: Plants medium-sized to robust, 12–35 cm tall, densely brownish aranose at base (Fig. 5). Leaves subcoriaceous, usually appressed to the ground (most often erect-patent in var. *iranicum*), densely tomentose-aranose beneath, relatively densely aranose above, leaf surface often swollen at hair base (forming a low protuberance or a short ridge), not shiny, dark green to greyish green, not spotted, sometimes suffused purplish above; leaf blade oblong, elliptical to obovoid, usually 12–20 × 2.5–5.5 cm (10–15 × 2–4 cm in var. *iranicum*), either entire, obtusely acute to rounded at apex, densely irregularly denticulate, or pinnatifid to pinnatisect; terminal leaf segment triangular to broadly ovate, rounded to obtusely acute, distal margin convex, denticulate, proximal margin straight to concave, denticulate, patent to recurved, lateral segments (3) 4–6, large, \pm triangular, patent to subhamate, both margins denticulate, distal one convex, proximal one \pm straight or concave; interlobes \pm short, irregularly denticulate, margins raised, mid-vein pale green to pale brownish pink; petiole short, usually 1 (–2) cm long, usually light pink-purple. Scapes over topping leaves, irregularly densely floccose-aranose. Capitulum small to medium-sized, ca. 3 cm in diam., \pm flat, light to bright yellow; involucre cylindrical (Fig. 6), outer phyllaries 30–46 (26–35 in var. *iranicum*), linear-lanceolate, 6–8 × (1.0–) 1.3–1.8 mm, imbricate, appressed or loosely appressed at base, arcuate-recurved in upper half, green to grey-green, usually suffused pink or light brownish purple, middle part darker, bordered pale green, usually \pm evenly densely ciliate, \pm flat. Ligules flat, outer ones abaxially striped brown-purple. Pollen developed, pollen grains of \pm uniform size; stigmas yellow. Achenes of various colours, usually pale greyish straw-brown, but also yellowish straw-coloured, olivaceous greyish, pinkish pale brown, medium brown or silvery whitish, sometimes also pale ochraceous, narrowly turbinate, gradually narrowing at both ends, 4.4–6.8 (–7.2) mm long (incl. cone), (0.8–) 0.85–1.1 mm wide, wider in upper 3/5–2/3 of achene length, achene body very gradually, almost indistinctly narrowing into the cone; cone ca. (0.7–) 0.8–1.4 (–2.0) mm long; rostrum (5–) 7–9 (–10.5) mm (to 11–13 mm in var. *iranicum*), pappus 6–8 (–10) mm (5.5–6 (–7) mm in var. *iranicum*), pale brownish, yellowish-brownish or dirty whitish. Flowering optimum late summer.

Reproduction: As proven by Gustafsson (1932), *T. serotinum* is not an autonomous apomict. Numerous experiments (carried out also by T. Černý and J. Štěpánek, not presented here) with isolated capitula showed that there is no tendency to unassisted autogamy, either. The character of self-incompatibility remains to be tested; the absolutely prevailing allogamy seems to be proven.

Distribution: The largest region of the continuous distribution of *T. serotinum* subsp. *serotinum* extends from eastern Romania and Bulgaria through Ukraine and SE European Russia to NW Kazakhstan (in the NW and near the Caspian coast); there is another large part of its range in the NW Pannonian region (reaching Moravia and NE Austria) and Anatolia, Lebanon and Syria. Smaller, more or less isolated regions of its occurrence are in other parts of the Balkans, in Transcaucasia, N Iran and adjacent parts of Turkmenistan and Afghanistan.

Material studied: We have seen over 800 herbarium specimens of subsp. *serotinum* from all the regions listed above. The lists of specimens are available upon request from JK or JŠ.

Variation: As may be expected for a sexually reproducing taxon with a large geographical range, the variation is relatively extensive, lower near the NW limit of its range, higher in some regions, such as Bulgaria and adjacent countries (a variation involving even achene colour). With a single exception, the variation does not form any population units.

The exception is *T. serotinum* in Iran where the plants studied are distinct in having shorter pappus and longer rostrum (much higher values of the rostrum/pappus ratio). We recognize plants with such aberrant achenes as a separate variety:

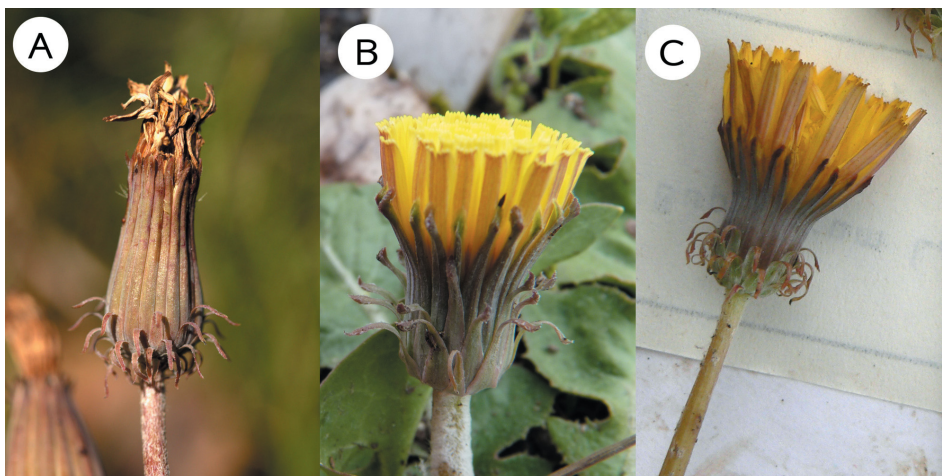


Fig. 6. – Involucre of *Taraxacum serotinum* subsp. *serotinum* (A), population Ce (Czech Republic, photo by VZ at the locality), *T. serotinum* subsp. *tomentosum* (B), cultivation (cult. no. 9198, photo by JŠ) and *T. haussknechtii* (C), cultivation (cult. no. 8293 m photo by JŠ); see Table 1 and Fig. 1 for details.

Taraxacum serotinum* var. *iranicum Kirschner, Štěpánek, Zeisek et Amini Rad, **var. nova**

Type: “Iran [Mazandaran Province], 25 m. S of Amol. Central Elburz N slopes. Rocky slopes”, 4000–5000 ft, 21 August 1966, P. Furse 9054 (holotype: K, no. det. 12021).

Diagnosis: *A varietate typica rostro longiore et pappo brevior differt.*

Brief description: Plants less robust, with slightly narrower, erect-petent leaves, usually deeply divided into denticulate lateral lobes, slightly smaller capitula and involucre, lower number of outer phyllaries (26–35) and achenes with rostrum usually 9.5–11 (–13) mm long and pappus 5.5–6 (–7) mm long.

Comments: Both the genetic relationships (inferred from SSRs analyses) and the morphology of the specimens analyzed indicated a relatively distinct position for the Iranian plants. However, because there are overlaps between the ranges in the variation in the diagnostic characters, and the material used does not show any population variation, we treat these plants as a variety of *T. serotinum*.

Distribution: The material studied is confined to the N to NE part of Iran, provinces of Mazandaran, Semnan and Khorasan. It is a region quite isolated from the nearest area where *T. serotinum* occurs.

Specimens studied: Iran: Golestan National Park, E. Mazandaran, N. Semnan, Tanggol, 37°22'30"N, 55°56'E, 670 m, 16 Nov 1996, H. Akhani 12296 (herb. Akhani, no. det. 26458). – Golestan National Park, E Mazandaran, N Semnan, ca. 14 km SW of Lohondor, Koilar, 37°30'N, 55°50'E, 1300 m, 9 Jul 1995, H. Akhani 11705 (herb. Akhani, no. det. 26457). – Golestan National Park, E Mazandaran, N Semnan, ca. 500 m E of Alu-Baq spring, 1700 m, 8 Aug 1995, 37°19'N, 55°53'30"E, H. Akhtani 11917 (herb. Akhani, no. det. 26456). – Mazandaran, Kojur, Kohnah-Lashak, 1600–1980 m, 6 Jul 1982, Termeh, Moussavi & Tehrani (IRAN, no. det. 28788). – [Mazandaran] Elbourz, Tchalmish [mt. Chal Mish], 2300 m, 23 Jul 1948, Behboudi & Aellen (IRAN, no. det. 28785). – [Semnan] Shahrud, Khosh-yeilagh, Gardaneh-ye Olang, 1950–2000 m, 18 Aug 1978, Termeh, Moussavi & Tehrani (IRAN, no. det. 28786). – Semnan, Shahmirzad [to] Sari, 31 km [of] Shahmirzad, Has-Kouh, 2250–2350 m, 14 Jul 1988, Termeh & Karavar (IRAN, no. det. 28792). – Semnan, Shahmirzad towards Chashm, 15 km [of] Shahmirzad, 2400 m, 28 Jun 1992, Termeh, Moussavi & Tehrani (IRAN, no. det. 28790). – Khorasan, Shirvan, Namanlou, Golul, Tcheshmeh-Gabri, 2400 m, 19 Jul 1986, Termeh, Moussavi & Tehrani (IRAN, no. det. 28783). – Khorasan, Neyshahur, Sheykt, Binaloud, 1500–2250 m, 30–31 Jul 1976, Termeh & Tehrani (IRAN, no. det. 28794).

b. *Taraxacum serotinum* subsp. *tomentosum* Nyman, Consp. Fl. Eur. 2: 437 (1879).

- ≡ *Taraxacum pyrrophappum* Boiss. et Reut., Diagn. Pl. Nov. Hisp. 19 (1842)
- ≡ *Taraxacum tomentosum* Lange, Vidensk. Meddel. Naturhist. Foren. Kjöbenhavn 1861: 101 (1861), nom. illeg., Art. 52.1, 52.2
- ≡ *Taraxacum serotinum* subsp. *pyrrophappum* (Boiss. et Reuter) Bolós et al., Fl. Paisos Catalans 1215 (1990), nom. illeg. “*pyropappum*”. – Type indication: p. 20: “Hab. in argillosis ad vias propè Matritum infra Caravanchel, inter Ocana et Aranjuez, et propè le Guardia, etc.” – Type: [a gathering of two herbarium sheets in herb. Boissier] “Entre Ontigola et Ocana ... ad vias. Junio 1841, Reuter” (lectotype: G, no. det. 18319, designated by Burdet et al. 1983: 801). – Residual syntype: “Aranjuez, in argillosis.”, Jun 1841, Reuter (BM, no. det. 9790).
- = *Taraxacum neyrautii* Debeaux, Bull. Soc. Hist. Natur. Toulouse 25: xii (1891) (? Jun.); etiam Bull. Soc. Bot. Fr., Paris, 38 (ser. 2, vol. 13): IX (1891) (? Jul.) et Rev. Bot. 9: 255 (1891) (? Jul.-Oct.), “Neyrauti”. – Type indication: [plants collected by J. Neyraut on June 10, 1888, and on August 15, 1890, at Mt. Alaric]. Type: “Plantes de France. Comigne (Aude). Mont Alaric, de la bergerie au sommet de la montagne.”, 15 Aug 1890, E. J. Neyraut (**lectotypus, hic designatus**: MPU, no. det. 20361). – Residual syntype: “Alaric, Aude ... [illegible], feuilles radicales.”, Jun 1888, [E. J. Neyraut] (MPU, no. det. 20347). – Further authentic material: “de Capendu à Moux (Aude.), sur le mont Alaric.”, 12 Jun 1888 [E. J. Neyraut] (MPU, no. det. 20360).

Note: There are certain doubts about the priority of the various publications by O. Debeaux that appeared in 1891. The Bull. Soc. Bot. Fr. publication cites the Toulouse description (without page reference) and there is a separate booklet publication [Debeaux O. (1891): Note sur plusieurs plantes nouvelles ou peu connues de la région méditerranéenne et principalement des Pyrénées-Orientales. – Paul Klincksieck, Paris, 8 vol, 53 pp., n. v., Tax. Lit. 29344, probably Jul. 1891, corresponding to the Rev. Bot. publication] also cited in Rev. Bot. For the time being, we ascribe the priority to the Toulouse publication but a detailed bibliographic search might change this conclusion. It is important that all the three publications cite the material collected by J. Neyraut, first in June 1888 and then in August 1890.

- ≡ *Taraxacum serotinum* var. *spathulifolium* Rouy, [scheda, exs.:] Société Rochelaise 1891, no. 3101 (1892) ut “*spathulaefolium*”, see also Rouy, Fl. Fr. 9: 192 (1905) [the exsiccate seen in MPU, no. det. 20358 & 20350; P 4304008 & 4304986, photo!].
- = *Taraxacum serotinum* var. *breviscapum* Schultz-Bip. in Willkomm, Sertum Fl. Hispan. 93 (1852). – Type indication: “Pl. exs. coll. ven. n. 460” [= Willkomm, Iter Hisp. Secunda, no. 460]; also cited *T. pyrrophappum* Boiss. et Reuter, and the following localities: “... prope Daroca ..., ... inter Pozondón et Celda ..., ... circa Molina ..., ... inter Tarrascosa et Carancón ..., in Castella vetere ..., ... prope monasterium el Paulár ...”. – Type: “[Hispania] In argilloso-arenosis inter Molina et Chera et alibi in Castella Nova.”, Aug 1850, Willkomm, Iter Hisp. Secunda, no. 460 (**lectotypus, hic designatus**: P 3726134, photo!; isolectotype: G, no. det. 22590; PRC 403195, no. det. 26948). – Residual syntypes: “In argillosis sterilibus prope Dasoon in Arragonia.”, Jul 1850, Willkomm (P 3726135, photo!). – “In argilloso-arenosis in silvis Juniperi Sabinae inter Pozondón et Celda in Arragonia australi.”, Aug 1850, Willkomm (P 3726135, photo!). Icon.: Fig. 7.

Description: Plants small to medium-sized, usually 5–12 cm tall, densely brown aranose at base, the base also covered with remnants of old petioles (Fig. 7). Leaves subcoriaceous, leaf rosettes similar to those of *T. obovatum*, smaller than those of *T. serotinum*, with narrower, leaves usually appressed to the ground, light greyish-green, initially ± densely whitish tomentose-aranose, later glabrescent, leaf surface usually swollen at hair base; leaf blade broadly oblong-spatulate, usually 6–11 × 2.5–4 cm, margin (including that of lateral segments) usually irregularly denticulate, blade often undivided, frequently pinnatilobed to pinnatipartite, rarely pinnatisect, terminal segment usually large, dominant, ± obtuse, often with a minute mucro, lateral segments usually 2–4 (–5), broadly triangular to triangular-lingulate, short, patent to subrecurved, rarely subhamate; blade gradually narrowed into 1–4 cm long, narrow, pale to pink-brown, densely hairy petiole; mid-vein pale to paled pinkish-brownish, initially densely floccose-aranose. Scapes short at anthesis, usually conspicuously shorter than leaves, often only 2–4 cm long, usually remaining short during fruit ripening, light green, often suffused bronze, wholly tomentose-aranose or densely floccose-aranose. Capitulum small to medium-sized, imperfectly opening and therefore only 1.5–2.5 cm wide, flat, ± pale yellow; involucre rounded to subtruncate at base, ca. 7–8 mm in diam., light olivaceous-green, usually suffused pinkish, slightly pruinose; outer phyllaries 26–35 (–38), linear-lanceolate to linear, (4–) 5–8 × (0.8–) 1.0–1.7 (–2.3) mm appressed at base, upper half arcuate-recurved, in general very similar to those of *T. serotinum* in shape, size and coloration but relatively sparsely ciliate, usually only near phyllary apex, inner phyllaries to ca. 10 mm long, corniculate, longitudinally striped purplish, pruinose. Ligules flat, outer ones abaxially striped grey-pink to grey orange, apical

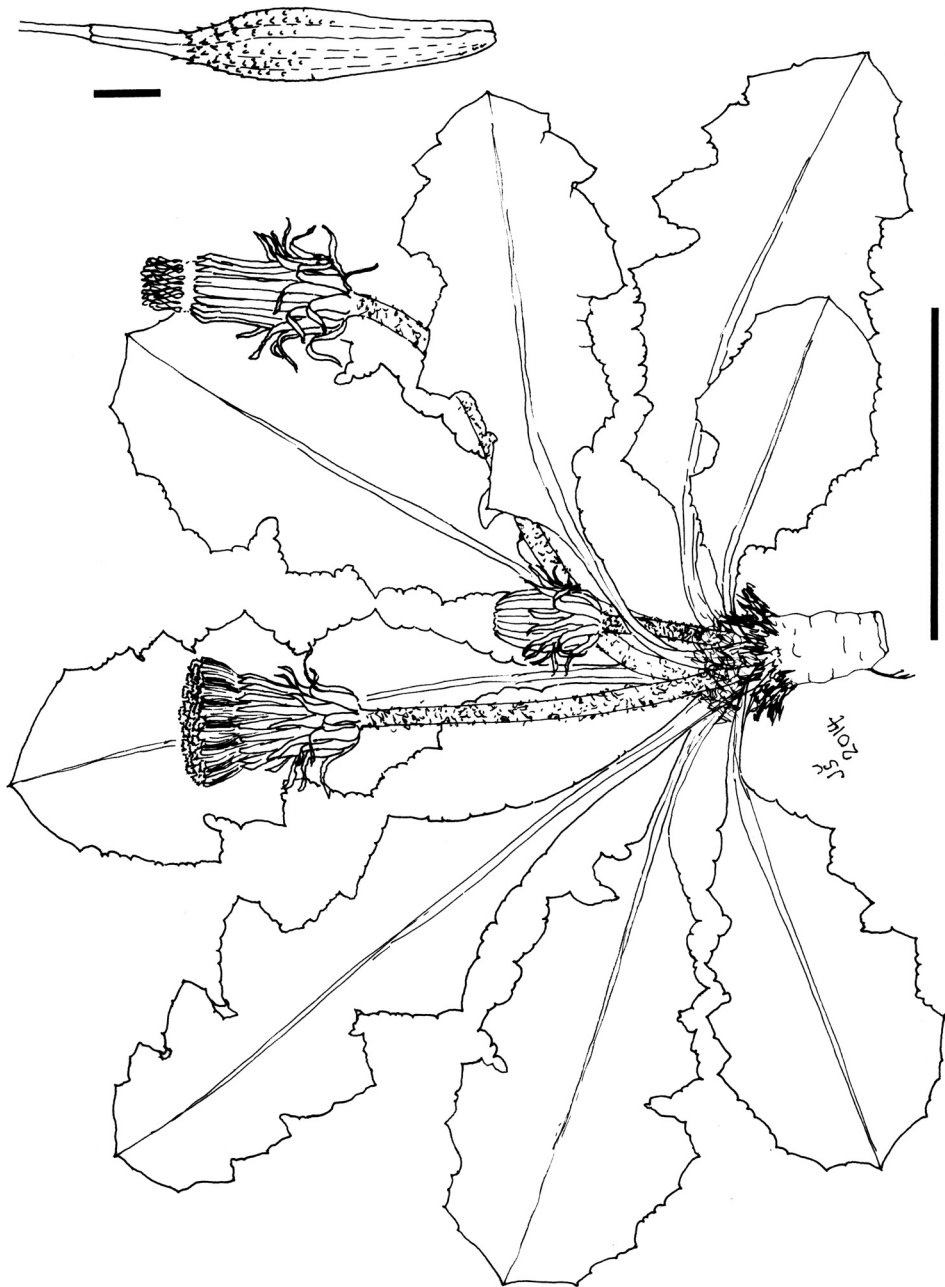


Fig. 7. – *Taraxacum serotinum* subsp. *tomentosum*. Habit (A), scale bar = 5 cm, and achene (B), scale bar = 1 mm. Drawn by J. Štěpánek.

teeth yellow. Pollen developed, pollen grains uniform in size; stigmas yellow. Achenes (yellowish) light greyish pale straw-brown, narrowly turbinate, 4.6–5.9 mm long including cone, 0.8–1.05 mm wide, achene body with upper 1/3–1/4 covered with sparse to subdense short spinules (less often squamules), otherwise smooth, very gradually narrowing into subconical to subcylindrical cone ca. 0.8–1.5 mm long; rostrum 4–8 mm long, pappus 4.5–7 mm long, \pm invariably yellowish light brown. Flowering optimum: summer to late summer.

Note: It is not easy to distinguish from *T. serotinum* subsp. *serotinum* (for details, see Table 4). In general, plants of *T. serotinum* subsp. *tomentosum* are smaller, leaves have a relatively longer petiole, leaf lateral lobes are less rounded (more “angled”), scapes shorter, not elongating, capitulum not fully opening.

Reproduction: Both the imperfectly opening capitula and the almost complete homozygosity indicate autogamy.

Distribution: Widely distributed in CE and SE Spain, in S France and, probably introduced, at a single site in N Morocco (e.g. van Soest 1954).

Specimens studied: France: Aude. In pascuis elatioribus montis Mont-Alaric supra Comigne, Jul 1899, E. J. Neyraut. Dörfler, Herb. Norm., no. 3948 (BRNU 6744, no. det. 742; E, no. det. 11849; G, no. det. 22591; LD, no. det. 17828; MPU, no. det. 20356; P 4142844 & 4320000, photo!; PR, no. det. 456; PRC, no. det. 21155; S, no. det. 23429; WU, no. det. 22123; Z, no. det. 24515; ZT, no. det. 24556). – Aude: Mts Alaric, pentes entre Comigne et Mouse., 12 Aug 1904, herb. L. Marty (ZT, no. det. 24554). – Aude. Mt. Alaric: pentes rocheuses faces à Comigne, 11 Sep 1910, L. Marty (P 4272371, photo!). – Plantes de France. Comigne (Aude). Mont Alaric, de la bergerie au sommet de la montagne, 26 Jul 1899, E. J. Neyraut (MPU, no. det. 20357; S, no. det. 23474; WU, no. det. 22126; ZT, no. det. 24555). – Aude: mont Alaric, autour des bergeries situées au SSE, du village de Comigne, 12 et 26 Jul 1891, E.-J. Neyraut. Magnier, Fl. Selecta Exs., no. 2770. (G, no. det. 22592; MPU, no. det. 20353, 20351, 20349 & 20348; P 4453687, 4319999 & 3314530, photo!; S, no. det. 23475; WRSL, no. det. 28540; WU, no. det. 22125 & 22121). – Moux (Aude), sur le trajet du four à chaux à la métairie St. Antoine située au pied du Mont Aric, 3 Jul 1892, [E. J. Neyraut] (G, no. det. 22593). – Montpelier, Port Juvenal, 1829, coll.? (MPU, no. det. 20537). – Bizaneti (Aude), Alentours de Bouquig, 19 May 1901, E. J. Neyraut (MPU, no. det. 20355). – Aude, à Ste. Eugénie (Cne. de Peyriac), 26 May 1901, E. J. Neyraut (MPU, no. det. 20354). – Cucugnan (Aude), château de Quiribus, et Maury (Pyrénées orientales), en suivant le route de Maury à Cucugnan, 7 Jul 1908, E. J. Neyraut (MPU, no. det. 20359; P 4121414, photo!). – Aude, Montagne d’Alaric entre Heure et Moux, 11 Sep 1910, L. Marty 1720. (MPU, no. det. 20346; P 4272367, photo!). – Aude: mont Alaric, 12 Jul 1891, [E. J. Neyraut] (MPU, no. det. 20352). – Aude: Laroque-de-Fa, coteaux secs, bords des chemins., Aug-Sep, J. Delpont (P 4131406, photo!).

Spain: Province de Teruel. Sierra de Valacloche, pelouses arides, sur le calcaire, 1,600 mètres, 1893, E. Reverchon, Pl. Espagne, prov. Teruel, no. 836 (E, no. det. 11848; P 3726148, photo!; PR, no. det. 449 & 28610; PRC, no. det. 21148; UPS, no. det. 24226 & 24232; WU, no. det. 22120; P 4304090, 3726152 & 3726155, photo!; Z, no. det. 24514). – Castille: Bujedo, chemins, 7 Aug 1907, H. Elias (BRNU 29253, no. det. 921; MPU, photo!; P 3726144, photo!). – Castille: Obarenes, dans le bois près d’une bergerie, 11 Sep 1907, H. Elías (P 3726154, photo!). – Almeria, s. dato, Rigo 306 (Z, no. det. 24665). – Plantae Aragoniae australis, Jul 1863, F. Loscos 23 (UPS, no. det. 24227). – Bailo (Espagne, prov. Huesca), 2 km au nord du petit village nommé Alastuey, lieu-dit Pardina de Villanovilla, 30T XN 8411, alt. 670 m, 16 Aug 1969, P. Montserrat (JACA 544069). Soc. Éch. Pl. Vascul. Eur. Bassin Méditerr., fasc. 23, no. 14703. (B, no. det. 22212; RU, no. det. 11650; P 4121240, photo!). – Prov. Almeria, loc. herbicida circa Maria, et Sierra de Baza, sol. calcar. 500–800 m s. m., 23 et 30 Jul 1895, Porta et Rigo, Iter IV. Hispanicum 1895, no. 306. (MPU, photo!; P 3726145, photo!; PR, no. det. 28608; WU, no. det. 22127). – Ad vias viarum reg. inf. juxta Castelserás. Aragonia, 20 Jul 1876, F. Loscos (WU, no. det. 22124). – Ad vias juxta Albarracín (Aragonia), 20 Sep 1886, Pau (WU, no. det. 22122). – Castille: Bujedo, 24 Oct 1906, Elias. Sennen, Pl. d’Espagne, no. 193 (MPU, photo!; WU, no. det. 22119). – Castille: Bujedo, 1907, Elias (MPU, photo!). – Fiscal, Aragon, Aug 1878, Bordère (MPU, no. det. 20536; P 3268584, photo!). – [Flora Aragonensis] ad vias viarum reg. inf. Castelserás, Jul 1876, F. Loscos (MPU, photo!). – Aragon, Aug 1909, Caruel (MPU, photo!). – In collibus calcareis ad Burgos, Aug 1851, [J. Lange] (G, no. det. 22588). – Ad vias prope Parador de Villanuble (pr. Valladolid), 7 Jul 1852, [J. Lange] (G, no. det. 22589). – Aragon, Castelseras, Jun 1876, F. Loscos 134 (LE, no. det. 17773). – Castelserás, 20 Jul 1876, F. Loscos 34 (MPU, photo!; P 3314626 & 3726156, photo!; PRC 401808, no. det. 25139; WRSL, no. det. 28542). – Aragon, El Puerto, 31 Aug 1909, F. Sennen, Pl. d’Esp., no. 193 (PRC 401809, no. det. 25138). – Aragon: Teruel, Aug 1909, [Fr. Sennen] (MPU, photo!). – Oto, Aragon, Jul 1883, Bordère (PR, no. det. 28404). – In collibus calcareis ad Burgos., 14. X. 1851, [J. Lange] (P 3726132, photo!). – Medina del Rioseco, 7 Jul 1851 vel 1852, J. Lange (P 3726135, photo!). – Teruel, entre Linares de Mora et Noguerauelas, alt. 1500 m, 24 Jul 1976, B. de Retz 73626 (P 4121241, photo!). – Murcia, Bullias, 1896, M. Gandoger, Fl. Hisp. Exs., no. 347. (P 4304985, photo!). – Bujaraloz, Hostal del Cervio, 19 May 1972, S. Barrier 72-322 (P 4121225, photo!). –

Prov. Huesca, Broto, zwischen Fiscal und Boltaña, an der N260, 4 Aug 2007, F. G. Dunkel (herb. F. G. Dunkel Du-20343-1, no. det. 26428).

2. *Taraxacum haussknechtii* Uechtr. in Hausskn., Mitt. Thür. Bot. Ver. 7: 49 (1895).

≡ *Taraxacum serotinum* subsp. *haussknechtii* (Uechtr.) Gajić in Fl. SR Srbije 7: 298 (1975). – Type indication: “Hab. in schistosis P. T. pr. Malakasi, a medio Jul. florens.” – Type: “C. Haussknecht. Iter Graecum 1885. Pindus Tymphaeus: pr. Malakasi in serpentin.”, 18 Jul 1885, C. Haussknecht ut *T. Haussknechtii* Uechtr. (**lectotypus, hic designatus**: JE, no. det. 28528; isolectotype: “Graecia: Pindus Tymphaeus, pr. Malakasi, in serpentin.”, 18 Jul 1885, C. Haussknecht (S, no. det. 23504); “Pindus Tymphaeus: in schistos. pr. Malakasi.”, Jul 1885, C. Haussknecht ut *Taraxacum Haussknechtii* Uchtr. (BM, no. det. 8829).

= *Taraxacum gracile* Formánek, Verh. Naturforsch. Ver. Brünn 37(1898): 158 (1899). – Type indication: “Habitat ad pagum Gewgeli in M. [Macedonia]” – Type: “Gewgeli, Macedonia.”, 24 Aug 1898, E. Formánek (holotype: BRNM 5274/36, no. det. 21605).

Icon.: Fig. 8.

Description: Plants small to medium-sized, usually 8–15 cm tall (in cultivation, they sometimes reach 25 cm); plant base densely brownish aranose, base not covered with remnants of old petioles (Fig. 8). Leaf rosettes large (leaves much more numerous than in the other taxa of this section) with numerous scapes, leaves usually erect-patent, some of them may be appressed to the ground, conspicuously narrow, usually 6–12 × 0.5–2 cm, subcoriaceous, light green, not spotted, less often with little brown-purple spots, sparsely to ± densely aranose; leaf blade linear-lanceolate, linear-oblongeolate to linear-elliptical in outline, almost always pinnatisect, rarely ± pinnatilobed; terminal segment relatively small, usually 7–15 × 4–10 mm, triangular to broadly so in outline, or helmet-shaped, often with a sagittate base, acute to acuminate, sometimes mucronate, distal margin ± straight or concave or sigmoid, entire or with several acute teeth, rarely with an incision, proximal margin ± straight or concave or sigmoid, entire or with 1–2 minute acute teeth; lateral segments 5–8 (–9) pairs, opposite or alternate, triangular to narrowly so, relatively small, usually 4–8 × 3–10 mm, slightly recurved to patent, acute; interlobes of variable length, usually narrow, (0–) 5–10 × 1–4 mm, not densely dentate to lobulate, margins raised, often bordered brown-purple; mid vein pale or brownish; petiole narrow or narrowly winged, pale greenish or suffused brownish pink, usually 1.5–2 cm long. Scapes very numerous (over 20 even in small plants), sub-equal leaves, densely aranose, pale greenish to suffused bronze. Capitulum small, 1.5–2.5 (–3) cm in diam., ± flat, golden yellow to light yellow (rarely to light ochraceous yellow). Involucre very small, narrowly cylindrical, 4–5 (–6) mm wide, rounded to ± truncate at base; outer phyllaries (15–) 18–34, linear to linear-lanceolate, 4–7 × 0.6–1.2 (–1.4) mm, imbricate, relatively regularly arranged, appressed in lower part, distal part of phyllary arcuate to arcuate-recurved, flat to callose near apex, light green to pale pinkish to light purplish, paler towards margins, with 0.05–0.15 mm wide whitish-membranous border, not ciliate or sparsely ciliate, if so, then more densely towards the apex; inner phyllaries 13–25, usually 8–11 mm long, of equal width, light olivaceous green, later becoming pink. Outer ligules flat, striped pale to very pale greyish-pinkish, greyish-purplish to greyish olivaceous outside, apical teeth usually deep yellow or ± reddish, inner ligules canalliculate, with apical teeth yellow; stigmas deep yellow, pale yellow pubescent outside; pollen abundant, pollen grains uniform in size. Achenes usually (yellowish) light greyish pale straw-brown, narrowly turbinate, (4.2–) 5.0–6.2 (–7.0) mm long including cone, 0.9–1.1 mm wide, achene body with upper 1/3–1/4 covered with sparse to sub-dense short spinules, otherwise ± smooth, very gradually narrowing into subconical to subcylindrical cone 0.8–1.5 (–1.7) mm long; rostrum (4–) 6–9 (–10.5) mm long, pappus (5–) 6–8 mm long, yellowish light brown to pale greyish-brownish, sometimes with a pinkish hue. Flowering optimum: summer to late summer.

Distribution: *T. haussknechtii* is centered in the Republic of Macedonia and adjacent parts of Greek Macedonia and Thessaly, rarely in other parts, and marginally reaches Albania, Serbia and Bulgaria. See Fig. 9 for map of distribution of the species.

Reproduction: The results of population analyses point to the absolutely prevailing allogamy. Isolated capitula (tested by J. Štěpánek and T. Černý, not presented here) did not yield well developed achenes without forced autogamy.

Specimens studied: Bulgaria: In collibus Konjovo ad Kistendyl, Aug 1904, Mrkvička (PRC 403305, no. det. 26993). – M. Golo Bardo: in lapidosis calcareis supra refugium Slavej, 28 Aug 1970, N. Vihodcevski (KRAM 229235, no. det. 3278). – Pernik, Golo Bardo, chalet Orlite, 1986, B. Kuzmanov 8634 (PRA, no. det. 27405). – Pernik, Golo Bardo, between Slavej and Orlite, 25 Sep 1976, B. Kuzmanov (PRA, no. det. 27404). – Montes Rodopi centr., Chepelare, 26 Sep 1987, B. Kuzmanov 8746, cult. as JŠ 3138 (PRA, no. det. 25348, 25347). – Ad vias prope Radomir, Aug 1887, J. Velenovský (PR, no. det. 28600).

Greece: Macedonia, Lithochori, 9 Aug 1891, P. Sintenis et J. Bornmüller, Iter Turcicum 1891, no. 1333 (BP 470653, no. det. 25248; BRNM 5288/36, no. det. 21604; G, no. det. 18977; JE, no. det. 28535; OXF, no. det.

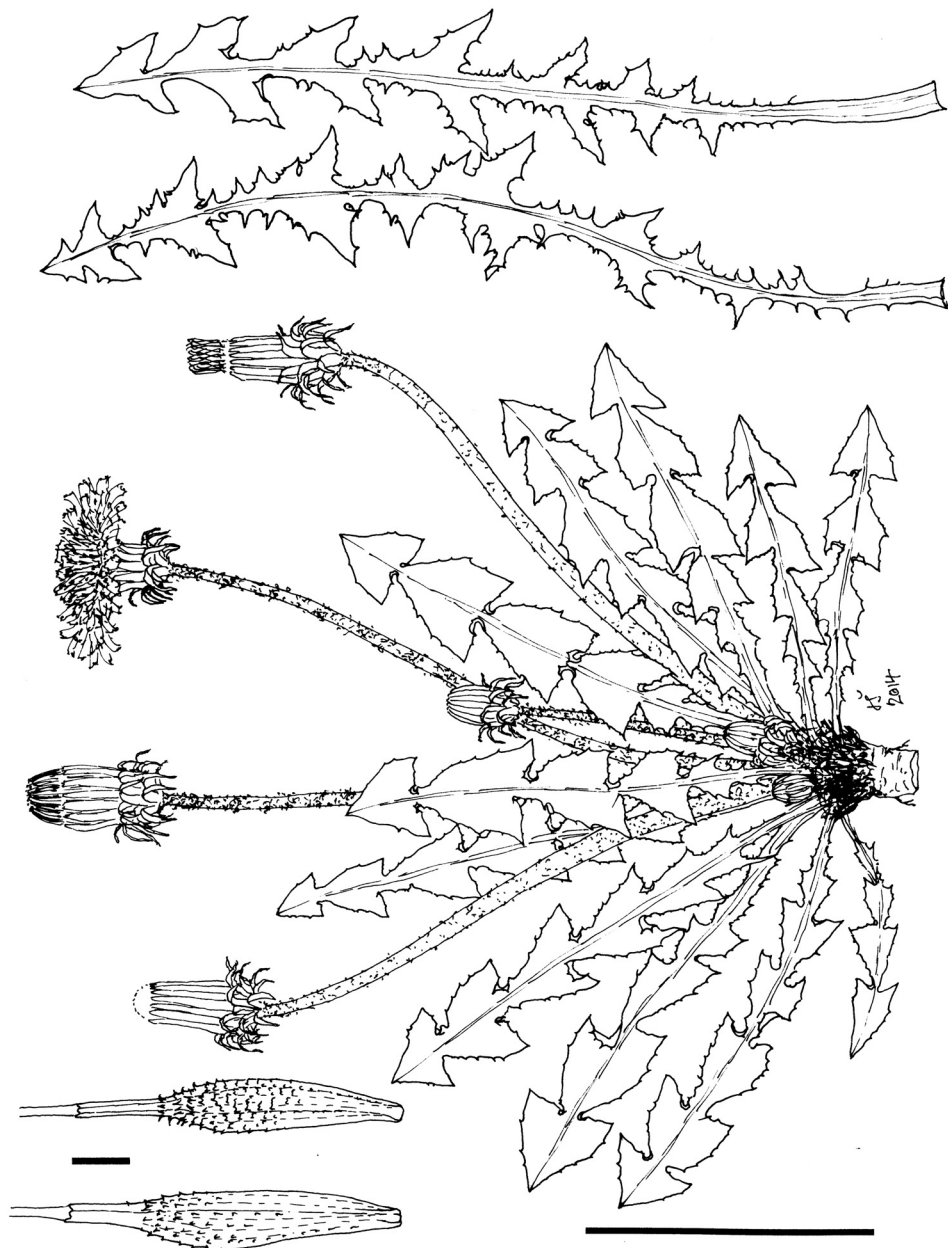


Fig. 8. – *Taraxacum haussknechtii*. Habit (A), scale bar = 5 cm, leaves of two different morphotypes (B) and two achenes (C), scale bar = 1 mm. Drawn by J. Štěpánek.

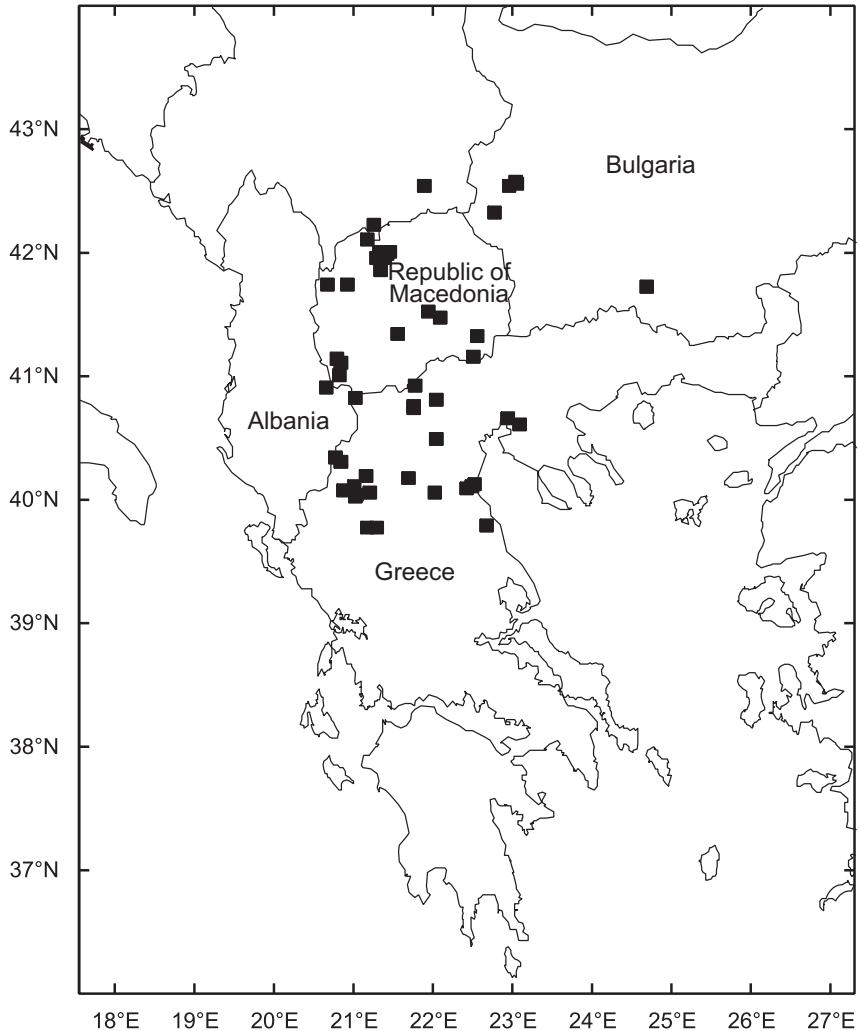


Fig. 9. – Distribution of *Taraxacum haussknechtii* based on herbarium specimens (see the text).

11980; PR, no. det. 28592; PRC, no. det. 21145; W 1892-9551, no. det. 21192; WU, no. det. 21914; WU, no. det. 21989). – M. Korthiati in Macedonia, Aug 1898, E. Formánek (BRNM 5286/36, no. det. 21603). – M. Ossa in Thessalia, 1 Aug 1889, E. Formánek (BRNM 5284/36, no. det. 21601). – Xerolivadon pl. in Macedonia, Aug 1899, E. Formánek (BRNM 5278/36, no. det. 21594). – Karaferia in Macedonia, Aug 1898, E. Formánek (BRNM 5277/36, no. det. 21593). – Thessalien, Prov. Trikala, NE Malakasi, etwas oberhalb des Ortes, ca. 900–1000 m, 17 Jul 1985, W. Burri & F. Krendl (W, no. det. 21459). – Nomos Grevena, westlicher Ortsrand von Samarina, 1559 m, 40°06'23.2"N, 21°00'38.8"E, 27 Jul 2009, T. Gregor & L. Meierott TG5443 (FR, no. det. 25182). – Nomos Grevena, 2.7 km NE Distrata, N Vasilitza-Berg, 1370 m, 40°02'50.2"N, 21°02'11.4"E, 29 Jul 2009, T. Gregor & L. Meierott TG5522 (FR, no. det. 24499). – Nomos Ioannina, Grammos, 0.8 km NW Aetomilitsa, 1475 m, 40°18'50.4"N, 20°50'49.8"E, 3 Aug 2009, T. Gregor & L. Meierott TG5678 (FR, no. det. 24498). – Nomos Florina, 0.4 km SW Psorades, 850 m, 40°49'35.7"N, 21°01'45.2"E, 6 Aug 2009, T. Gregor & L. Meierott TG5803 & TG5805 (FR, no. det. 24497 & 24496). – Nomos Florina, Uferbereich des Vegoritida-Sees 1.5 km N Agios Panteleimonas, 513 m, 40°44'20.0"N, 21°45'24.6"E, 6 Aug 2009, T. Gregor & L. Meierott

TG5809 (FR, no. det. 24495). – N. Pindos, W ober Samarina gegen Smolikas, 1550 m, 27. VII. 2009, L. Meierott & T. Gregor LM GR-09/55 (herb. L. Meierott, no. det. 22724). – Prespa See, NW Psarades, 850 m, 6 Aug 2009, L. Meierott & T. Gregor LM GR-09/359 (herb. L. Meierott, no. det. 22723). – Limni Visovitici NE Ayos Pantaleimon, 6 Aug 2009, L. Meierott & T. Gregor LM GR-09/366 (herb. L. Meierott, no. det. 22722). – N Pindos (Gramos), Aetomilitsa (1400 m), 3 Aug 2009, L. Meierott & T. Gregor LM GR-09/262 (herb. L. Meierott, no. det. 22721). – N Pindos, SE Smolikas, NE ober Dhistratos, 1370 m, 29 Jul 2009, L. Meierott & T. Gregor LM GR-09/118 (herb. L. Meierott, no. det. 22720). – N Pindos, NW ober Metsovon, 1350 m, 26 Jul 2009, L. Meierott & T. Gregor LM GR-09/38 (herb. L. Meierott, no. det. 22719). – N Pindos, zw. Grevena u. Samarina, 830 m, 26 Jul 2009, L. Meierott & T. Gregor LM GR-09/46 (herb. L. Meierott, no. det. 22718). – Macedonien, bei Saloniki, Aug 1873, T. Pichler (BP 470652, no. det. 25255). – Olympus: Hagios Dionysios, 13 Sep [18]89, P. Sintenis, Iter Orient. 1889, no. 1828 (WU, no. det. 21995). – Macedonia, in loc. pinguibus pr. Salonicum, Jul 1873, T. Pichler (G, no. det. 18976; W 1889-99616, no. det. 20887; WU, no. det. 21917). – Macedonia, Felstriften des Korthiać-Gebirges bei Saloniki, Bergregion, Jul 1906, L. Adamović (WU, no. det. 21913). – Auf fetten Grund bei Salonik, Aug 1873, T. Pichler 191 (G, no. det. 18981). – Thessalia, Olympus, ca. 900 m, 14 Aug 1934, J. Wagner (W 1934-7781, no. det. 21191). – Thessalia, Olympus, 900 m, Herolakki, 14 Aug 1934, J. Wagner (PR, no. det. 28590). – In montis Olympi Thessaliae pede, circa Litochoron 250-350 m, 14 Jul 1927, H. Handel-Mazzetti (W, no. det. 20888). – Montes Smolikas, in declivitatibus merid., 1500 m, a. 1997, A. J. Richards, cult. as JŠ 7074 (PRA, no. det. 27402). – Nom. Ioannina/Kastoria, Pendelofos Pass, Kastoria – Ioannina road, 1500 m, 21 Jul 1997, A. J. Richards (PRA, no. det. 25349). – Voilya, Grammos Mts., Macedonia, 4500 ft, 9 Sep 1937, Balls & Balfour Gowrley B4012 (E, no. det. 11834). – Mt. Vourinos, E of Exarchos, Grevenon, 95 m, 18 Aug 1983, I Hagemann, H. Ketelhut & H.-J. Wolf 1056, Soc. Éch. Pl. Vasc. Eur. Bass. Méditerr., no. 16609 (P 4133326, photo!). – Thessalie, Larissa, Elasson, à 21 km au de la localité, près de la route à Kozane, 700 m, D. Podlech 25970, Soc. Éch. Pl. Vasc. Eur. Bass. Méditerr., no. 8028, ut *T. serotinum*. (P 4436993, photo!). – Massif du Kadmaktchalan (Macédonie), Ostrovo, Sep 1938, H. Humbers & S. Topali H396 (P 4278442, photo!).

Republic of Macedonia: Skopje, 17 Aug 2007, P. Petřík (digit. photo, no. det. 19378). – Držilov [?Držilovo] pr. Skoplje, 9 Aug 1922, K. Vandas (PR, no. det. 28607). – Rosomani, 19 Aug 1893, E. Formánek (BRNM 5285/36, no. det. 21602). – Ůskub [Skopje], 20 Aug 1887, E. Formánek (BRNM 5283/36, no. det. 21600). – Ůskub [Skopje], Aug 1889, E. Formánek (BRNM 5282/36, no. det. 21599). – Vodena [Vodno], Aug 1899, E. Formánek (BRNM, no. det. 21597). – Lukavec, Aug 1899, E. Formánek (BRNM 5280/36, no. det. 21596). – Gorničava pl. [planina], Aug 1898, E. Formánek (BRNM 5276/36, no. det. 21592). – Gorničava pl., Aug 1897, E. Formánek (PR, no. det. 28609) – Ohrid, E von Peštani, 800-1000 m, 15 Jul 1976, E. Krendl & F. Krendl (W, no. det. 21464). – N von Valandovo, gegen den Melki Rid, 300–500 m, 14 Jul 1977, E. Krendl & F. Krendl (W, no. det. 21432). – In aridis apricis montis Vodno (dit. Ůsküb), 300–800 m, 20 Aug 1917, J. Bornmüller, Plantae Macedoniae, no. 1381 (BP 470650, no. det. 25254; JE, no. det. 28531; PRC 402564, no. det. 26836; B, no. det. 22196). – Dolnja Voda prope Ueskueb, O. Bierbach (BP 470651, no. det. 25256). – In campis ditionis Ůsküb, inter Jostoff et Saraj, c. 300 m, 24 Aug 1917, J. Bornmüller, Plantae Macedoniae, no. 1380 (B, no. det. 22197; WU, no. det. 21911; PRC 402563, no. det. 26837; JE, no. det. 28533). – Raduše (Serpentin) am Šar-dagh, 3 Jul 1936, O. Behr & E. Behr (B, no. det. 22194). – Auf Serpentin bei Raduše, 3 Jul 1936, O. Behr & E. Behr (G, no. det. 18942; JE, no. det. 28527; PR 272501, no. det. 28594). – Ad Raduše (ad fluv. Wardar), 300–400 m, 13 Jul 1916, J. Bornmüller, Plantae Macedoniae, no. 4251 (JE, no. det. 28529). – Heraklea, 23 Aug 2007, P. Petřík, cult. as JŠ 8288 (PRA, no. det. 27396; distributed also as *Taraxaca* Exs., no. 880, e.g. PRA, no. det. 23845, and no. 881, e.g. PRA, no. det. 23846). – Matka, 17 Aug 2007, P. Petřík, cult. as JŠ 8289 (PRA, no. det. 27397; distributed also as *Taraxaca* Exs., no. 882, e.g. PRA, no. det. 23847, and no. 883, e.g. PRA, no. det. 23848). – Skopje, 17 Aug 2007, P. Petřík, cult. as JŠ 8290 (PRA, no. det. 27398; distributed also as *Taraxaca* Exs., no. 884, e.g. PRA, no. det. 23849, and no. 885, e.g. PRA, no. det. 23850). – Ad arcem Ohrid, 22 Aug 2007, P. Petřík, cult. as JŠ 8291 (PRA, no. det. 27399; distributed also as *Taraxaca* Exs., no. 886, e.g. PRA, no. det. 23851, no. 887, e.g. PRA, no. det. 23852, and no. 888, e.g. PRA, no. det. 23853). – Prilep, 25 Aug 2007, P. Petřík, cult. as JŠ 8292 (PRA, no. det. 27400; distributed also as *Taraxaca* Exs., no. 889, e.g. PRA, no. 23854). – Negotino, 28 Aug 2007, P. Petřík, cult. as JŠ 8293 (PRA, no. det. 27401; distributed also as *Taraxaca* Exs., no. 890, e.g. PRA, no. det. 23855). – Skopje, pagus Matka, monasterium Sv. Andrej sub lacu structili Matka, 29 Jul 1985, V. Skalický & A. Skalická (PRC 402569, no. det. 26831). – Skopje, monasterium Nerezí, in planitie montis Vodno 1080 m, 19 Aug 1979, V. Skalický & V. Rejzlová (PRC 402568, no. det. 26832). – Skopje, below Gazibaba, 22 Jun 1937, F. Weber (PRC 402567, no. det. 26833). – Ohrid ... [ruins], 730 m, 1 Jul 1937, F. Weber (PRC 402565, no. det. 26835). – Skopje, montes Vodno, supra Kozle, Aug 1993, D. Fišerová, cult. as “JŠ VODNO” (PRA, no. det. 27395). – Skopje, slopes of Vodno mountains, D. Fišerová, cult. as JK 3710 (PRA, no. det. 25912 & 28598). – Prilep, 25 Jul 1937, F. Weber (PRC 402566, no. det. 26834).

– Blagusch-Gebirge b. Weseli, Sep 1916, K. Koppe (JE, no. det. 28526). – Mt. Korab ad Ničpur, 1400 m, Aug 1937, A. Pilát (PR, no. det. 28641). – In valle fluminis Treska prope Monastýr Matka procul Skoplja, 500 m, Jul 1937, M. Deyl (PR, no. det. 28639). – Raduša prope Skoplja, 500 m, Jul 1937, M. Deyl (PR, no. det. 28636). – Prilep, 26 Jul 1937, F. Weber (PR, no. det. 28633). – Montes Galičica, in declivibus supra vicum Ramne haud procul ab oppido Ohrid, 1000-1500 m, 2 Jul 1937, I. Klášterský (PR, no. det. 28631).

Albania/Republic of. Macedonia: Ochrida, 1909, Dimonie, 7 Sep 1911, cult. Handel-Mazzetti (WU, no. det. 21916). – Ohrida, 200–500 m, Jul 1908, Dimonie (WU, no. det. 21912).

Albania: Pogradec (Ohrida-lacus), 13 Aug 1938, P. Černjavski (W, no. det. 20886).

Serbia: Coška pr. Vranja [Vranje] in Serbia, 23 Aug 1889, E. Formánek (BRNM, no. det. 21598; PR, no. det. 28605). – Vranja, Jul 1878, [illegible, Janka?] (WRSL, no. det. 28653). – Vranja, Aug 1878, Pančić (G, no. det. 18980).

Kosovo: M. Scardo or., ad basin montis Ljubatrin [Ljuboten] prope Katschanik, 23. VII. 1918, J. Bornmüller, Pl. Maced., no. 4248 (WU, no. det. 21915; B, no. det. 22195).

Excluded name

There is a name referred to the sect. *Dioszegia* (as sect. *Serotina*) by Arrigoni (2012). It is *Taraxacum vallis-nibulae* Arrigoni, a name undoubtedly belonging to sect. *Taraxacum* (= sect. *Ruderalia* Kirschner, H. Øllgaard et Štěpánek) but represented by plants collected at the stage of second, summer flowering.