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A conspectus of *Tephroseris* (*Asteraceae*: *Senecioneae*) in Europe outside Russia and notes on the decline of the genus

Abstract: *Tephroseris* is generally considered a difficult genus. Based on the examination of extensive herbarium material and considering the existing literature, we recognize seven species in Europe outside Russia. These are *T. palustris*, *T. integrifolia* with subsp. *integrifolia*, subsp. *aurantiaca*, subsp. *capitata*, subsp. *maritima*, subsp. *serpentini* and subsp. "*tundricola*", *T. balbisiana*, *T. crispa*, *T. helenitis*, *T. longifolia* and *T. papposa*. Phylogenetic analysis of ITS and ETS sequences showed that these species fall into three lineages. These are: (1) *T. palustris*, clearly related to Arctic species of the genus; (2) *T. integrifolia*; and (3) the remaining species. Molecular dating of the *T. integrifolia* lineage resulted in a crown group age of 1.76 (0.85–2.87) million years. Possible reasons for taxonomic difficulties in the genus in Europe outside Russia may include its young phylogenetic age and extensive migration and genetic admixture in the Quaternary. The decline of the genus in Europe outside Russia is documented and discussed. We consider it possible that its decline is related to rising global temperatures.

Key words: *Asteraceae*, *Compositae*, ETS, Europe, glacial relic, global change, habitat loss, ITS, *Senecioneae*, *Tephroseris*

Introduction

Tephroseris (Rchb.) Rchb., estimated to contain approximately 50 species by Nordenstam (1978, 2007), is widely distributed in temperate and arctic parts of the northern hemisphere (Meusel & Jäger 1992). In Europe, the *Flora europaea* treatment by Chater & Walters (1976) recognized seven species in the group (treated as *Senecio* sect. *Tephroseris* (Rchb.) Hallier, Wohlf. & W. D. J. Koch), with 14 subspecies in addition to the typical subspecies and a number of additional taxa mentioned incidentally. To these must be added *T. palustris* (L.) Rchb., which was included by Chater & Walters (1976) in *S.* sect. *Eriopappus* (Du-

mort.) Schischk. Cufodontis (1933), as the last monographer of the genus, stated that "Delimitation of species … is not entirely satisfactory" (our translation), and Chater & Walters (1976) preceded their *Flora europaea* treatment by noting "An extremely difficult group, in which most of the taxa are very variable. The following treatment is conservative, and an attempt has been made to evaluate most of the more commonly recognized taxa; it is not, however, possible to key more than a proportion of the material involved and the treatment must be regarded as very provisional." At the same time, as will be described and discussed in greater detail below, several European red lists noted the decline of essentially all species of the genus.

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Tephroseris, first introduced as an unranked sub-group of *Cineraria* L. by Reichenbach (1830–1832) and raised to generic rank by the same author (Reichenbach 1841), has often been included in *Senecio* L. even in the fairly recent past (e.g. Chater & Walters 1976). It now is a well-established part of *Senecioneae* subtr. *Tussilagininae*, as first shown in a cladistic analysis of morphological characters by Bremer (1994), and later confirmed in molecular analyses (Pelser & al. 2007; Nordenstam & al. 2009). Morphological characters in support of the placement of *Tephroseris* in subtr. *Tussilagininae*, far removed from *Senecio* of subtr. *Senecioninae*, include its capitula without outer involucral (supplementary) bracts (ecalyculate), slender anther collars ("cylindrical", Drury 1967), endothecial cells with anticlinal wall thickenings only at their poles ("polarized", Drury 1967) and style branches with continuous stigmatic areas. Of these characters, the ecalyculate capitula and the continuous stigmatic areas of the style branches can be easily observed without a microscope. In subtr. *Tussilagininae*, *Tephroseris* is most closely related to *Nemosenecio* (Kitam.) B. Nord. and parts of *Sinosenecio* B. Nord. from Asia (Liu & al. 2006; Pelser & al. 2007; Wang & al. 2009; Ren & al. 2017). This group of three genera had been classified as subtr. *Tephroseridinae* C. Jeffrey & Y. L. Chen by Jeffrey & Chen (1984), a subtribe abandoned since, and is part of what is now known as the well-supported *Ligularia-Cremanthodium-Parasenecio* (*L-C-P*) complex sensu Liu & al. (2006). The most recent molecular systematic study of *Tephroseris*, aimed mainly at investigating its circumscription (Wang & al. 2009), found that *Sinosenecio koreanus* (Kom.) B. Nord. and *Sinosenecio newcombei* (Green) J. P. Janovec & T. M. Barkley fall into *Tephroseris*, whereas *T. changii* B. Nord. falls outside. Close relationships of *Sinosenecio koreanus* and *S. newcombei* to *Tephroseris* had previously been shown by Golden & al. (2001), and a close relationship of *T. changii* to parts of *Sinosenecio* had been suspected by Jeffrey & Chen (1984), as discussed by Nordenstam & Pelser (2011). Because *Sinosenecio koreanus* and *S. newcombei* were considered to have palmately veined leaves (not strictly palmate in *S. newcombei* according to Golden & al. 2001), whereas leaf venation in *Tephroseris* has been considered pinnate by Nordenstam (2007), Wang & al. (2009) concluded that leaf venation, used for the delimitation of *Nemosenecio*, *Sinosenecio* and *Tephroseris*, is a homoplastic character. However, closer inspection of leaf venation in *Tephroseris* revealed that it is best considered derived from palmate leaf venation (Kadereit & Bohley 2020).

In Europe, *Tephroseris* can be easily distinguished from *Senecio* and *Jacobaea* Mill. (if recognized as generically distinct) by its ecalyculate capitula, which are arranged in pseudoumbels (not in *T. palustris*) or are very rarely solitary, and the continuous stigmatic areas. Ecalyculate capitula can sometimes be found in European *Senecio* and *Jacobaea* (Chater & Walters 1976), but the

relevant species of *Senecio* (*S. gallicus* Chaix, *S. minutus* (Cav.) DC., *S. petraeus* Boiss. & Reut.) are annuals mostly from southwestern Europe, with capitula not arranged in pseudoumbels, and those of *Jacobaea* have capitula not arranged in pseudoumbels (*J. incana* (L.) Veld.) or large solitary capitula (*J. uniflora* (L.) Veldk. = *S. halleri* Dandy).

In the latest revision of the genus (as *Senecio* sect. *Tephroseris* Rchb. and excluding *T. palustris* (L.) Rchb.) by Cufodontis (1933), who recognized altogether 15 species but confessed limited knowledge of the genus in Asia, nine species were considered to occur in Europe. These were *S. balbisianus* DC., *S. brachychaetus* DC., *S. coincyi* Rouy, *S. elodes* DC., *S. helenitis* (L.) Schinz & Thell., *S. integrifolius* (L.) Clairv., *S. ovirensis* (W. D. J. Koch) DC., *S. papposus* (Rchb.) Schur and *S. rivularis* (Waldst. & Kit.) DC. With few exceptions, this treatment of *Tephroseris* (as *S.* sect. *Tephroseris*) in Europe was also adopted by Chater & Walters (1976) in *Flora europaea*, who, as noted above, treated *T. palustris* (as *S. congestus* (R. Br.) DC.) as part of a different section of *Senecio*. *Tephroseris palustris* had already been treated as a distinct subgroup (*Heloseris* Rchb.) of *Cineraria* and later *Tephroseris* by Reichenbach (1830–1832, 1841). Unlike Cufodontis (1933), Chater & Walters (1976) included *S. brachychaetus* in *S. ovirensis* and did not treat *S. coincyi* as a numbered species but pointed out its similarities to *S. balbisianus*. In their account of the distribution of *Tephroseris* (as *S.* sect. *Tephroseris*) in Europe, Meusel & Jäger (1992) adopted essentially the same treatment as Chater & Walters (1976), and except for additionally recognizing *T. crassifolia* (Schult.) Griseb. & Schenk and including *T. palustris*, the treatment of the genus in Europe by Greuter (2006+) is, at species rank, identical to that by Chater & Walters (1976). As will be discussed in detail in the taxonomic account below, essentially all modern European floras recognized the species listed above.

Although species recognition therefore appears fairly uncontroversial, more or less every account and floristic treatment of the genus emphasizes great difficulties in species delimitation. Apart from Cufodontis (1933) and Chater & Walters (1976) cited above, Holub (1973), combining several names in *Tephroseris*, noted "… species (which are difficult to define and often correspond to subspecies in other genera) …", and Nordenstam (1978) concluded that "*Tephroseris* is a homogeneous and natural group comprising closely-related taxa … A modern biosystematic study of the whole genus is urgently needed".

The very close relationship among species as the possibly major source of taxonomic difficulties is reflected in all phylogenetic accounts of the genus irrespective of their sampling. For example, Wang & al. (2009), using nuclear ribosomal Internal Transcribed Spacer (ITS) sequences in the analysis of 12 species of *Tephroseris* (incl. *Sinosenecio koreanus* and *S. newcombei*, see above) from across its range, but including only three European species, obtained no supported phylogenetic resolution

apart from one well-supported clade of Asian species. Skokanová & al. (2019), also using ITS sequences but analysing nine European and two Asian species, identified three clades of European species. *Tephroseris coincyi* was identified as supported sister to two larger clades, one containing only *T. integrifolia* (with a number of European and extra-European subspecies), and the other containing, in the nomenclature of Skokanová & al. (2019), *T. crispa*, *T. helenitis* (L.) B. Nord., *T. integrifolia* subsp. *aucheri* (DC.) B. Nord., *T. italica* Holub, *T. longifolia* (Jacq.) Griseb. & Schenk, *T. papposa*, *T. pseudocrispa* (Fiori) Holub and *T. tenuifolia* (Gaudin) Holub. Little supported phylogenetic resolution was obtained in the latter clade, and it was found, across their phylogeny, that single species contained several ribotypes and that ribotypes were shared among species. In their phylogenetic analysis of mainly Arctic species and again using ITS sequences, Golden & al. (2001) obtained a polytomy of four lineages of which one, however, contained three species. Interestingly, Skokanová & al. (2019) performed a molecular dating analysis in which they found that the split of their two major clades took place 1.75 (0.77–3.69) million years ago (ma), and that diversification of the two major clades started 1.23 (0.46–2.7) ma and 1.30 (0.53–2.83) ma, respectively. This firmly places diversification of *Tephroseris* in the Quaternary and illustrates the very young geological age of all species as a possible explanation for limited morphological differentiation.

Against this background, the aim of this paper is threefold. First, after the study of large numbers of herbarium specimens, and with the help of some molecular phylogenetic data, we want to critically discuss the recognition and distinction of species and subspecies in Europe outside Russia. Species cannot easily be keyed out, as already noted by Chater & Walters (1976), but, in our opinion, also cannot be reliably distinguished quantitatively based on morphometric analyses as claimed by Olšavská & al. (2015) and Skokanová & al. (2019). In consequence, we will strongly rely on the illustration of morphological variation, mainly leaf shape, in addition to descriptions and the discussion of characters. However, because distinction of species and subspecies remains very difficult with morphological characters alone, our key will also use geographical and ecological information. Second, we want to explore possible causes for the evident difficulties in distinguishing species. Thirdly, we want to outline the evidence for the decline of the genus in Europe and discuss its possible causes.

Material and methods

Herbarium material

Altogether approximately 1700 herbarium specimens from B, E, H, HAL, O, S and WU were examined by one of us (JWK). As the morphology of florets (except for presence/absence of ray florets) and fruits (except for indumentum) is invariable among the taxa studied,

examination was limited to gross morphology (habit, leaves, branching) and indumentum. Specimens used for photographs and leaf drawings are named in the respective figure captions, and a selection of specimens seen is listed for every taxon.

Geographical distribution

As a result of the strong decline of *Tephroseris* in the area considered (see below for details), recently collected herbarium material is extremely rare and did not allow us to draw meaningful distribution maps. Accordingly, the geographical distribution of taxa as shown in Fig. 5 and 15 is based mainly on Meusel & Jäger (1992). The extant distributions of taxa will be much more scattered than shown in these maps but not different in their latitudinal and longitudinal limits. When available, reference is made to up-to-date distribution data in the species accounts.

Conservation status

Unless otherwise stated, conservation status of taxa was taken from the IUCN (2021), which includes national assessments from Austria, the Czech Republic, France, Germany, Hungary, Lithuania, the Netherlands, Norway, Spain, Sweden, Switzerland and the United Kingdom. For Poland, assessments followed Snowarski (2002–2021), and for Italy Orsenigo & al. (2020).

Molecular analysis

For the molecular analysis, leaf material of 38 accessions of *Tephroseris* was collected in nature or sampled from herbarium specimens (Table 1). GenBank accession numbers of all material used are found in Table 2.

DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol including recommendations for increased DNA yield. Polymerase chain reactions were carried out for five markers: nuclear ribosomal ITS and ETS and plastid spacers *trnT-trnL*, *trnL-trnF* and *rpl32-ndhF*. For ITS, we used the forward primers ITS5 (Markos & Baldwin 2001) or ITS18S (Pelser & al. 2007) and the reverse primer ITS4 (White & al. 1990). For ETS, we used the forward primers 18S-ETS or 18S-E (Baldwin & Markos 1998) and the reverse primers AST1 (Markos & Baldwin 2001) or the newly designed primer Tim-1 (5′-GAT CAT CAC GCA GGT ACG AG-3′). For *trnT-trnL* (TabA, TabB) and *trnL-trnF* (TabC, TabF), primers from Taberlet & al. (1991) were used. The plastid spacer *rpl32-ndhF* was amplified in full length using optimized primers by Ren & al. (2017): modified rpl32-117F (5′-CGG TAG AAA GAG ATT TCC CTA ATG-3′) and modified ndhF-104R (5′- AAG CCC ACA TAC GAC GAA GAC-3′). In some cases, the extracted DNA was too degraded and *rpl32-ndhF* had to be amplified in two pieces, using the additional optimized internal primers rpl32-119F

Table 1. Origin of plant material used for DNA sequencing. "Protected population" indicates that there is no voucher specimen; in these cases we were allowed to collect small leaf samples but not specimens.

Taxon	Abbrev.	Locality	Collection	Voucher
Tephroseris balbisiana	Tep2	Spain, Salamanca	*Vogt 3516*	B 10 0673631
	Tep3	Spain, Sierra Nevada	*Vogt 4214*	B 10 0673632
	Tep10	Italy, Piemonte	*Schönswetter & al. 32286*	WU 0030833
Tephroseris crispa	Tep32	Austria, Niederösterreich	*Pachschwöll & Hehenberger CP774*	WU 0070676
	Tep33	Poland, Mazovia	*Bartoszek & al. s.n.*	WU 5087
	Tep34	Poland, Dolny Śląsk	*Vogt 4426*	B 10 0673634
	Tep35	Austria, Steiermark	*Vitek s.n.*	B 10 0185539
Tephroseris helenitis	Tep8	Austria, Salzburg	*Schmall 2018-001*	MJG 028199
	Tep22	Germany, Bayern	*Vogt 6275*	B 10 0673638
	Tep23	France, Pyrénées-Atlantiques	*Lazare s.n.*	B 10 0525766
	Tep24	France, Languedoc-Roussillon	*Vogt 16676*	B 10 0490365
	Tep25	Spain, Navarra	*Chizzola s.n.*	WU 4823
Tephroseris integrifolia subsp. *capitata*	Tep38	France, Alpes-Maritimes	*Schönswetter & Tribsch 32564*	WU 0030837
	Tep39	Italy, Piemonte	*Ristow & al. 789/09*	B 10 0356292
	Tep43	Austria, Steiermark	*Tribsch s.n.*	O 9066
	Tep44	Austria, Steiermark	*Fest s.n.*	B 10 0625668
Tephroseris integrifolia subsp. *integrifolia*	Tep6	Germany, Thüringen	*Kadereit & Schwarzberg 2018-553*	protected population
	Tep9	Germany, Thüringen	*Kadereit & Pusch 2018-534*	protected population
	Tep11	United Kingdom, Bedfordshire	*Preston & Stroh*	protected population
	Tep12	United Kingdom, Wiltshire	*Gurney & Preston*	protected population
	Tep18	Germany, Thüringen	*Kadereit & Schwarzberg 2018-532*	protected population
	Tep19	Germany, Thüringen	*Kadereit & Pusch 2018-535*	protected population
	Tep45	United Kingdom, Yorkshire	*Meinertzhagen s.n.*	BM
	Tep46	United Kingdom, Yorkshire	*Salman s.n.*	BM
	Tep47	United Kingdom, Lincolnshire	*Fowler s.n.*	BM
	Tep48	United Kingdom, Durham	*Bennett s.n.*	BM
Tephroseris integrifolia subsp. *maritima*	Tep14	United Kingdom, Anglesey	*Shaw s.n.*	protected population
	Tep16	United Kingdom, Anglesey	*Shaw s.n.*	protected population
	Tep21	United Kingdom, Anglesey	*Griffith & Bangor*	WU
Tephroseris integrifolia subsp. *serpentini*	Tep37	Austria, Burgenland	*Fischer & Fischer s.n.*	WU 5214
Tephroseris integrifolia subsp. "*tundricola*"	Tep42	Norway, Troms og Finnmark	*Arnstein Lye 12866*	O 9051
Tephroseris longifolia	Tep36	Italy, Emilia-Romagna	*Luccioli & Padovina s.n.*	B 10 0630751
	Tep41	Italy, Veneto	*Schönswetter & Tribsch 5271*	WU 0040178
Tephroseris palustris	Tep7	United States, Alaska	*2018-00641*	protected population
Tephroseris papposa	Tep27	Kosovo, Prizren	*Hartvig & al. 10013*	B 10 0630792
	Tep29	Greece, Ditikí Makedonía	*Schuler 99/803*	B 10 0162245
	Tep30	Greece, Kentrikí Makedonía	*Greuter s.n.*	B 10 0630793
	Tep31	Greece, Ditikí Makedonía	*Willing 6045*	B 10 0525937

(5′-GGC TTG TAA AYT TTT GCC TAA TA-3′) and ndhF-118R (5′-TTA TCA AAC CAC GTA TCT TTA A-3′; modified from Ren & al. 2017). PCR reactions were carried out in 25 μL volumes containing 1μL DNA template, 1 × reaction buffer, 1.2 mM MgCl$_2$, 0.1 mM dNTPs, 0.8 μM of each primer, 1 U Taq DNA Polymer-ase (NEB, Frankfurt, Germany) and 0.25–2 μL bovine serum albumin (10 mg/mL). PCR cycles started with an initial denaturation step at 94 °C for 60 s, followed by 35 cycles of denaturation at 94 °C for 20 s, annealing at 52–58 °C (depending on primer combination) for 30 s, and synthesis at 72 °C for 60 s. PCRs were finished with a

final synthesis step at 72 °C for 6 min. The PCR products were cleaned with ExoSap-IT PCR Clean-Up (Affymetrix, Santa Clara, CA, U.S.A.) and were sequenced in both directions with the same primers as used for the PCRs by StarSEQ (Mainz, Germany).

Chromatograms were checked manually and sequences aligned automatically with MAFFT v7.402 (Katoh & Standley 2013) with minor manual corrections. ITS alignments were complemented with publically available sequences in GenBank (Table 2). Phylogenetic reconstructions were carried out with the maximum likelihood (ML) algorithm using RAxML v.8.2.12 (Stamatakis 2014). Each marker was analysed individually under the GTRGAMMA model and bootstrapping was stopped automatically. The resulting phylogenies of nuclear ribosomal ITS and ETS were checked manually for supported conflicts (bootstrap support in both phylogenies ≥70). The phylogenies of the plastid markers were also checked for supported conflicts. In both cases topologies were congruent, and nuclear ribosomal markers and plastid markers were each combined in one dataset, respectively. Samples that had only data for one marker were removed from the combined datasets. Phylogenetic ML analyses were carried out for the nuclear ribosomal (nr) and the plastid dataset in RAxML with the same settings as for the individual markers. Bayesian Inference (BI) analyses of the ITS and the nr dataset were carried out using BEAST v2.6.3 (Bouckaert & al. 2019) on XSEDE (CIPRES Science Gateway; Miller & al. 2010). We used jModeltest2 (Darriba & al. 2012) on XSEDE to infer the optimal substitution model under the Akaike Information Criterion in BEAST, resulting in the models TIM2ef+G (ITS dataset) and TIM1+G (nr dataset). Initial values for gamma shape were taken from jModeltest2 results. The BI analyses were run three times each under the speciation birth-death-model using a strict clock model (for the nr dataset) for 10 million generations.

For the ITS dataset we used an uncorrelated relaxed log-normal clock and a substitution rate with a uniform distribution between 0.00251–0.00783 substitutions/site/million years (Kay & al. 2006) to obtain an age estimate for the phylogeny. Trees were sampled every 1000th generation. Convergence of each run was checked using Tracer v1.6 (Rambaut & al. 2014) to ensure that the effective sampling size was ≥ 200. A maximum clade credibility (MCC) tree with mean heights was constructed for each run in TreeAnnotator v1.8.4 (Rambaut & Drummond 2015) while removing 10% of the trees as burnin. The MCC trees were visualized in FigTree v1.4.2.8 (http://tree.bio.ed.ac.uk/software/figtree/).

Results

Molecular phylogeny

In our BI analysis of combined ITS and ETS sequences (Fig. 1), three major clades were resolved. Clade I,

the *Tephroseris integrifolia* clade, contains *T. palustris* as sister to *T. integrifolia*. Of the 17 accessions of *T. integrifolia*, the Finnmark material (subsp. "*tundricola*", one accession only) is highly supported sister to the remaining accessions of the species, which form a highly supported clade including accessions of subsp. *capitata* (non-monophyletic), subsp. *integrifolia* (non-monophyletic), subsp. *maritima* (non-monophyletic) and subsp. *serpentini* (one accession only). Clade II contains *T. pseudosonchus* (Vaniot) C. Jeffrey & Y. L. Chen, *T. flammea* (DC.) Holub, *T. rufa* (Hand.-Mazz.) B. Nord. and *T. kirilowii* (DC.) Holub from East Asia. Clade III, the *T. longifolia* clade, contains all material of *T. balbisiana* from its three disjunct partial ranges, which together are sister to a clade with four accessions of *T. papposa* (possibly monophyletic), two accessions of *T. longifolia* (non-monophyletic), five accessions of *T. helenitis* (non-monophyletic) and four accessions of *T. crispa* (non-monophyletic). Relationships among these three clades could not be resolved.

In our analysis of ITS alone (Fig. 2), which contains a larger sample, many relationships were not resolved. However, in a large and supported clade of *Tephroseris integrifolia* (not including one sequence of subsp. *capitata* obtained from GenBank), the Finnmark accession of the species again was sister to the remaining material, and this clade also contained two accessions of subsp. *aurantiaca*. *Tephroseris palustris*, sister to *T. integrifolia* in the combined ITS/ETS analysis, was recovered as strongly supported sister to the arctic *T. yukonensis* (A. E. Porsild) Holub. Clade III of the ITS/ETS analysis did not receive support, but the material of *T. balbisiana* from its three disjunct partial ranges again had very high support as a clade. No phylogenetic resolution was obtained using the plastid data.

The age of the *Tephroseris integrifolia* clade (clade I excluding *T. palustris* and *T. yukonensis*) was found to be 1.76 (0.85–2.87) ma. Clade III, as in our ITS analysis (Fig. 2) could not be resolved as supportedly monophyletic and could not be dated. However, comparison in a chronogram (not shown) showed that it is slightly older than the *T. integrifolia* clade.

Discussion

Phylogeny of *Tephroseris* in Europe outside Russia

Based on our combined ITS/ETS phylogeny (Fig. 1) and the phylogeny of a larger sample using only ITS (Fig. 2), we conclude that European *Tephroseris* consists of three lineages. The first lineage (clade I of our ITS/ETS phylogeny except *T. palustris*) consists of *T. integrifolia* with all the subspecies recognized here. This lineage, by also containing *T. integrifolia* subsp. *karsiana* (Matthews) B. Nord., *T. integrifolia* subsp. *caucasigena* (Schischk.) Greuter and *T. integrifolia* var. *leiocarpa* (Boiss.) B. Nord. in our ITS phylogeny (Fig. 2), is also distributed

Table 2. GenBank accession numbers of all material used in this study. * = newly sequenced in this study; na = not applicable.

Taxon	Country	GenBank accession number				
		ITS	ETS	rpl32-ndhF	trnT-trnL	trnL-trnF
Nemosenecio formosanus	China	KU696044	KU696167	KU750161	KY970818	na
N. nikoensis	Japan	na	na	na	na	GU818038
N. yunnanensis	China	KU696047	KU696170	KU750163	KY970975	na
Sinosenecio euosmus	China	GU818710	GU818310	KY970276	KY970898	GU818092
S. globiger	China	AY176159	KU696223	KY970187	KY970809	AF468170
Tephroseris atropurpurea	Russia	na	KU696279	na	na	na
T. balbisiana Tep2	Spain	MW779492*	MW796234*	MW796272*	MW796345*	MW796309*
T. balbisiana Tep3	Spain	MW779497*	MW796235*	MW796273*	MW796346*	MW796310*
T. balbisiana Tep10	Italy	MW779487*	MW796233	MW796271*	MW796344*	MW796308*
T. crispa	Czech Republic	EF538407	na	na	na	na
T. crispa	Czech Republic	MN625361	na	na	na	na
T. crispa Tep32	Austria	MW779493*	MW796236*	MW796274*	MW796347*	MW796311*
T. crispa Tep33	Poland	MW779494*	MW796237*	MW796275*	MW796348*	MW796312*
T. crispa Tep34	Poland	MW779495*	MW796238*	MW796276*	MW796349*	MW796313*
T. crispa Tep35	Austria	MW779496*	MW796239*	MW796277*	MW796350*	MW796314*
T. flammea	China	KU696137	KU696280	na	KY970976	KU750662
T. frigida	Canada	MG219080	na	na	na	na
T. helenitis Tep8	Austria	MW779502*	MW796244*	MW796282*	MW796355*	MW796319*
T. helenitis Tep22	Germany	MW779498*	MW796240*	MW796278*	MW796351*	MW796315*
T. helenitis Tep23	France	MW779499*	MW796241*	MW796279*	MW796352*	MW796316*
T. helenitis Tep24	France	MW779500*	MW796242*	MW796280*	MW796353*	MW796317*
T. helenitis Tep25	Spain	MW779501*	MW796243*	MW796281*	MW796354*	MW796318*
T. integrifolia subsp. *aurantiaca*	Slovakia	MN625399	na	na	na	na
T. integrifolia subsp. *aurantiaca*	Slovakia	MN625410	na	na	na	na
T. integrifolia subsp. *capitata*	Slovakia	MN625430	na	na	na	na
T. integrifolia subsp. *capitata*	Slovakia	MN625435	na	na	na	na
T. integrifolia subsp. *capitata*	Austria	MN638857	na	na	na	na
T. integrifolia subsp. *capitata* Tep38	France	MW779488*	MW796245*	MW796283*	MW796356*	MW796320*
T. integrifolia subsp. *capitata* Tep39	Italy	MW779489*	MW796246*	MW796284*	MW796357*	MW796321*
T. integrifolia subsp. *capitata* Tep43	Austria	MW779490*	MW796247*	MW796285*	MW796358*	MW796322*
T. integrifolia subsp. *capitata* Tep44	Austria	MW779491*	MW796248*	MW796286*	MW796359*	MW796323*
T. integrifolia subsp. *caucasigena*	Armenia	MN638856	na	na	na	na

Taxon	Country	ITS	ETS	rpl32-ndhF	trnT-trnL	trnL-trnF
T. integrifolia subsp. integrifolia	cultivated	EF538408	na	na	na	na
T. integrifolia subsp. integrifolia	Czech Republic	MN625370	na	na	na	na
T. integrifolia subsp. integrifolia	Slovakia	MN625428	na	na	na	na
T. integrifolia subsp. integrifolia Tep6	Germany	MW779508*	MW796257*	MW796294*	MW796366*	MW796330*
T. integrifolia subsp. integrifolia Tep9	Germany	MW779509*	MW796258*	MW796295*	MW796367*	MW796331*
T. integrifolia subsp. integrifolia Tep11	United Kingdom	MW779511*	MW796249*	MW796287*	MW796360*	MW796324*
T. integrifolia subsp. integrifolia Tep12	United Kingdom	MW779512*	MW796250*	MW796288*	MW796361*	MW796325*
T. integrifolia subsp. integrifolia Tep18	Germany	MW779503*	MW796251*	MW796289*	MW796362*	MW796326*
T. integrifolia subsp. integrifolia Tep19	Germany	MW779504*	MW796252*	MW796290*	MW796363*	MW796327*
T. integrifolia subsp. integrifolia Tep45	United Kingdom	MW779506*	MW796253*	MW796291*	MW796364*	MW796328*
T. integrifolia subsp. integrifolia Tep46	United Kingdom	MW779507*	MW796254*	MW796292*	MW796365*	MW796329*
T. integrifolia subsp. integrifolia Tep47	United Kingdom	na	MW796255*	MW796293*	na	na
T. integrifolia subsp. integrifolia Tep48	United Kingdom	na	MW796256*	na	na	na
T. integrifolia subsp. karsiana	Turkey	MN638860	na	na	na	na
T. integrifolia subsp. maritima Tep14	United Kingdom	MW779514*	MW796259*	MW796296*	MW796368*	MW796332*
T. integrifolia subsp. maritima Tep16	United Kingdom	MW779515*	MW796260*	MW796297*	MW796369*	MW796333*
T. integrifolia subsp. maritima Tep21	United Kingdom	MW779522*	MW796261*	MW796298*	MW796370*	MW796334*
T. integrifolia subsp. serpentini Tep37	Austria	MW779516*	MW796262*	MW796299*	MW796371*	MW796335*
T. integrifolia subsp. "tundricola" Tep42	Norway	MW779505*	MW796263*	MW796300*	MW796372*	MW796336*
T. kirilowii	China	AY176165	KU696281	KY970352	KY970974	AF468164
T. kjellmanii	Canada	MG218569	na	na	na	na
T. koreana	China	na	KU696282	KY970278	KY970900	na
T. longifolia	Italy	MN625363	na	na	na	na
T. longifolia	Austria	MN625371	na	na	na	na
T. longifolia (subsp. brachychaeta = T. italica)	Italy	MN625372	na	na	na	na
T. longifolia (subsp. brachychaeta = T. italica)	Italy	MN625433	na	na	na	na
T. longifolia (subsp. longifolia)	Austria	MN625418	na	na	na	na
T. longifolia (subsp. moravica)	Slovakia	MN625368	na	na	na	na
T. longifolia (subsp. pseudocrispa)	Italy	MN625392	na	na	na	na
T. longifolia Tep36	Italy	MW779517*	MW796264*	MW796301*	MW796373*	MW796337*
T. longifolia Tep41	Italy	MW779518*	MW796265*	MW796302*	MW796374*	MW796338*
T. palustris	Canada (1) and China (2)	MG220070 (1)	KU696283 (2)	na	na	na

Table 2 (continued from previous page)

Taxon	Country	GenBank accession number				
		ITS	ETS	rpl32-ndhF	trnT-trnL	trnL-trnF
T. palustris Tep7	United States	MW779519*	MW796266*	MW796303*	MW796375*	MW796339*
T. papposa	Turkey	GU818724	GU818319	na	na	GU818100
T. papposa	Turkey	MN638855	na	na	na	na
T. papposa Tep27	Kosovo	MW779521*	MW796267*	MW796304*	MW796376*	MW796340*
T. papposa Tep29	Greece	MW779510*	MW796268*	MW796305*	MW796377*	MW796341*
T. papposa Tep30	Greece	MW779520*	MW796269*	MW796306*	MW796378*	MW796342*
T. papposa Tep31	Greece	MW779513*	MW796270*	MW796307*	MW796379*	MW796343*
T. phaeantha	unknown	na	na	na	na	EU195521
T. pierotii	China	EU195498	na	na	na	EU195522
T. pseudosonchus	China	KU696139	KU696284	na	na	na
T. rufa	China	AY176166	KU696285	KY970351	KY970973	AF468180
T. stolonifera	unknown	na	na	na	na	EU195523
T. subdentata	unknown	na	na	na	na	EU195524
T. yukonensis	Canada	MG218262	na	na	na	na

in SW Asia where these three taxa occur. Inclusion particularly of Russian species of *Tephroseris* may reveal a much wider geographical distribution of this lineage. The second lineage is represented by *T. palustris*, which in our ITS phylogeny is closely related to the Arctic *T. yukonensis*. Such relationship may be supported by the very dense indumentum of long arachnoid hairs on peduncles and capitula of both these species. The third lineage is formed by what we treat here as *T. balbisiana*, *T. crispa*, *T. helenitis*, *T. longifolia* and *T. papposa*, and appears to be an entirely European lineage. However, further species sampling outside Europe may reveal that this conclusion is not justified. The sister relationship between *T. balbisiana* on the one hand and the other four species on the other hand is perfectly plausible from a morphological point of view, because *T. balbisiana* is quite similar particularly to Apennine material of *T. longifolia* (see also below).

The phylogenetic results obtained are not helpful for species or subspecies delimitation because only *Tephroseris integrifolia* (with non-monophyletic subspecies), *T. balbisiana* and *T. papposa* were resolved as monophyletic. These results essentially confirm what had already been shown by Skokanová & al. (2019). These authors also obtained little supported phylogenetic resolution and found, across their phylogeny, that single species contained several ribotypes and that ribotypes were shared among species. Our treatment of clade I as one species (*T. integrifolia* with several subspecies) and of clade III as five species (*T. balbisiana*, *T. crispa*, *T. helenitis*, *T. longifolia*, *T. papposa*) may appear unbalanced in view of the somewhat similar phylogenetic structure of the two clades, i.e. their comparable lack of phylogenetic resolution. Because of lack of phylogenetic resolution, delimitation of species and subspecies here mainly followed morphology, geographical distribution and ecology and also made an attempt to follow recent taxonomic practice in the genus in Europe. As intermediate forms exist among essentially all species recognized in clade III, it also would be justifiable to treat the entire clade (apart from *T. balbisiana*) as one species (*T. longifolia*) with several subspecies. Such treatment would also reflect the more or less allopatric distributions of *T. crispa*, *T. helenitis*, *T. longifolia* and *T. papposa* (Fig. 15), as also discussed by Meusel & Jäger (1992). Whereas *T. helenitis* is western to central European, and *T. papposa* is clearly southeastern European, *T. crispa* and *T. longifolia* are found between these two, with *T. crispa* having a more northern distribution at lower altitudes and *T. longifolia* a more southern distribution at mostly higher altitudes. Although our ITS/ETS and ITS phylogenies did not succeed in resolving species and species relationships in many instances, the use of more variable markers and a very broad sample of the genus in Europe might achieve this aim. For example, the use of AFLP markers by Skokanová & al. (2019) demonstrated that genetic groups congruent with taxa recognized by them can be resolved better than with ITS (but see discussion under *T. longifolia*).
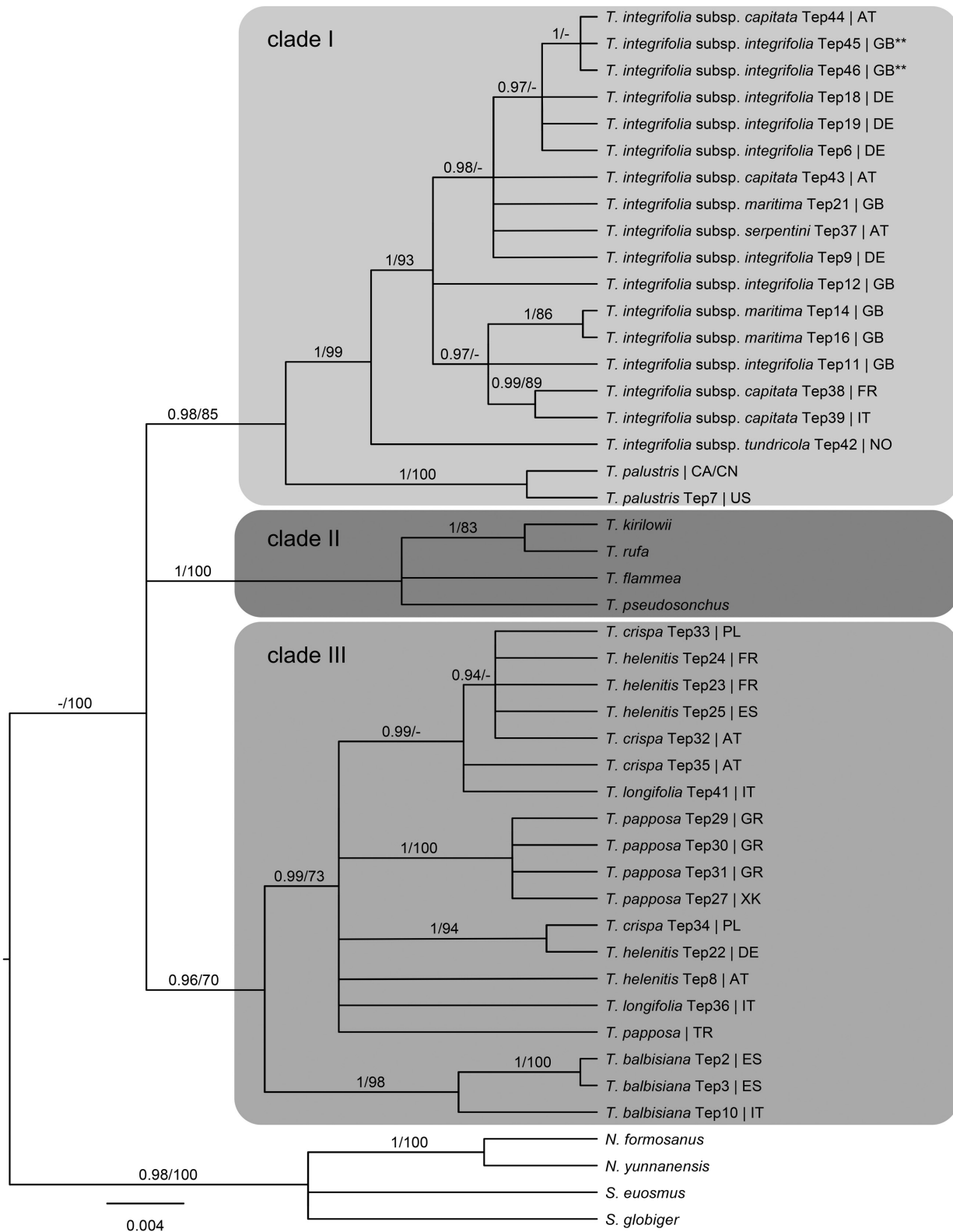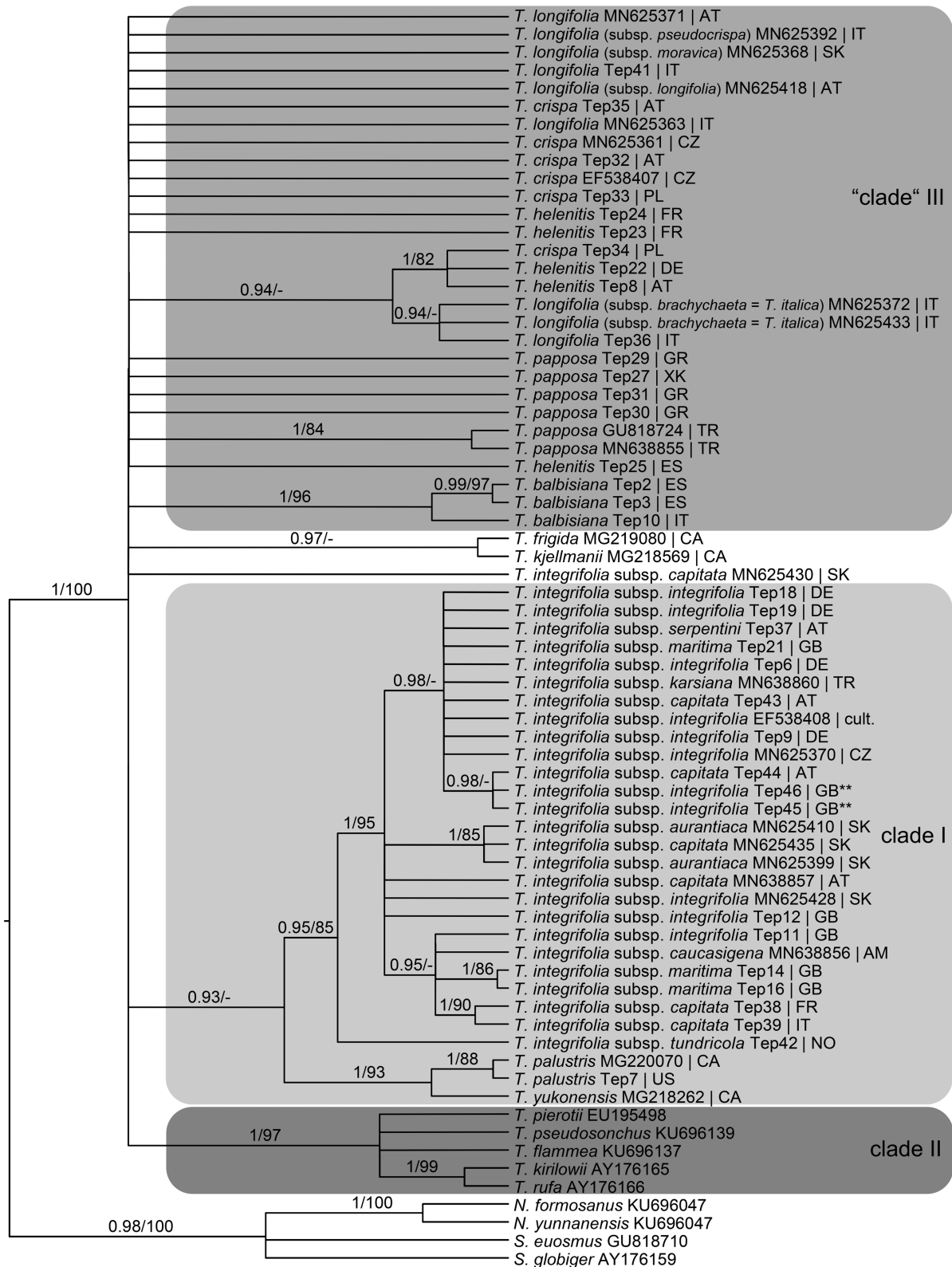
Fig. 1. Phylogeny of *Tephroseris* p.p. based on combined ITS and ETS sequences. The sample includes mainly taxa from Europe outside Russia plus some extra-European taxa. Support values > 0.9 (posterior probability) and ≥70% (ML bootstrap) are indicated.

Species identification

Except for our treatment of *Tephroseris balbisiana*, *T. coincyi* and *T. elodes* as one species, i.e. *T. balbisiana*, the species we recognize here do not differ from those recognized in major European treatments (Chater & Walters 1976; Meusel & Jäger 1992; Greuter 2006+). We hope, however, that our discussion and comparison of charac-

Fig. 2. Phylogeny of *Tephroseris* p.p. based on ITS sequences. The sample includes mainly taxa from Europe outside Russia plus some extra-European taxa. Support values > 0.9 (posterior probability) and ≥ 70% (ML bootstrap) are indicated.

ters, our identification key, which also uses geographical distribution and ecology, and particularly our illustrations of specimens and leaves will be of more assistance in species identification than any existing key. Although

Jäger (2011) hypothesized (for *T. integrifolia* subsp. *vindelicorum* Krach) that long isolation had resulted in ecologically and morphologically differentiated populations, which then have often been recognized as distinct taxa

(a plausible hypothesis considering the rather scattered distribution of essentially all species), no support for this could be found in population genetic analyses of *T. integrifolia* (Isaakson 2009; Meindl 2011) and *T. helenitis* (Pflugbeil 2012).

The molecular dating analysis of *Tephroseris* by Skokanová & al. (2019) and us places diversification of the genus well in the Quaternary, confirming the long-held view that *Tephroseris* in Europe is best interpreted as a glacial relic (*T. integrifolia*: Engler 1879; Böcher & al. 1946; Pigott & Walters 1954; *T. palustris*: Engler 1879; *T. helenitis*: Pflugbeil 2012). We believe that the weak morphological differentiation among the species has mainly two explanations. First, the species are of very young age and have had little time for differentiation. Second, the climatic oscillations of the Quaternary have led to substantial changes in geographical distribution resulting in between-lineage contact and genetic exchange (Anderson 1948; Anderson & Stebbins 1954; Hewitt 2011), which may have repeatedly blurred boundaries among diverging entities. Both these factors, as incomplete lineage sorting in a geologically young lineage and/or as admixture among lineages, would explain sharing of ribotypes between species and ribotype polymorphisms within species as reported by Skokanová & al. (2019).

Taxonomic account

Key to the species and subspecies of *Tephroseris* in Europe outside Russia

1. Plants annual, axis conspicuously hollow with an often bulbous base, leaves often pinnatifid, capitula mostly in panicles, nodding after anthesis, pappus much elongated after anthesis, plants with very dense indumentum of very long hairs above; plants from wet or drying open ground (Fig. 3, 4D, E) . . . .   **1. *T. palustris***
– Plants perennial, leaves entire to coarsely dentate-serrate, capitula in pseudoumbels, very rarely solitary **2**
2. Lower leaves mostly 25–45 cm long, long petiolate, petiole often up to twice as long as blade; plants from wet places in S Spain (Sierra Nevada), C Spain (Sanabria, Sierra de Villafranca, Sierra de Gredos) or Maritime Alps (Fig. 4A–C, 16) . . . .   **3. *T. balbisiana***
– Lower leaves mostly shorter; plants from elsewhere **3**
3. Blade of lower leaves mostly with more or less cordate base, sometimes almost hastate, mature leaves mostly glabrous, lower leaf surface distinctly lighter than upper surface, with dark network of veins; plants from wet places in C and E Europe (Fig. 19, 20) . . . .
. . . .   **5. *T. crispa***
– Blade of lower leaves mostly not with distinctly cordate or hastate base, mostly with more or less dense arachnoid or floccose indumentum **4**
4. Plants locally endemic in Wales (Anglesey), Austria (Steinstückl near Redlschlag/Burgenland) or Norway (Finnmark) **5**

– Plants from elsewhere **7**
5. Plants from Wales (Anglesey; Fig. 11, 12C, D) . . . .
. . . .   **2d. *T. integrifolia* subsp. *maritima***
– Plants not from Wales **6**
6. Plants from Austria (Steinstückl near Redlschlag/Burgenland), on serpentine (Fig. 12A, B, 13) . . . . .
. . . .   **2e. *T. integrifolia* subsp. *serpentini***
– Plants from Norway (Finnmark; Fig. 12E, 14) . . . .
. . . .   **2f. *T. integrifolia* subsp. *"tundricola"***
7. Involucral bracts mostly purple, purplish or with purple tips, florets orange **8**
– Involucral bracts mostly green throughout, florets mostly yellow **9**
8. Leaves mostly densely arachnoid; plants from high altitudes (1500–2440 m) in Alps and Carpathians (Fig. 9C–E, 10) . . . .   **2c. *T. integrifolia* subsp. *capitata***
– Leaves mostly almost glabrous, rarely sparsely arachnoid or somewhat floccose; plants from dry to humid grassland at lower altitudes (Fig. 8, 9A, B) . . . .
. . . .   **2b. *T. integrifolia* subsp. *aurantiaca***
9. Leaves mostly entire, lowest leaves mostly persistent and more or less appressed to ground, leaf blades mostly as long as or longer than petiole, leaf indumentum mostly dense and persistent, more rarely sparsely arachnoid or floccose; plants mostly from calcareous grassland (Fig. 6, 7) . . . .
. . . .   **2a. *T. integrifolia* subsp. *integrifolia***
– Leaves entire or dentate, sinuate-dentate to dentate-serrate, lowest leaves when present not appressed to ground, leaf indumentum dense or sparse **10**
10. Leaves much more densely arachnoid on lower than on upper surface, upper leaf surface often rugose, blade margin mostly narrowly revolute; plants from W to C Europe (Fig. 21, 22) . . . .   **6. *T. helenitis***
– Leaf indumentum similar on upper and lower leaf surfaces, blade margin not revolute **11**
11. Margin of lower leaves mostly coarsely and irregularly dentate to dentate-serrate, sometimes denticulate, leaves mostly sparsely arachnoid, glabrescent, sometimes particularly lower leaf surface densely arachnoid and sometimes floccose; plants from SE Central Europe and Italy (Fig. 17, 18C–F) . . . .
. . . .   **4. *T. longifolia***
– Margin of lower leaves entire to sinuate-dentate, leaves mostly densely and persistently arachnoid to floccose; plants from SE Europe (Fig. 18 A, B, 23)
. . . .   **7. *T. papposa***

1. *Tephroseris palustris* (L.) Rchb., Fl. Saxon.: 146. 1842 ≡ *Othonna palustris* L., Sp. Pl.: 924. 1753. – Lectotype (designated by Jeffrey & Chen in Kew Bull. 39: 284. 1984): Herb. Linn. No. 1000.13 (LINN). – Fig. 3, 4D, E.
= *Cineraria congesta* R. Br., Chlor. Melvill.: 21. 1823 ≡ *Senecio congestus* (R. Br.) DC., Prodr. 6: 363. 1838. – Holotype: Canada, 1819–1820, *Parry s.n.* (BM 001041631).

Fig. 3. *Tephroseris palustris* – [Netherlands], Noord Holland, Ankeveen, 17 May 1959, *G. Een s.n.* (S).
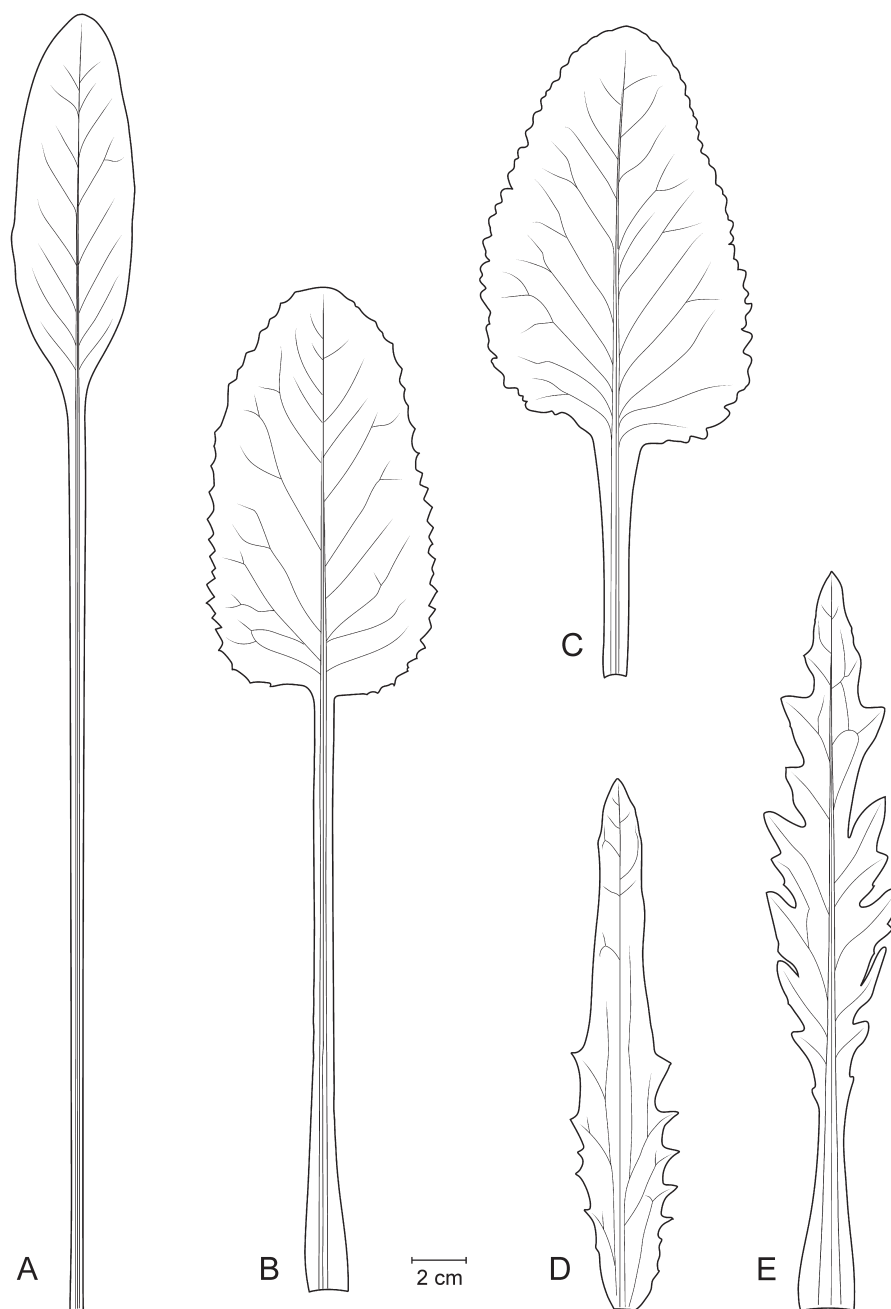
very coarsely and distantly dentate-serrate to pinnatifid, margin often undulate; basal and lower cauline leaves withered at anthesis; cauline leaves decreasing in size toward apex, upper cauline leaves lanceolate to oblong or linear, often entire, often somewhat amplexicaul; basal and lower leaves mostly glabrous, upper leaves with increasingly dense indumentum toward apex. Capitula rarely few (and then sometimes in pseudoumbels), mostly very many in very dense panicles, nodding after anthesis until fruiting time. Involucral bracts 16–24, 4–10 mm long. Base of capitula and involucral bracts mostly with dense indumentum of very long arachnoid hairs, rarely indumentum sparse. Ray florets 14–21, 5.5–10 × 1.5–2.5 mm, light yellow. Achenes 3.5–4.5 mm long, glabrous, light brown; pappus conspicuously elongating after anthesis, up to 20 mm long, white.

Chromosome number — 2n = 48 (Watanabe 2002).

Phenology — Flowering and fruiting from May to August.

Habitat — The species grows on wet or drying and essentially completely open ground on the shores of lakes or ditches, in peat bogs or on raw soils where it often can be found in great numbers, but only transitionally.

Fig. 4. Leaves of *Tephroseris balbisiana* – A: Spain, Granada, Sierra Nevada, an der Strasse Capileira–Mulhacén, 31 Aug 1985, *R. Vogt 4214* (B); B: [Italy], Piemonte, Prov. Cuneo, in humidis montis M. Mascaron supra Val Pesio, Jun 1899, *C. Bicknell s.n.* (WU); C: [Spain], Prov. d'Avila, Sierra de Villafranca, Puerto de la Peña Negra, 19 Jun 1979, *B. de Retz 79344* (H); and of *T. palustris* – D: [Netherlands], Noord Holland, Ankeveen, 17 May 1959, *G. Een s.n.* (S); E: [Germany], Mark Brandenburg, Beetzer See, 11 Oct 1992, *Erzberger s.n.* (B).

Description — Plants annual, 20–100 cm tall, sometimes taller, erect, unbranched below or occasionally branched from base. Axis hollow, conspicuously thickened to almost bulbous at base particularly in large plants, with numerous short adventitious roots. Axis often reddish/purplish, mostly glabrous at base and with increasingly dense indumentum toward apex. Lower leaves 7–30 × 0.5–4.5 cm, rarely larger, oblanceolate, gradually narrowing toward base, mostly without distinct petiole, entire to

Distribution — For distribution in Europe and globally see Meusel & Jäger (1992, sub *Senecio congestus*). For more detailed distribution see: Snowarski (2000–2021, Poland, sub *S. congestus*), NDFF & FLORON (2021, Netherlands), Bundesamt für Naturschutz (BfN) (2021, Germany).

Conservation status — Following Kochjarová (2006), the species is extinct in the United Kingdom, the Czech Re-

public, Hungary, Slovakia and Romania. The species is critically endangered in Sweden, endangered in France, vulnerable in the Netherlands, rare in Lithuania and not endangered in Germany (but in danger of extinction in parts of it). In Poland the species also is not endangered (Snowarski 2000–2021). The possible decline of *Tephroseris palustris* in the Netherlands has been discussed by van der Slikke (1998).

Remarks — Of all species of *Tephroseris* in Europe, *T. palustris* is most distinct by its annual habit, its indumentum, plants mostly glabrous below but densely arachnoid with long hairs above, the arrangement of its capitula (unless there are only very few) in panicles rather than in pseudoumbels, mostly rather short ray florets, capitula nodding after pollination, and a pappus that elongates very strongly and to up to 2 cm long after anthesis. The leaves can be more or less clearly dissected, which cannot be seen in any other European species. The species has often been described as viscid. This we cannot confirm after examination of living material (Kadereit pers. obs.) although very short glandular hairs with a minute glandular head are present on all parts that have an indumentum. Although the species has been described as annual, biennial or perennial (e.g. Chater & Walters 1976), the most detailed account of its habit (Hayek 1928) described it as a winter annual (einjährig-überwinternd) that grows into large rosettes in autumn and starts flowering in the following summer. Cultivation of the species showed that plants developed from germination to flowering within four months, after which they died (Kadereit pers. obs.). Although the species is self-incompatible (Kadereit pers. obs.), its annual habit, the large number of capitula and the rather small ray florets all are best interpreted as characters related to its colonizing life style. It can colonize newly available habitats in vast numbers, as presently in the construction of the Marker Wadden in the Marken Meer (Netherlands), where very large populations of the species can be seen (S. Claessens, 's-Graveland, pers. comm.). Its colonizing ability but transient presence are also well illustrated in the accounts by Runge (1960–1987), who described the massive appearance of the species in NW Germany, apparently originating from a newly constructed polder in the Netherlands (Flevoland, Zuidersee), and its subsequent disappearance.

Although Reichenbach (1841) had treated *Tephroseris palustris* as part of *Tephroseris*, but in a different infrageneric group (*Heloseris* unranked) than the other species (*Tephroseris* unranked), the species was, as described above, excluded by later authors. However, irrespective of its unusual and quite divergent morphology, it is clearly part of *Tephroseris* as is evident from molecular phylogenetic accounts of the genus (Golden & al. 2001; Wang & al. 2009). Considering our own molecular results, where the species was found to be sister to the Arctic *T. yukonensis* in our analysis of ITS (Fig. 2), and

those of Golden & al. (2001), where a supported clade with the Arctic *T. fuscata* as sister to *T. palustris* plus the Arctic *T. yukonensis* was resolved, it seems very likely that *T. palustris* is of Arctic origin. Indeed, the species is very widespread across the Arctic of the Old and New Worlds (Meusel & Jäger 1992, sub *Senecio congestus*), where it has been described as frequent in all but one of the subareas used in the panarctic flora (Elven 2021). In the Arctic, the species has often been treated (or labelled on herbarium sheets) as *S. congestus* (based on *Cineraria congesta*). This taxon has never been combined into *Tephroseris* at specific rank, but only at subspecific rank as *T. palustris* subsp. *congesta* (R. Br.) Holub. Although the Arctic material has pinnatifid leaves more commonly than the European material, Arctic material is highly variable and cannot be separated from European material. In consequence, no separate taxon should be recognized for the Arctic material, as was also concluded by Barkley & Murray (2006).

Selected specimens seen — [France], parties inondées des marais des dunes de Monchaux près Quend (Somme), 28 May 1867, *B. de Brutelett s.n.* (B); Belgium, Liège, Lanaye, au pied du Thier de Lanaye, plaine alluvial de la Meuse, 20 May 1971, *J. Duvigneaud 71 B 195* (H); [Netherlands], Noord Holland, Ankeveen, 17 May 1959, *G. Een s.n.* (S); [Netherlands], Ankeveense polder near Bussum, floating sod, peaty soil, 19 Jun 1955, *A. J. M. Leeuwenberg & al. s.n.* (H); [Germany], Mark Brandenburg, Beetzer See, 11 Oct 1992, *Erzberger s.n.* (B); [Germany], Rathenow, Graben nordwestlich vom Kleßener See, 1 Jul 1980, *D. Benkert s.n.* (B); [Belarus], in pratis ad ripas fluminis Struma prope vicum Szarkowszczyzna, 6 Jul 1938, *I. Dabkowska s.n.* (B); [Latvia], Rēzekne region, Ančupani hills, in a gravel pit, 15 Jun 1980, *G. Klavina 53291* (B); Estonia, Tartu province, Kallaste village, ruderal area on shore, 16 Aug 1993, *R. Lampinen 18124* (H).

2. *Tephroseris integrifolia* (L.) Holub in Folia Geobot. Phytotax. 8: 173. 1973 ≡ *Othonna integrifolia* L., Sp. Pl.: 925. 1753. – Type: not designated. – Protologue: "Habitat in Alpibus Pyrenaicis, Helveticis, Austriacis, Sibiricis". – Fig. 6–14.

Tephroseris integrifolia as understood by us comprises clade I of Fig. 1, except for *T. palustris*, and clade I of Fig. 2, except for *T. palustris* and *T. yukonensis*. The species can be recognized mostly by its leaves and inflorescence. The leaves are commonly entire, the lowest ones often persistent until flowering and more or less appressed to the ground with blades that are commonly as long as or longer than the petiole. Leaf size mostly decreases rather sharply in the basal quarter of the axis and leaves commonly become sessile in that part of the axis. The species also mostly has a rather dense and persistent arachnoid indumentum. The inflorescence often consists of rather few and often small capitula that are rather densely ag-
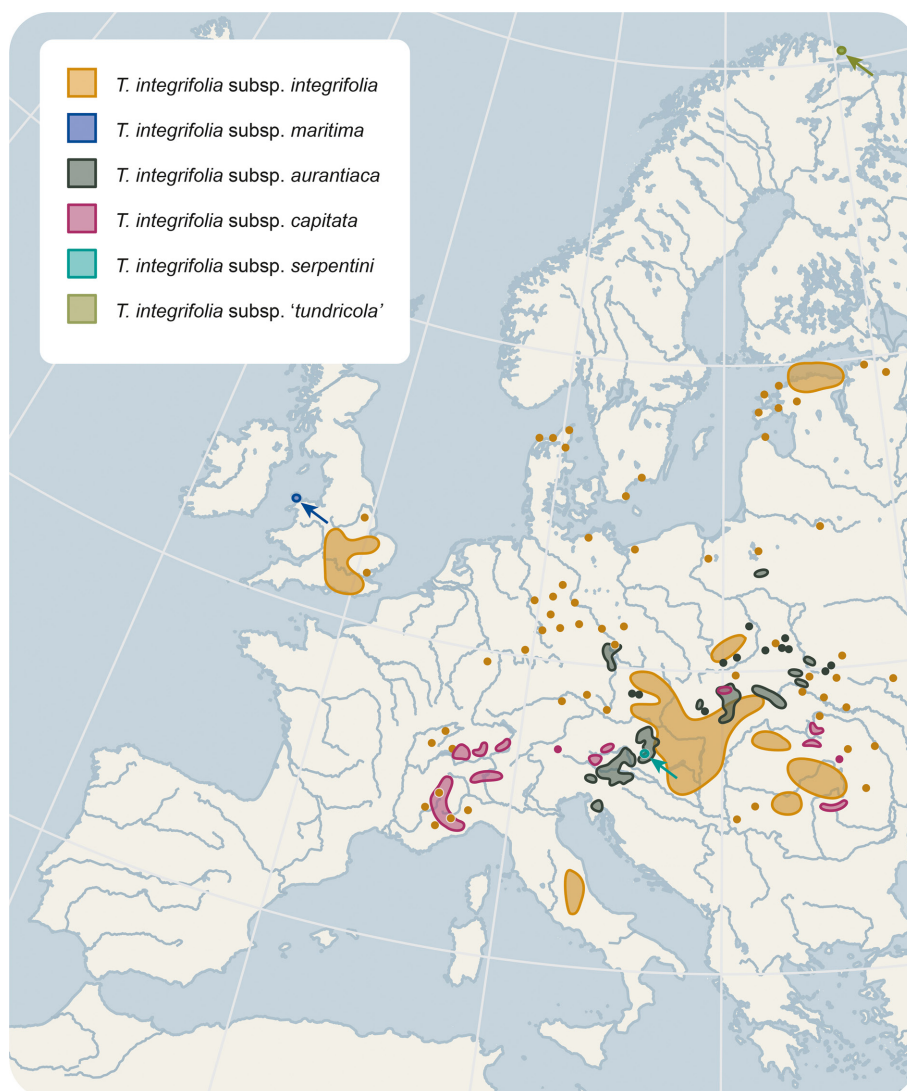
Fig. 5. Geographical distribution of *Tephroseris integrifolia* (modified from Meusel & Jäger 1994).

Legend:
- T. integrifolia subsp. *integrifolia*
- T. integrifolia subsp. *maritima*
- T. integrifolia subsp. *aurantiaca*
- T. integrifolia subsp. *capitata*
- T. integrifolia subsp. *serpentini*
- T. integrifolia subsp. *'tundricola'*

more rarely as long as blade, blade mostly broadly ovate, mostly entire or more rarely denticulate to sinuate-denticulate; lower cauline leaves up to 16 × 2 cm, mostly long petiolate, blade narrowly ovate, obovate or elliptic, mostly entire; cauline leaves increasingly sessile toward apex, mostly entire, upper cauline leaves lanceolate to linear; lower leaves sparsely to densely arachnoid or floccose on both surfaces, upper leaves increasingly white arachnoid. Capitula 2–8 in pseudoumbel, rarely 1 in very small specimens, mostly rather densely aggregated at flowering time; peduncle mostly 1–2.5 cm long at anthesis, rarely longer. Involucral bracts 18–32, 5.5–8 mm long, usually green. Capitula often white arachnoid at base; involucral bracts often glabrous or very sparsely white arachnoid in upper half. Ray florets 10–15, 6–13 × 2–3 mm, yellow, spreading. Capitula sometimes discoid. Achenes 2.5–3.5 mm long, pubescent, brown; pappus 5–9 mm long, white.

Chromosome number — 2*n* = 48, 96 (Watanabe 2002).

Phenology — Flowering and fruiting from (April to) May to June.

Habitat — Subspecies *integrifolia* mostly grows in dry calcareous grassland at low altitudes.

Distribution — For overall distribution see Meusel & Jäger (1992) and Fig. 5. For more detailed distribution see: Snowarski (2000–2021, Poland, sub *Senecio integrifolius*), Bartha & al. (2021, Hungary), Online Atlas of the British and Irish Flora (2021, United Kingdom), Bundesamt für Naturschutz (BfN) (2021, Germany), Tela Botanica (2021, France), Bartolucci & al. (2018, Italy), Sârbu & al. (2005, Romania, sub *S. integrifolius* subsp. *integrifolius*), Pladias (2014–2021, Czech Republic); see also Kochjarová (1997).

Conservation status — The subspecies is vulnerable in

gregated at flowering time. Capitula are mostly densely arachnoid at the base with involucral bracts that are often glabrous or very sparsely arachnoid at least in their upper half. There are exceptions to all these characters (see subspecies). We recognize six subspecies.

2a. ***Tephroseris integrifolia*** subsp. ***integrifolia*** – Fig. 6, 7.

= *Tephroseris integrifolia* subsp. *vindelicorum* Krach in Mitt. Bot. Staatssamml. München 27: 76. 1988. – Holotype: Germany, Jun 1908, *F. Vollmann s.n.* (M 0030348).

Description — Plants perennial, 9–90 cm tall, erect, mostly unbranched below. Rootstock short, erect or oblique. Axis glabrescent, sparsely to more rarely densely white arachnoid or floccose at base at flowering time, increasingly densely white arachnoid toward apex. Lowermost leaves at flowering time 2–7 × 1–3 cm, more or less appressed to ground, petiole mostly shorter than blade,

Fig. 6. *Tephroseris integrifolia* subsp. *integrifolia* – [Austria], Pannonischer Bezirk, Ebreichsdorf, 25 May 1964, *Schönbeck s.n.* (WU).
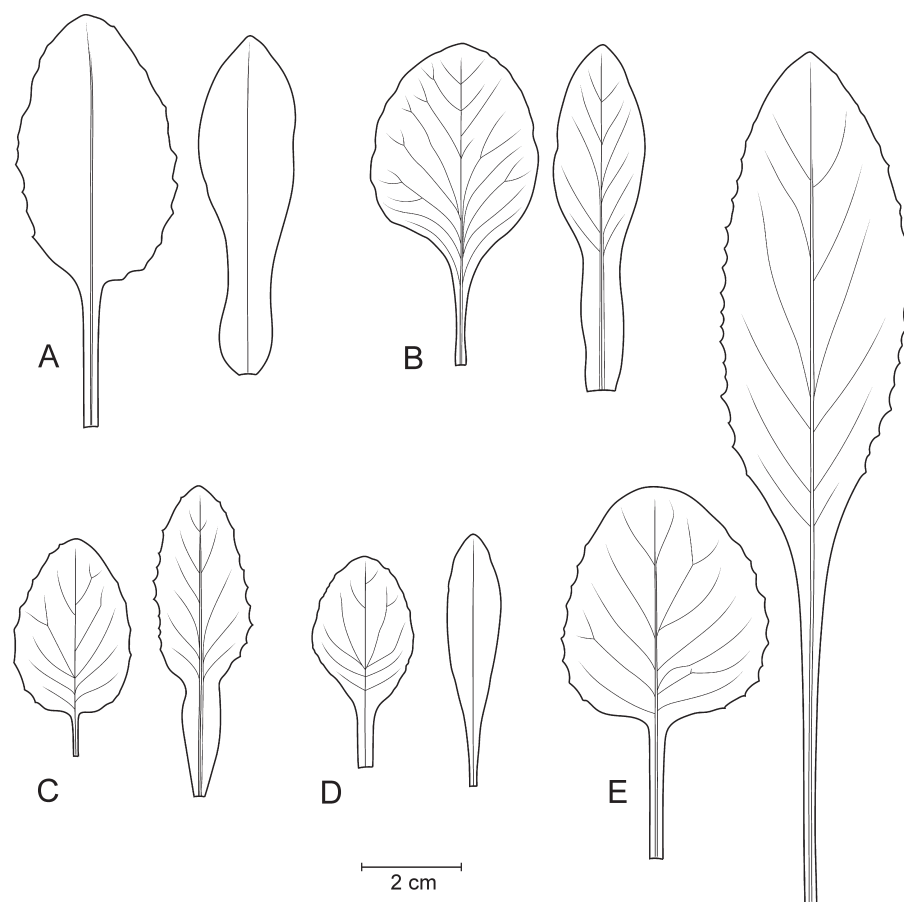
Fig. 7. Leaves of *Tephroseris integrifolia* subsp. *integrifolia* – A: [Switzerland], audessus d'Arzier, Jul 1874, *Bernet s.n.* (H); B: [Austria], Pannonischer Bezirk, Ebreichsdorf, 25 May 1964, *Schönbeck s.n.* (WU); C: [Austria], Flora Austriae infer., an der Donau, 15 May 1915, *s.coll. s.n.* (O); D: [France], Montchambert, 20 Jun 1869, *Davall s.n.* (B); E: [Hungary], bei Budapest, 12 May 1906, *E. Janchen s.n.* (WU).

lia. As a result of an AFLP analysis of a large sample of *T. integrifolia* from Bavaria, where populations classified as subsp. *vindelicorum* could not be separated from populations classified as subsp. *integrifolia*, Meindl (2011) concluded that taxonomic recognition of the Lechfeld plants is not justified. We agree with this conclusion and do not recognize subsp. *vindelicorum* as a separate taxon. For Europe outside Russia, Greuter (2006+) listed *T. integrifolia* subsp. *aucheri* (DC.) B. Nord. as an additional subspecies of *T. integrifolia*. This taxon is here treated as *T. papposa* (see below).

Selected specimens seen — [Switzerland], audessus d'Arzier, Jul 1874, *Bernet s.n.* (H); [Switzerland], Vaud, Montchaubert, 1090 m, 20 Jun 1869, *Davall s.n.* (B); [Switzerland], Vaud, Col de Marchairuz, 1320 m, Weideland mit Tannen, 4 Jul 1973, *M. Nydegger s.n.* (H); [United Kingdom], Hampshire, Winchester, St Catherine's Hill, 11 Jun 1909, *B. T. Lowne s.n.* (K); [United Kingdom], Westmoreland, limestone range nr Brough, 1200–1500 ft, 1880, *J. B. jun. & W. E. B. s.n.* (E); [Germany], Lechfeld bei Augsburg, Aug 1871, *A. Eyler s.n.* (WU); Germany, Thüringen, Badra, 260 m, lichtes *Betula*-Gehölz über Gips, 20 May 2014, *R. Hand 6496* (B); [Austria], Pannonischer Bezirk, Ebreichsdorf, 25 May 1964, *Schönbeck s.n.* (WU); [Austria], Flora Austriae infer., an der Donau, 15 May 1915, *s.coll. s.n.* (O); Hungary, bei Budapest, 12 May 1906, *E. Janchen s.n.* (WU); Poland, Distr. Pinczów, Krzyżanowice village, xerothermic grassland, 26 May 1986, *A. Rostański s.n.* (B); Estonia, zwischen Nomme und Reval, 11 Jun 1912, *H. Lindberg s.n.* (H); [Denmark], Jylland, Himmerland, Aug 1947, *B. Hjorth-Olsen s.n.* (O); [Sweden], Skåne, Lackalange, May 1895, *A. Nordström s.n.* (O).

Poland (Snowarski 2000–2021), endangered/critically endangered in Sweden, endangered in Switzerland, endangered in the Czech Republic, vulnerable/endangered in the United Kingdom, endangered and regionally critically endangered in Austria, critically endangered and extremely rare and strongly declining in Germany and (subsp. *vindelicorum*, see below) in danger of extinction in Germany.

Remarks — Populations of *Tephroseris integrifolia* from Lechfeld, a fluvial gravel plain south of Augsburg (Germany), were described as *T. integrifolia* subsp. *vindelicorum* by Krach (1988). These plants, according to Krach (1988), differ from subsp. *integrifolia* mainly by their smaller size in all vegetative characters and by often having discoid capitula, but mainly in their different chromosome number. This is $2n = 96$ in subsp. *vindelicorum* but $2n = 48$ in subsp. *integrifolia*. The longer anthers and larger stomata of subsp. *vindelicorum* may be related to this difference in ploidy level. However, Krach (1988) also reported counts of $2n = 96$ from two other populations geographically remote from Lechfeld, at least one of which (Grettstadt) was classified as subsp. *integrifo-*

2b. *Tephroseris integrifolia* subsp. ***aurantiaca*** (Willd.) B. Nord. in Opera Bot. 44: 44. 1978 ≡ *Cineraria aurantiaca* Willd., Sp. Pl. 3: 2081. 1803. – **Lectotype (designated here):** Austria, 10 Jun, *Hoppe s.n.* (B-W 16008-010; isolectotype: W-Rchb. 1889-0029807). – Fig. 8, 9A, B.

Fig. 8. *Tephroseris integrifolia* subsp. *aurantiaca* – [Austria], Kärnten, Glantschach, s.d., *s.coll. s.n.* (WU).
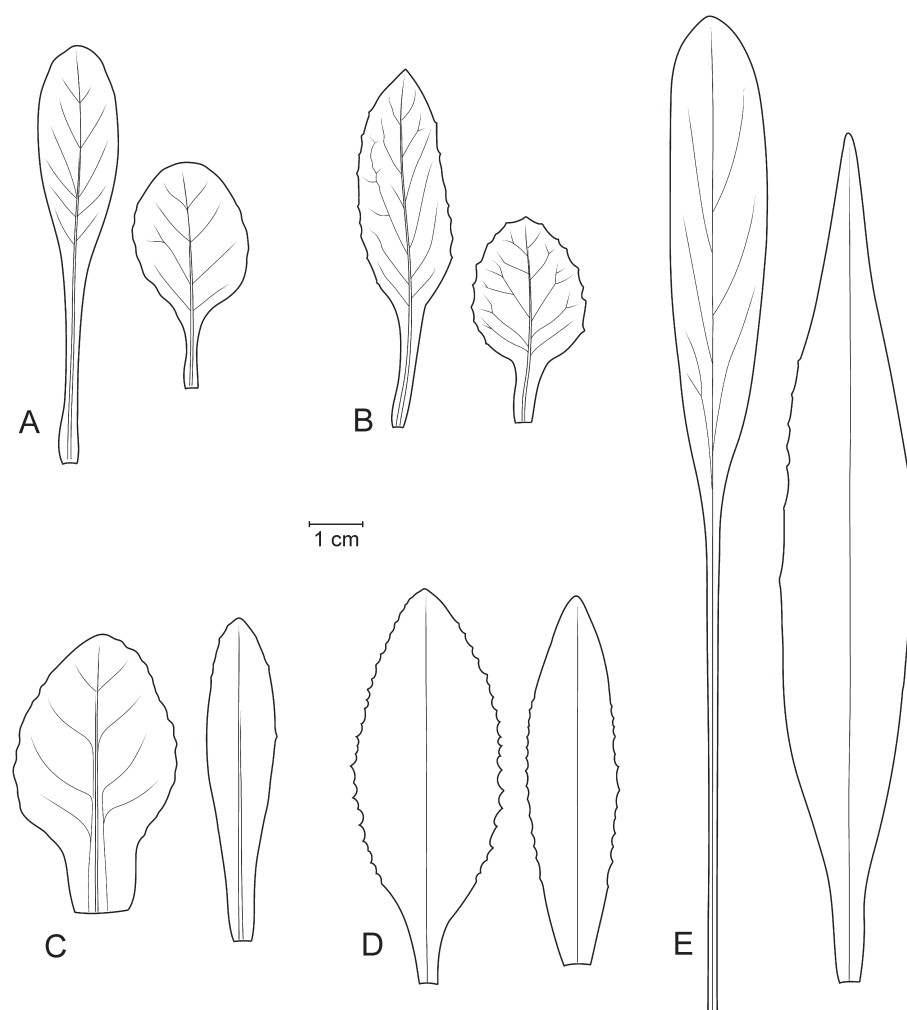
Fig. 9. Leaves of *Tephroseris integrifolia* subsp. *aurantiaca* – A: [Austria], Kärnten, Glantschach, s.d., *s.coll. s.n.* (WU); B: [Austria], Stiria, Ober-Thal procul a Gratz, s.d., *J. C. Eques a Pittoni s.n.* (WU); and of *T. integrifolia* subsp. *capitata* – C: [Austria], Stiria superior, in pratis montis Gregerlnock (sive Rotkofel) prope pagum Turrach, Jul 1905, *B. Fest s.n.* (WU); D: [Austria], Kärnten, Aug 1880, *Jabornegg s.n.* (WU); E: [France], See-Alpen, Baisse Peyrefique, 8 Jul 1998, *W. Gutermann, P. Schönswetter, A. Tribsch 32564* (WU).

Description — Plants perennial, 13–55 cm tall, erect, unbranched below. Rootstock short, erect or oblique. Axis sparsely arachnoid at base at flowering time, increasingly white arachnoid toward apex. Lower leaves 3–15 × 1.5–3.5 cm, distinctly petiolate, petiole mostly shorter than blade, rarely as long as blade, blade broadly to narrowly ovate to obovate, entire, distantly denticulate, dentate, coarsely dentate or sinuate; basal leaves often persisting until anthesis; cauline leaves increasingly sessile toward apex, mostly entire, upper cauline leaves lanceolate to linear; lower leaves mostly almost glabrous, rarely sparsely arachnoid or somewhat floccose, upper leaves increasingly white arachnoid. Capitula (1 or)2–6 in pseudoumbel; peduncle 1–2.5 cm long at anthesis, rarely longer, not extending much at fruiting time. Involucral bracts 14–26, 5–10 mm long, often purple, purplish or with purple tip. Capitula often white arachnoid at base; involucral bracts often glabrous or very sparsely

white arachnoid in upper half. Ray florets 12–16, 5–11 × 1–3 mm, mostly deep orange, spreading. Capitula sometimes discoid. Achenes c. 3 mm long, pubescent, brown; pappus 7–10 mm long, white.

Chromosome number — 2*n* = 48, 96 (Watanabe 2002).

Phenology — Flowering and fruiting from May to June, rarely later.

Habitat — The subspecies mostly grows in dry to humid meadows from 450 to 1000 m.

Distribution — For overall distribution see Meusel & Jäger (1992, sub *Senecio integrifolius* subsp. *aurantiacus*) and Fig. 5. For more detailed distribution see: Snowarski (2000–2021, Poland, sub *S. aurantiacus*), Bartha & al. (2021, Hungary, sub *Tephroseris aurantiaca*), Pladias (2014–2021, Czech Republic, sub *T. aurantiaca*); see also Kochjarová (1997).

Following Meusel & Jäger (1992), and largely confirmed by the herbarium material we have seen, the subspecies occurs in the southeastern Alps and adjacent areas to the south (Istria) and southeast (Hungary) and in the Tatry mountains (Poland/Slovakia). Further north and east it can be found in southeastern Poland and western Ukraine. We cannot confirm occurrences further west in the Erzgebirge (Germany/Czech Republic).

Conservation status — The subspecies is endangered in Hungary, in danger of extinction in Austria, critically endangered in the Czech Republic, rare and declining since the beginning of the 20th century in Slovenia (Leban & Anderle 2012), and endangered in Poland.

Remarks — *Tephroseris integrifolia* subsp. *aurantiaca* can be distinguished from subsp. *integrifolia* by the mostly sparse indumentum of its lower leaves and its mostly purplish or purplish tipped involucral bracts and deep orange florets. The taxon is rather invariable across its

Fig. 10. *Tephroseris integrifolia* subsp. *capitata* – [Austria], Stiria superior, in pratis montis Gregerlnock (sive Rotkofel) prope pagum Turrach, Jul 1905, *B. Fest s.n.* (WU).

range. The two accessions of subsp. *aurantiaca* included in our ITS analysis (Fig. 2) were resolved as a supported clade with one accession of subsp. *capitata*.

Selected specimens seen — [Austria], Kärnten, Glantschach, s.d., *s.coll. s.n.* (WU); [Austria], Stiria, Ober-Thal procul a Gratz, s.d., *J. C. Eques a Pittoni s.n.* (WU); [Austria], Carinthia, in pratis ad pedem montis Singer-Berg prope Unterbergen, 450 m, s.d., *Jabornegg s.n.* (H); [Austria], Trockenwiese oberhalb Robesch, Karawanken, Kleinobir-N, 750 m, 27 Jun 1990, *G. H. Leute 9452/4* (WU); [Slovakia], in jugis montium Muramje fensik cottus Gömör, 4 Jun 1906, *Filarszky & Kümmerle s.n.* (H); [Slovenia], Sveta planina in Krain, s.d., *H. Freyer s.n.* (H); [Ukraine], Galicia orient., Jaryna prope Janów, 14 Jun 1897, *E. Wołoszczak s.n.* (WU).

2c. *Tephroseris integrifolia* subsp. ***capitata*** (Wahlenb.) B. Nord. in Opera Bot. 44: 45. 1978 ≡ *Cineraria capitata* Wahlenb., Fl. Carpat. Princ.: 271. 1814. – Lectotype (according to Sweden's Virtual Herbarium, designation not indicated): Slovakia, 21 Aug 1813, *G. Wahlenberg s.n.* (UPS V-081606 n.v.). – Fig. 9C–E, 10.

Description — Plants perennial, 15–45 cm tall, erect, mostly unbranched below. Rootstock short, erect or oblique. Axis mostly densely arachnoid or floccose at base at flowering time, increasingly densely white arachnoid toward apex. Lowermost leaves at flowering time 2–8 × 1.5–3 cm, petiole mostly shorter than blade, broadly winged, blade mostly broadly ovate, mostly dentate to sinuate; lower cauline leaves up to 16 × 2 cm, mostly long petiolate, blade narrowly ovate, obovate or elliptic, mostly entire; cauline leaves increasingly sessile toward apex, mostly entire, upper cauline leaves lanceolate to linear; lower leaves mostly densely arachnoid to somewhat floccose, upper leaves increasingly white arachnoid. Capitula 2–6 in pseudoumbel; peduncle 1–2.5 cm long at anthesis, rarely longer. Involucral bracts 18–24, 8–12 mm long, purple, purplish or with purple tip. Capitula often white arachnoid at base; involucral bracts often glabrous or very sparsely white arachnoid in upper half. Ray florets 12–17, 5–12 × 2–3 mm, mostly deep orange, spreading. Capitula sometimes discoid. Achenes 3–4 mm long, pubescent, brown; pappus 7–10 mm long, white.

Chromosome number — $2n$ = 48, 64, 96 (Watanabe 2002; Mráz 2005).

Phenology — Flowering and fruiting from July to August.

Habitat — The species mostly grows in subalpine to alpine dry to humid meadows from 1500 to 2440 m.

Distribution — For overall distribution see Meusel & Jäger (1992, sub *Senecio integrifolius* subsp. *capitatus*) and Fig. 5. For more detailed distribution see: Snowarski (2000–2021, Poland, sub *S. capitatus*), Tela Botanica (2021, France), Info flora (2021, Switzerland, sub *Tephroseris capitata*), Bartolucci & al. (2018, Italy), Sârbu & al. (2005, Romania, sub *S. integrifolius* subsp. *capitatus*); see also Kochjarová (1997).

The subspecies is distributed mainly in two areas of the Alps, namely Kärnten and Steiermark (Austria) in the east and mainly the Maritime Alps in the west. We have seen some specimens (e.g. Kellerjoch, Tirol, Austria; Mt Generoso, Switzerland) from outside these two major ranges.

Conservation status — The subspecies is endangered in Austria, vulnerable to endangered in Switzerland and vulnerable in Poland.

Remarks — *Tephroseris integrifolia* subsp. *capitata* differs from subsp. *integrifolia* mainly in the colour of its involucre and florets and in its altitudinal distribution. Also, those lower leaves present at flowering time in subsp. *capitata* are not appressed to the ground, the petiole is mostly quite broadly winged, and the leaf margin is mostly dentate to sinuate. The distinction between subsp. *aurantiaca* and subsp. *capitata*, both of which mostly have capitula with an at least partly purple involucre and deep orange florets, is also fairly straightforward. Subspecies *capitata* has a much denser indumentum than subsp. *aurantiaca*, and the two subspecies differ in leaf morphology. In subsp. *aurantiaca* the lower leaves persist and are appressed to the ground in much the same way as in subsp. *integrifolia* and also have a short but mostly narrow petiole; they are also often entire. In contrast, the lower leaves of subsp. *capitata* are as described above. Importantly, the altitudinal distribution of the two subspecies is also different: subsp. *aurantiaca* grows between 450 and 1000 m, whereas subsp. *capitata* grows between 1500 and 2440 m.

The four accessions of *Tephroseris integrifolia* subsp. *capitata* included in our molecular analysis (Fig. 1, 2) were not resolved as closest relatives to each other. Interestingly, a chromosome number of $2n$ = 64 was reported for subsp. *capitata* by Váchová (1970) and Kochjarová (1997; see Mráz 2005). This number differs from the commonly reported chromosome numbers of $2n$ = 48 and $2n$ = 96 found in the genus and also in subsp. *capitata* and implies, as suggested by Mráz (2005), a basic number of x = 8. Diploid ($2n$ = 16) or tetraploid ($2n$ = 32) species based on this number have not been reported in *Tephroseris*, but tetraploid species are known in *Ligularia* (Watanabe 2002).

Selected specimens seen — [Austria], Stiria superior, in pratis montis Gregerlnock (sive Rotkofel) prope pagum Turrach, Jul 1905, *B. Fest s.n.* (WU); [Austria], Kärnten, Aug 1880, *Jabornegg s.n.* (WU); Austria, Steiermark, Wölzer Tauern, Klosterneuburgerhütte–Niederer Zinken–Hoher Zinken–Schießeck, 1880–2275 m, basenrei-

Fig. 11. *Tephroseris integrifolia* subsp. *maritima* – [United Kingdom], Anglesey, in scopulis prope Holyhead, Jun 1889, *J. E. Griffith s.n.* (H).
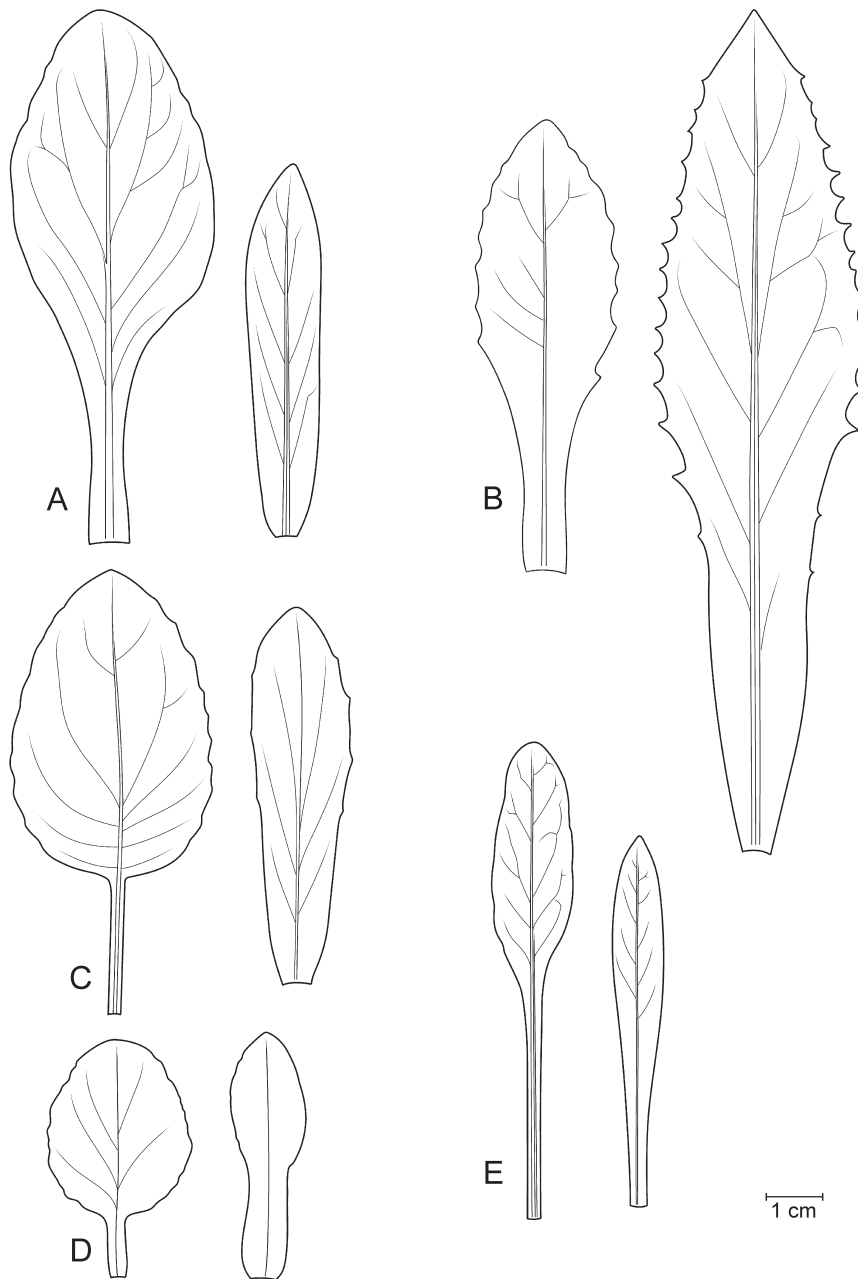
(O); [France], Hautes Alpes, Tal der Aigue Blanche, SE von St Véran, 17 Jul 1970, *D. Müller-Doblies & Döbbeler 8676* (B); [France], Val Casterino, Tenda, Alp. Mar. Liguria, 2100 m, 11 Jul 1897, *C. Bicknell s.n.* (H); [Romania], Flora Transsilvanica, in reg. alp. montis Butschetsch, supra Busteni, 10 Jun 1912, *J. Bornmüller s.n.* (B); [Slovakia], Bel. Tatra, 1600 m, in hochalpinen Bergwiesen, 16 Jul 1966, *W. Hempel s.n.* (B).

There exist three very locally distributed taxa, which we recognize here as subspecies of *Tephroseris integrifolia*.

2d. *Tephroseris integrifolia* subsp. *maritima* (Syme) B. Nord. in Opera Bot. 44: 45. 1978 ≡ *Senecio campestris* var. *maritimus* Syme in Sowerby, Engl. Bot., ed. 3, 5: 90. 1866. – Type: not designated. – Protologue: "on maritime rocks near Holyhead, Anglesea". – Fig. 11, 12C, D.

This perennial subspecies, known only from South Stack to Porth Ruffydd in Anglesey, Wales (Fig. 5; Stroh 2016), and originally described as *Senecio campestris* var. *maritima* Syme, somewhat resembles *Tephroseris helenitis*. Similarity to *T. helenitis* is most obvious in leaf morphology: the indumentum of the lower leaf surface is clearly more dense than that of the upper leaf surface, the upper leaf surface is somewhat rugose

Fig. 12. Leaves of *Tephroseris integrifolia* subsp. *serpentini* – A, B: [Austria], Burgenland, Bernsteiner Gebirge, zwischen Redlschlag und Bernstein, 14 May 2011, *G. & M. A. Fischer s.n.* (WU 2 sheets); and of *T. integrifolia* subsp. *maritima* – C: [United Kingdom], sea cliffs near the South Stack nr Holyhead, 14 Jun 1930, *A. Wilson 968* (S); D: [United Kingdom], Anglesey, in scopulis prope Holyhead, Jun 1889, *J. E. Griffith s.n.* (H); and of *T. integrifolia* subsp. "tundricola" – E: [Norway], Finnmark, Vardø, Hestmannes, 1 km Ø f Austerelva i Persfjord, 28 Jul 1987, *K. A. Lye 12866* (O).

cher Rasen, 19 Jul 2003, *A. Tribsch 9066* (O); [France], See-Alpen, Baisse Peyrefique, 8 Jul 1998, *W. Gutermann, P. Schönswetter, A. Tribsch 32564* (WU); Italy, Piemonte, Cuneo, Valle Stura di Delmonte, c. 5 km NE of Sambuco, Monte Omo, 2440 m, 17 Jul 2009, *M. Ristow 789/09 & al.* (B); France, Alpes de Haute Provence, Kottische Alpen, Bec de Liévre, 2720 m, 12 Jul 2003, *M. Wiedermann 9202* (WU); [France], Basses-Alpes, Col de Larche, 2000 m, 28 Jun & 6 Jul 1897, *G. Vidal s.n.* (well illustrated in Babington 1882) and the leaf margin is often narrowly revolute and somewhat sinuate-dentate. Babington (1882) had classified this population as *S. spathulifolius*, a synonym of *T. helenitis*, and we expected subsp. *maritima* to be part of *T. helenitis* considering its morphology and its ecology, which is clearly different from that of *T. integrifolia* subsp. *integrifolia* (see below). Interestingly, plants from coastal populations of *T. helenitis* in Normandy, classified as *S. helenitis* subsp.

Fig. 13. *Tephroseris integrifolia* subsp. *serpentini* – [Austria], Burgenland, Bernsteiner Gebirge, zwischen Redlschlag und Bernstein, 14 May 2011, *G. & M. A. Fischer s.n.* (WU).

candidus (Corb.) Brunerye by Brunerye (1969), now *T. helenitis* subsp. *candida* (Corb.) B. Nord., look similar to subsp. *maritima*. Much to our surprise, our molecular data clearly place subsp. *maritima* in the *T. integrifolia* clade, where the three accessions sequenced are not closest relative to each other (Fig. 1, 2). Such relationship may be supported by the ratio of petiole to blade – the petiole of basal leaves is mostly shorter than the blade in *T. integrifolia* but mostly longer in *T. helenitis* – and by the rather short peduncles at flowering time – these are often rather short (< 2 cm) in *T. integrifolia* but often longer in *T. helenitis*. However, none of these characters is sufficiently distinct quantitatively to be absolutely reliable for taxon differentiation and for recognition of relationships. Subspecies *maritima* is ecologically very distinct from subsp. *integrifolia*. Whereas subsp. *integrifolia* in England and in much of its overall range is a plant of calcareous grassland (Smith 1979; Stroh & al. 2017), subsp. *maritima* is found on the tops of cliffs formed from mica schists, sandstone and shale, where the soil is derived chiefly from glacial drift, is rich in organic matter and has a pH of 5.5–7 (Smith 1979). Considering its limited and disjunct distribution and morphological and ecological distinctness, we believe it is justified to treat the Welsh population as a subspecies of *T. integrifolia*. However, its inclusion in *T. integrifolia* makes it even more difficult to distinguish *T. integrifolia* from *T. helenitis*, a distinction considered unconvincing by, e.g., Pigott & Walters (1954). It would be interesting to grow subsp. *maritima* in order to determine to what extend its morphology is the result of phenotypic plasticity.

Chromosome number — 2*n* = 48 (Smith 1979).

Conservation status — The one population known of subsp. *maritima* has been assessed as vulnerable.

Remarks — Material of *Tephroseris* from Westmorland and Yorkshire, now apparently extinct (Smith 1964; Halliday 1997), had also been classified as *T. helenitis* by Babington (1882, as *Senecio spathulifolius*), and Halliday (1997) considered these northern populations to be more similar to subsp. *maritima* than to subsp. *integrifolia*. The material we have seen of these northern populations is in our opinion partly very similar to subsp. *integrifolia* and partly more similar to subsp. *maritima*. Our molecular results (Fig. 1, 2) clearly place this material in *T. integrifolia* but, considering the lack of resolution in our trees, do not allow us to decide whether they are more closely related to subsp. *integrifolia* or to subsp. *maritima*.

Selected specimens seen — [United Kingdom], Holyhead, near South Stack, cliffs, Jun 1884, *J. E. Griffith s.n.* (WU); [United Kingdom], Anglesey, in scopulis prope Holyhead, Jun 1889, *J. E. Griffith s.n.* (H); [United Kingdom], sea cliffs near the South Stack nr Holyhead, 14 Jun 1930, *A. Wilson 968* (S).

2e. ***Tephroseris integrifolia*** subsp. ***serpentini*** (Gáyer) B. Nord. in Opera Bot. 44: 45. 1978 ≡ *Senecio serpentini* Gáyer in Vasvárm. Szombathely Város Kultúregyes. Vasvárm. Múz. Évk. 1: 7. 1925. – Type: not designated. – Protologue: "*S. Serpentini* (*S. spathulifolius* Waisb.) e mte Steinstückl ad Borostyánkö". – Note: the specimen BM 001025990 is indicated as "type" on JSTOR Global Plants, but the collection date (11 Jun 1928) is later than the publication date of *S. serpentini*. – Fig. 12A, B, 13.

An ecologically specialized population from serpentine has been treated as a subspecies of *Tephroseris integrifolia*, i.e. subsp. *serpentini* by, e.g., Fischer & al. (2005; for illustration and description see also Fischer & al. 2015). This population is known only from Steinstückl near Redlschlag in Burgenland, Austria (Fig. 5; Fischer & al. 2005; see also Punz & al. 2010). Plants from this population are perennial, between 20–60 cm tall, where tall plants > 40 cm are more frequent than smaller plants, and most conspicuously often have involucral bracts that are purplish-brownish throughout, or at least at their tips, and have orange florets. However, there are individuals that have entirely green involucral bracts and yellow florets. The population is quite variable in terms of indumentum, with plants commonly but not always glabrescent below, and is particularly variable in leaf shape. Whereas leaves can be entire and lower leaves can have a blade longer than the petiole, as in typical subsp. *integrifolia*, leaves can also have coarsely dentate or serrate margins (Fig. 12B) approaching the leaf shape of *T. longifolia*. Capitula at flowering time are not as tightly aggregated as in subsp. *integrifolia*. As stated by Fischer & al. (2005), this population requires further study. For the moment, as argued for subsp. *maritima*, it should be treated at subspecific rank because of its morphological and ecological distinctness combined with its very local distribution. Because plants from serpentine are in general often somewhat impoverished in comparison to conspecifics from non-serpentine (Macnair & Gardner 1998), the rather tall habit of subsp. *serpentini* may suggest that the population is well adapted to its habitat and not only a modification as discussed by Fischer & al. (2005).

Selected specimens seen — [Austria], Burgenland, Bernsteiner Gebirge, zwischen Redlschlag und Bernstein, 14 May 2011, *G. & M. A. Fischer s.n.* (WU); [Austria], Burgenland, Steinstückl bei Redlschlag, lichter Kiefernforst/Schlagflur, 30 May 2011, *B. Knickmann 20110530* (WU); [Austria], , Steinstückl, Bernstein, 27 May 1928, *G. Gáyer s.n.* (H).

2f. ***Tephroseris integrifolia*** subsp. ***"tundricola"*** (Tolm.) B. Nord. in Opera Bot. 44: 45. 1978 ≡ *Senecio tundricola* Tolm. in Dokl. Akad. Nauk SSSR 1928: 266. 1928. – **Lectotype (designated here):** Russia, 21 Aug 1926, *A. Tolmatchew 756* (S 16-55505; isolectotype: S 16-55496). – Note: The name might not be applicable
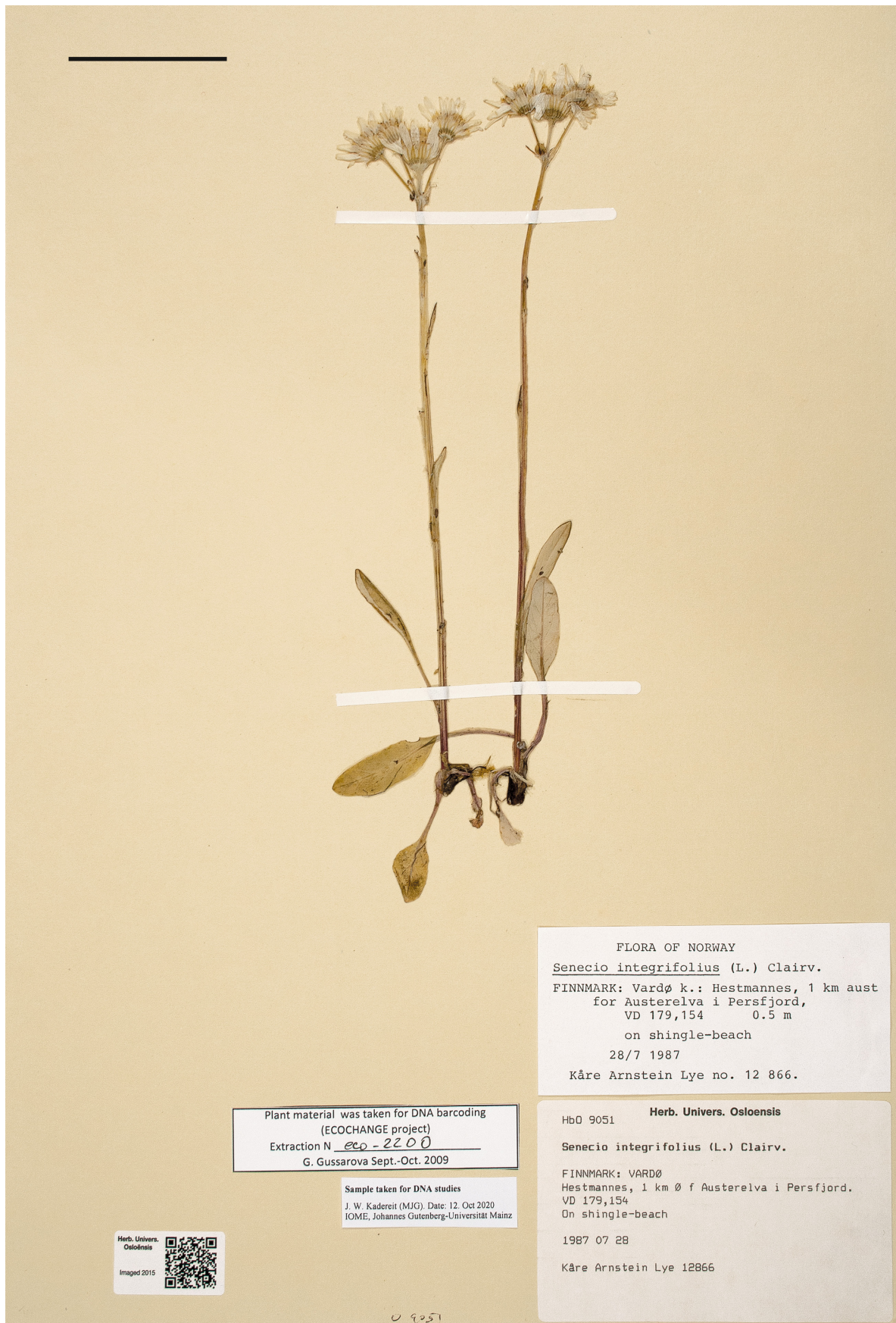
Fig. 14. *Tephroseris integrifolia* subsp. "*tundricola*" – [Norway], Finnmark, Vardø, Hestmannes, 1 km Ø f Austerelva i Persfjord, 28 Jul 1987, *K. A. Lye 1286*6 (O).
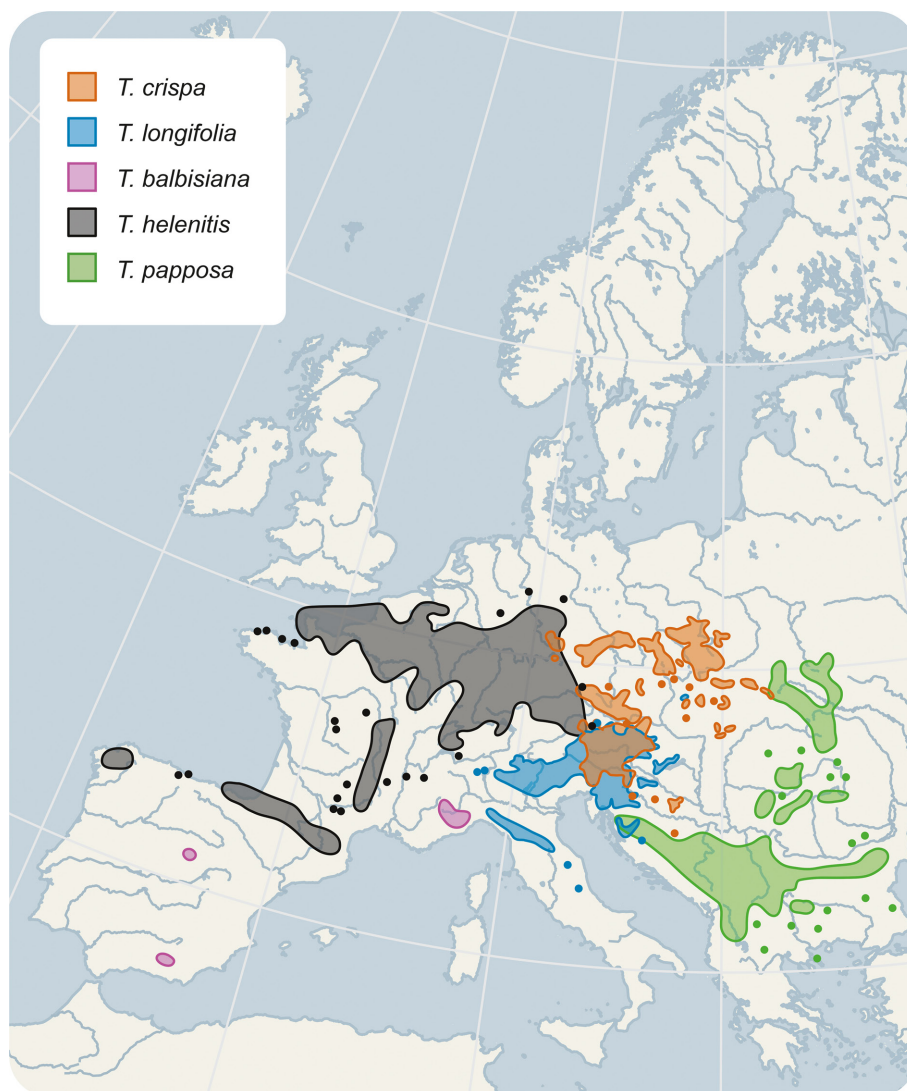
Fig. 15. Geographical distribution of *Tephroseris balbisiana*, *T. crispa*, *T. helenitis*, *T. longifolia* and *T. papposa* (modified from Meusel & Jäger 1994).

to the Finnmark material (see below for discussion). – Fig. 12E, 14.

In Scandinavia north of Denmark, *Tephroseris integrifolia* subsp. *integrifolia* is limited to southernmost Sweden (Widén 1987). However, the species also occurs in Finnmark in the very north of Norway (Fig. 5). The material we have seen from there differs from subsp. *integrifolia* mainly by having more or less glabrous lowermost leaves with rather long petioles and narrow blades. Interestingly, the one specimen of this material we sequenced was found to be well-supported sister to the remainder of *T. integrifolia* (Fig. 1, 2). Considering its morphology, its disjunct distribution in Arctic Scandinavia and its position in our phylogeny, we believe this material should be recognized as a distinct subspecies of *T. integrifolia*. The name subsp. *tundricola* for this taxon, described from Arctic Russia, has been used by Karlsson in 2004 (Checklista över Nordens kärlväxter; http://www2.nrm.se /fbo/chk/chk3.htm) but not in 2019 (A. Anderberg,

Stockholm, pers. comm.), and Greuter (2006+) indicated that this taxon is distributed in Norway. However, Chater & Walters (1976) did not list subsp. *tundricola* for Norway, and Solstad & Elven (2011) referred to the Finnmark material as *T. integrifolia* without subspecific allocation. Equally, no other species than *T. integrifolia* has been recorded in Finnmark according to the Norwegian Biodiversity Information Centre (https://www.biodiversity .no/). The type material of subsp. *tundricola* (NO-Küste der Gyda-Tundra, östlich vom Kap Leskin, 72°16'N, 21 Aug 1926, *A. Tolmatchew*, Museum Botanicum Academiae Scientiarum Petropolitanae No. 756, S!) has a denser indumentum than the Finnmark populations as well as purplish involucral bracts, so it remains open whether subsp. *tundricola* is the correct name for the Finnmark material. This has also been discussed by Høiland (1986). Following Chater & Walters (1976), Meusel & Jäger (1992) and Schischkin (1995), *T. integrifolia* (and probably several species listed by Schischkin [1995] that may eventually have to be included in *T. integrifolia*) is very widely distributed in Russia. Full understanding of subsp. "*tundricola*" may have to await a critical analysis of this Russian material. The Finnmark populations have been assessed as critically endangered (NBIC 2021).

Selected specimens seen — [Norway], Finnmark, Vardø, Hestmannes, 1 km Ø f Austerelva i Persfjord, 28 Jul 1987, *K. A. Lye 12866* (O); [Norway], Finnmark, Vardø, Persfjordens østside, 26 Aug 1982, *T. Berg s.n.* (O); [Norway], Finnmark, Vardø, Persfjorden, Hestmannes, 18 Jul 1993, *L. Borgen s.n.* (O); [Norway], Finnmark, Vardø. Vestre Persfjord E of Vestervelva, 2–40 m, low dolomite outcrops, meadow patches in cliffs, 26 Jul 2007, *R. Elven & al. s.n.* (O).

3. *Tephroseris balbisiana* (DC.) Holub in Folia Geobot. Phytotax. 8: 173. 1973 ≡ *Senecio balbisianus* DC.,

Fig. 16. *Tephroseris balbisiana* – [Italy], Piemonte, Prov. Cuneo, in humidis montis M. Mascaron supra Val Pesi, Jun 1899, *C. Bicknell s.n.* (WU).

Fig. 17. *Tephroseris longifolia* – Austria, Steiermark, Hochenegg SW von Leutschach, 28 May 1978, *G. Fischer s.n.* (WU).

Prodr. 6: 360. 1838. – **Lectotype (designated here):** Italy, 1804, *Balbis s.n.* (G-DC 00468425; isolectotype: G-DC 00468244). – Fig. 4A–C, 16.

= *Senecio elodes* Boiss. ex DC., Prodr. 7: 301. 1838 ≡ *Tephroseris elodes* (DC.) Holub in Folia Geobot. Phytotax. 8: 173. 1973. – **Lectotype (designated here):** Spain, Aug 1837, *Boissier s.n.* (G-DC 00468246; isolectotypes: G 00342262, G 00342263, G 00342264, K 000802953).

= *Senecio coincyi* Rouy in Bull. Soc. Bot. France 37: 163. 1890 ≡ *Tephroseris coincyi* (Rouy) Holub in Folia Geobot. Phytotax. 12: 308. 1977. – Type: not designated. – Prologue: "ESPAGNE: le « Pinar » de Hoyocasero, montagnes d'Avila (herbier Rouy, leg. de Coincy, 24 juin 1888)".
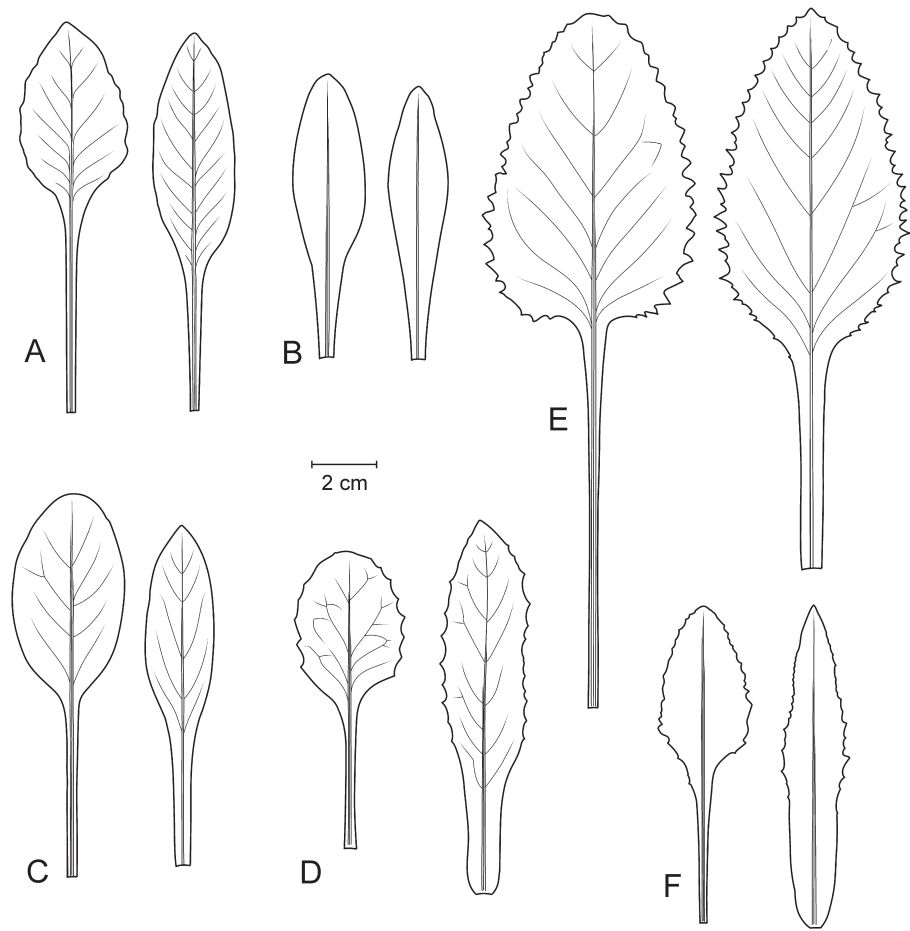

Fig. 18. Leaves of *Tephroseris papposa* – A: Serbia, Suva Planina, s.d., *S. Petrovic s.n.* (WU); B: Greece, Nom. Kastoria, 1.3 km NO Pano Arena, 8 Jun 1989, *Willing 6045* (B); and of *T. longifolia* – C: [Hungary], Hungaria merid.-orient., ad thermas Herkulis, s.d., *Degen s.n.* (WU); D: Austria, Steiermark, Hochenegg SW von Leutschach, 28 May 1978, *G. Fischer s.n.* (WU); E: [Italy], Bagni di Romagna, Réserve Naturelle de Sasso Fratino, 29 May 1990, *E. Luccioli & G. Padovani 15722* (B); F: Italy, Veneto, Karnische Alpen, Rif. Calvi–Hochalpjoch, gegen den M. Peralba, 2200–2500 m, 4 Jul 2000, *P. Schönswetter & A. Tribsch 5271* (WU).

Description — Plants perennial, 65–120 cm tall, erect, unbranched below. Rootstock short, erect or oblique. Axis conspicuously hollow, mostly glabrescent at base and increasingly white arachnoid-floccose toward apex. Lower leaves 25–45 × 3–8 cm, distinctly petiolate, petiole up to twice as long as blade, rarely longer, blade narrowly ovate to obovate, rarely almost entire, mostly somewhat sinuate to coarsely dentate-serrate; basal leaves absent at anthesis; cauline leaves increasingly sessile toward apex, upper cauline leaves lanceolate to linear, mostly entire, with cuneate to rounded base, very rarely slightly amplexicaul; lower leaves mostly sparsely arachnoid or somewhat floccose, upper leaves increasingly white arachnoid to somewhat floccose. Capitula (6–)8–16 in pseudoumbel, densely arranged at anthesis; peduncle elongating at fruiting time; commonly with single long-pedunculate capitula or 2- or 3-capitulate accessory pseudoumbels below terminal pseudoumbel. Involucral bracts 16–28, 7–11 mm long. Capitula mostly white arachnoid at base; involucral bracts sparsely to densely white arachnoid, glabrescent. Ray florets 12–21, 10–17 × 1–2.5 mm, mostly yellow, spreading. Achenes 3.5–4.5 mm long, glabrous, light brown; pappus 4–10 mm long, white.

Chromosome number — $2n = 40$ (Blanca & Cueto 1992).

Phenology — Flowering and fruiting from June to August.

Habitat — The species grows exclusively in very wet and oligotrophic to mesotrophic localities, such as wet and often peaty meadows, small peat bogs and along streams, on neutral to slightly acid soil from 400 to 2200 m.

Distribution — The species is distributed (Fig. 15) in southern Spain (Sierra Nevada: formerly *Tephroseris elodes*), central Spain (Sanabria, Sierra de Villafranca, Sierra de Gredos: formerly *T. coincyi*) and France and Italy (Maritime Alps: *T. balbisiana*). For distribution see also Meusel & Jäger (1992, sub *Senecio balbisianus*, *S. elodes*, *S. coincyi*), Tela Botanica (2021, France), (Bartolucci & al. 2018, Italy).

Conservation status — The species has been assessed as vulnerable to endangered in Spain, vulnerable in France

and least concern in Italy (Orsenigo & al. 2020). For detailed accounts of the ecology and status of the species in Spain see García López & Roa Medina (1988), Martínez-García & al. (2012, 2015) and Schnadelbach & al. (2016).

Remarks — This species is easily recognizable by its normally large size and large leaves in combination with its highly disjunct distribution in mostly very wet places in the Spanish Sierra Nevada, parts of central Spain (Sanabria, Sierra de Villafranca, Sierra de Gredos) and the Maritime Alps of Italy and France. *Tephroseris balbisiana* can be similar to *T. longifolia* from the Apennines (Italy; see below). The strong similarity between *T. coincyi* from central Spain and *T. elodes* from the Sierra Nevada had already been noticed by Rouy (1890), Cufodontis (1933) and Chater & Walters (1976), and indeed Aedo (2019) treated *T. coincyi* as *T. elodes* subsp. *coincyi* (Rouy) Aedo. The leaf margin of *T. coincyi* is sometimes more coarsely dentate-serrate than that of *T. elodes*, and the leaf blade is often broader, and Aedo (2019), when distinguishing *T. elodes* and *T. coincyi* at subspecific rank, used the leaf margin to differentiate these two taxa. However, we consider this character not sufficient for the recognition of two taxa, and both cannot be distinguished morphologically from *T. balbisiana*. Because these three entities form a well-supported clade (Fig. 1, 2), we include them in *T. balbisiana* without rank irrespective of their widely allopatric distribution. Rouy (1890), Cufodontis (1933) and Aedo (2019) also noted the strong similarity of *T. elodes*/*T. coincyi* to *T. balbisiana*.

The one chromosome count for this species of $2n = 40$ by Blanca & Cueto (1992, sub *Tephroseris elodes*) is highly unusual in this genus, where chromosome numbers are based on $x = 8$, at least in the European species. Chromosome numbers based on $x = 10$ are typical for *Senecio*. However, we have seen images of the voucher specimen for this count (Juan Lorite, Granada, pers. comm.) and can confirm its correct identification. It clearly would be desirable to re-examine *T. balbisiana* for its chromosome number.

Selected specimens seen — Spain, Granada, Sierra Nevada, an der Strasse Capileira–Mulhacén, 31 Aug 1985, *R. Vogt 4214* (B); [Spain], Regno Granatense, Sierra Nevada, Horcajo de Trévelez, 2300 m, 27 Jul 1923, *P. Font i Quer s.n.* (H); [Spain], Prov. d'Avila, Sierra de Villafranca, Puerto de la Peña Negra, 19 Jun 1979, *B. de Retz 79344* (H); [Spain], Ávila, inter Piedrahita et Puerto de Peña Negra, 1700 m, in humidis ad rivulum, 14 Jun 1980, *J. Fernández Casas s.n.* (B); Spain, Salamanca, Puerto de Peña Negra, Nordhang, Arroyo de Peña Negra, 1 Jul 1985, *R. Vogt 3516* (B); [Italy], Piemonte, Prov. Cuneo, in humidis montis M. Mascaron supra Val Pesi, Jun 1899, *C. Bicknell s.n.* (WU); [France], Alpes-Maritimes, St-Etienne de Tinée, Torrent du Rabuons, 2000 m, Aug 1915, *Ch. Duffour s.n.* (S); France, Mercantour, Talschluss der

Valle die Valetta S Terme di Valdieri, 1750–2000 m, 4 Jul 1998, *W. Gutermann & al. 32286* (WU).

4. *Tephroseris longifolia* (Jacq.) Griseb. & Schenk in Arch. Naturgesch. 18(1): 343. 1852 ≡ *Cineraria longifolia* Jacq., Fl. Austriac. 2: 49. 1774 ≡ *Senecio brachychaetus* DC., Prodr. 6: 362. 1838. – **Lectotype (designated here):** Austria, 1774, *Jacquin s.n.* (BM 001025995; isolectotype: BM 001025996). – Fig. 17, 18C–F.

= *Cineraria ovirensis* W. D. J. Koch in Flora 6: 507. 1823 ≡ *Tephroseris ovirensis* (W. D. J. Koch) B. Nord. in Opera Bot. 44: 45. 1978. – Type: not designated. – Protologue: "Auf der Alpe Ovir in Kärnthen von Dr. Rohde gesammelt, lag in Mertens Sammlung unter *C. campestris*".

= *Cineraria tenuifolia* Gaudin, Fl. Helv. 5: 307. 1829 ≡ *Senecio gaudinii* Gremli, Excursionsfl. Schweiz, ed. 8: 238. 1896 ≡ *Tephroseris tenuifolia* (Gaudin) Holub in Folia Geobot. Phytotax. 8: 174. 1973 ≡ *Tephroseris longifolia* subsp. *gaudinii* (Gremli) Kerguélen in Bull. Assoc. Informat. Appl. Bot. 1: 184. 1994. – Type: not designated. – Protologue: "Hab. in Alpibus australibus. Rarissimam plantam anno 1812 in itinere rhaetico ad M. Umbrail s. Wormserjoch descensum, supra Bormium in Hormini consortio legi. Eam ibidem quoque iamdudum invenerat Cl. Schleicher".

= *Senecio alpestris* var. *pseudocrispus* Fiori in Fiori & al., Fl. Italia 3: 220. 1903 ≡ *Senecio rivularis* subsp. *pseudocrispus* (Fiori) E. Mayer, Annum Hort. Bot. Labac. CL: 40. 1960 ≡ *Tephroseris longifolia* subsp. *pseudocrispa* (Fiori) Greuter in Willdenowia 33: 249. 2003. – Type: not designated. – Protologue: "Regione submontana del Friuli nei colli di Brazzano a 100m. (PIRONA!, GORTANI!) e dalla Stretta di Pradolino presso Stupizza a 470m. (GORTANI!)".

= *Tephroseris italica* Holub in Folia Geobot. Phytotax. 8: 173. 1973 – [*Senecio brachychaetus* sensu Cufod. in Repert. Spec. Nov. Regni Veg. Beih. 70: 101. 1933, non *Senecio brachychaetus* DC., Prodr. 6: 362. 1838]. – Holotype: FI. Exsicc. Ital., *Fiori, Béguinot & Pampanini 171* (F n.v.).

= *Tephroseris longifolia* subsp. *moravica* Holub in Preslia 51: 281. 1979. – Holotype: Czech Republic, 12 Jul 1973, *J. Holub s.n.* (PRA n.v.).

= *Tephroseris longifolia* subsp. *brachychaeta* Greuter in Willdenowia 33: 248. 2003. – Holotype: Italy, 1808, *Bertoloni s.n.* (G-DC 00468273).

Description — Plants perennial, 15–80 cm tall, erect, unbranched below. Rootstock short, erect or oblique. Axis frequently reddish/purplish at base and with reddish/purplish lines, mostly sparsely arachnoid, rarely densely arachnoid and then sometimes floccose. Lower leaves 6.5–25 × 2.5–4 cm, rarely much larger (up to 30 × 9 cm), distinctly petiolate, petiole mostly shorter than to as long as blade, rarely longer than blade, wingless or more rarely winged, denticulate to more or less coarsely dentate or

dentate-serrate, rarely more or less entire, blade mostly ovate to lanceolate, rarely almost truncate at base; basal leaves sometimes persisting until anthesis; cauline leaves increasingly sessile and margin increasingly entire toward apex, upper cauline leaves mostly entire and somewhat amplexicaul; leaves mostly sparsely arachnoid, sometimes particularly lower leaf surface densely arachnoid and sometimes floccose. Capitula 3–12 in pseudoumbel; peduncle 2–6 cm long at anthesis, extending at fruiting time; commonly with single long-pedunculate capitula or 2- or 3-capitulate accessory pseudoumbels below terminal pseudoumbel. Involucral bracts 14–26, 5–10 mm long, commonly with purple tip. Capitula mostly sparsely arachnoid, rarely densely arachnoid. Ray florets 12–25, 10–17 × 2–2.5 mm, rarely absent, yellow, often somewhat upright at anthesis. Achenes 2.5–3 mm long, glabrous or pubescent; pappus 7–8 mm long, white.

Chromosome number — $2n = 48$ (Watanabe 2002; see also Olšavská & al. 2015; Skokanová & al. 2019).

Phenology — Flowering and fruiting from May to August.

Habitat — The species grows in mesotrophic grasslands, tall-herb subalpine plant communities and in open forests and along forest margins (Janišová & al. 2018) from 400 to 2500 m.

Distribution — For overall distribution see Meusel & Jäger (1992, sub *Senecio brachychaetus*, *S. ovirensis*, *S. rivularis* subsp. *pseudocrispus*) and Fig. 15. For more detailed distribution see: Bartha & al. (2021, Hungary), Bundesamt für Naturschutz (BfN) (2021, Germany, sub *Tephroseris tenuifolia*), Info flora (2021, Switzerland, sub *T. tenuifolia*), Bartolucci & al. (2018, Italy, sub *T. italica*, *T. longifolia* subsp. *longifolia*, subsp. *gaudinii*, subsp. *pseudocrispa*), Pladias (2014–2021, Czech Republic); see also Skokanová & al. (2019) and Kochjarová (1997).

Conservation status — Critically endangered and close to extinction in Hungary (as *Tephroseris ovirensis*), regionally endangered in Austria, critically endangered in the Czech Republic (as *T. longifolia* subsp. *moravica*), endangered in Switzerland (as *Senecio tenuifolia*), least concern in Italy (as *T. longifolia* subsp. *longifolia* and subsp. *pseudocrispa*; Orsenigo & al. 2020).

Remarks — *Tephroseris longifolia* can be similar to *T. papposa* (see below) in leaf shape, but the leaf margin is very often coarsely and irregularly dentate to dentate-serrate, although frequently also entire. However, the leaf indumentum of *T. longifolia* is not persistent in the way it is in most *T. papposa*. In *T. longifolia* the ray florets are often rather long and narrow and often more or less erect at flowering time.

    Tephroseris longifolia, or rather what has been called the *T. longifolia* aggregate, has been subject to very

detailed studies using morphometric (Olšavská & al. 2015), ecological (Janišová & al. 2018) and molecular (Skokanová & al. 2019) approaches. Whereas Olšavská & al. (2015) recognized five subspecies within *T. longifolia*, i.e. subsp. *longifolia*, subsp. *moravica* Holub, subsp. *brachychaeta* Greuter, subsp. *gaudinii* (Gremli) Kerguélen and subsp. *pseudocrispa* (Fiori) Greuter (an intraspecific classification also used by Greuter [2006+]), Skokanová & al. (2019) treated subsp. *brachychaeta*, subsp. *gaudinii* and subsp. *pseudocrispa* as *T. italica* Holub, *T. tenuifolia* (Gaudin) Holub and *T. pseudocrispa* (Fiori) Holub, respectively. They also considered *T. crispa* to be part of the *T. longifolia* aggregate.

    In our opinion, neither treatment is supported by any of the published data. Although Olšavská & al. (2015) succeeded in separating the taxa investigated by them in a PCoA of morphometric data (separation of taxa is less obvious in their UPGMA analysis and very substantial overlap among taxa can be seen when looking at the variation of individual characters), the identification key provided by these authors will not allow the user to identify anything but extreme individuals. The lack of diagnostic characters or character combinations is also obvious from the tabular comparison (Skokanová & al. 2019: table 2) of the taxa investigated by Olšavská & al. (2015) plus *Tephroseris crispa*. In the molecular analysis by Skokanová & al. (2019), also including what these authors call *T. integrifolia* subsp. *aucheri* of the *T. longifolia* clade (see below, here classified as *T. papposa*), *T. helenitis* and *T. papposa*, ITS ribotypes are shared among taxa (N1: *T. crispa*, *T. longifolia* subsp. *longifolia* and subsp. *moravica*, *T. pseudocrispa*; N2: *T. crispa*, *T. tenuifolia*; N3: *T. crispa*, *T. pseudocrispa*, *T. tenuifolia*; N4: *T. crispa*, *T. longifolia* subsp. *moravica*; N6: *T. crispa*, *T. helenitis*; N8: *T. integrifolia* subsp. *aucheri*, *T. italica*, *T. papposa*), and several taxa are polymorphic for ITS ribotypes (*T. crispa*, *T. integrifolia* subsp. *aucheri*, *T. italica*, *T. longifolia* subsp. *moravica*, *T. papposa*, *T. pseudocrispa*, *T. tenuifolia*). Using AFLP data, some separation of taxa was achieved in neighbour-joining and neighbour-net analyses, partly without bootstrap support, but PCoA and Bayesian clustering of all samples of the *T. longifolia* aggregate (i.e. including *T. crispa* and excluding *T. integrifolia* subsp. *aucheri*, *T. helenitis* and *T. papposa*) resulted in three groups, namely *T. crispa*, *T. italica* + *T. tenuifolia*, and the remaining taxa as the third group. Finally, ecological differentiation among taxa is weak. Although Janišová & al. (2018) claimed that (among the morphotypes of the *T. longifolia* aggregate studied by them) "significant niche differentiation was confirmed for climatic, topographic, pedological, and vascular plant-based coenotic niches", they also noted that "all studied populations of *T. longifolia* agg. occur in very similar habitats including mesotrophic grasslands, tall-herb subalpine plant communities, open forests and forest margins, usually with deeper soils of intermediate pH values".

Fig. 19. *Tephroseris crispa* – [Austria], Feuchte Stelle mit Eschen im Fichtenforst unterhalb Köstinger, 31 May 1974, *M. A. Fischer s.n.* (WU).

Clearly, the data by Olšavská & al. (2015), Janišová & al. (2018) and Skokanová & al. (2019) are extremely valuable for understanding variation in the *Tephroseris longifolia* aggregate and reflect differentiation among the populations analysed by them. However, using these data to recognize taxa at subspecific or even specific rank is in our opinion not justified, particularly in view of the morphological variation of the species. In accordance with Skokanová & al. (2019), we treat *T. crispa* at specific rank here (see below). This is supported by its distinct morphology. Also, Janišová & al. (2018) noted that the habitats preferred by *T. longifolia* differ from those preferred by *T. crispa*, *T. helenitis* (both mainly in neutral to acidophilous wet meadows and fens) and *T. integrifolia* (mainly in nutrient-poor dry and semi-dry calcareous grassland and open forest communities). This in our opinion supports treatment of *T. crispa* at specific rank. As regards recognition of intraspecific taxa within *T. longifolia*, recognition particularly of subsp. *brachychaeta*, but also of subsp. *pseudocrispa*, should be considered. The former comprises often very tall and large-leaved plants from the Apennines, which also are somewhat distinct in their ITS ribotypes (Skokanová & al. 2019). This material is somewhat similar to *T. balbisiana* (see above). However, we have seen very little material from the Apennines. Interestingly, as described above, Skokanová & al. (2019) found the Apennine material to group with material from more western parts of the Alps classified by them as *T. tenuifolia*. Such a relationship is not reflected in morphological variation because in considerable contrast to the tall and large-leaved material from the Apennines, the material from more western parts of the Alps tends to be smaller than typical material of *T. longifolia*. Recognition of subsp. *brachychaeta* (but including *T. tenuifolia* = *T. longifolia* subsp. *gaudinii*) would be supported by the molecular data by Skokanová & al. (2019). As regards subsp. *pseudocrispa*, this is quite
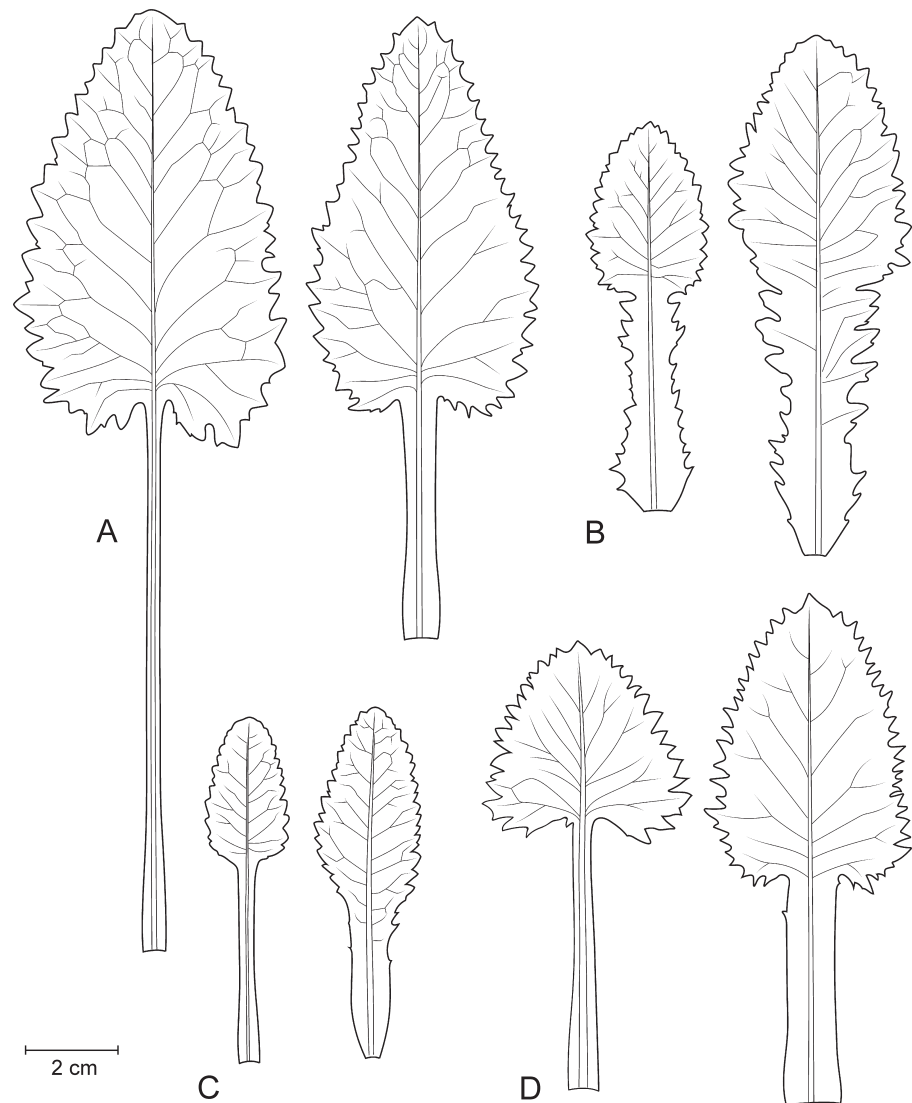

Fig. 20. Leaves of *Tephroseris crispa* – A: [Austria], Feuchte Stelle mit Eschen im Fichtenforst unterhalb Köstinger, 31 May 1974, *M. A. Fischer s.n.* (WU); B: [Austria], Steiermark, Söchau, s.d., *H. Sabransky s.n.* (WU); C: Austria, Oberösterreich, nordöstliches Mühlviertel, südöstlich von Unterwald, 18 May 2012, *W. Till 120115* (WU); D: [Austria], Flora Vindobonensis, bei Purkersdorf(?), 5 May 1872, *R. & A. L. v. Reuss s.n.* (WU).

distinct in leaf morphology by having basal leaves with an often cordate blade strongly resembling *T. crispa*. However, these plants have at least sparsely arachnoid leaves. Populations of such morphology occupy a small distribution range in northeastern Italy, northwestern Slovenia and adjacent Austria.

Selected specimens seen — [Hungary], Hungaria merid.-orient., ad thermas Herkulis, s.d., *Degen s.n.* (WU); Austria, Steiermark, Hochenegg SW von Leutschach, 28 May 1978, *G. Fischer s.n.* (WU); Austria, Niederösterreich, Bezirk Lilienfeld, wenig südöstlich von Naglreith, 796 m, 11 Jun 2010, *W. Till 100249* (WU); [Austria], Kärnten, Bleiburg, 21 May 1958, *E. Folkeson s.n.* (S); [Austria], Grazer Bergland, Stübinggraben, 4 km S Großstübing, 600 m, über Kalk, auf einer Schlagfläche

im Buchenwald, 22 May 1977, *W. Möschl & H. Pittoni s.n.* (S); [Italy], Bagni di Romagna, Réserve Naturelle de Sasso Fratino, 29 May 1990, *E. Luccioli & G. Padovani 15722* (B); [Italy], Longobardia, Prov. di Sondrio, in pratis montanis et subalpinis montium Oga et Tirindré, 1100–1700 m, 19–26 Jun 1904, *M. Longa s.n.* (WU); Italy, Veneto, Karnische Alpen, Rif. Calvi–Hochalpjoch, gegen den M. Peralba, 2200–2500 m, 4 Jul 2000, *P. Schönswetter & A. Tribsch 5271* (WU); Switzerland, Graubünden, Puschlav, Buco del Cavallo, 1900 m, 2 Aug 1967, *T. Eckardt 876* (B); [Switzerland], Graubünden, Oberengadin, Laviruns, 18 Jul 1920, *W. Schibler s.n.* (H).

5. *Tephroseris crispa* (Jacq.) Rchb., Fl. Saxon.: 147. 1842 ≡ *Cineraria crispa* Jacq., Fl. Austriac. 2: 48. 1774. – **Lectotype (designated here):** Austria, s.d., *Jacquin s.n.* (W-Jacq. 0032009; isolectotypes: BM 001025991, BM 001025992). – Fig. 19, 20.

= *Cineraria rivularis* Waldst. & Kit., Descr. Icon. Pl. Hung. 3: 265. 1812 ≡ *Senecio rivularis* (Waldst. & Kit.) DC., Prodr. 6: 359. 1838. – Type: not designated. – Protologue: "Crescit ad rivulos frigidos in vallibus Matrae umbrosis: velut infra Kis-Kut supra fodinas Oroszienses".

Description — Plants perennial, 17–70 cm tall, erect, unbranched below (very rarely with 1-capitulate lateral axes at base). Rootstock short, erect or oblique. Axis mostly with reddish/purplish lines, mostly glabrous at base and increasingly white arachnoid toward apex. Lower leaves 3.5–15 × 1.4–6 cm, rarely much larger, distinctly petiolate, petiole up to twice as long as blade, distinctly winged, entire to coarsely dentate-serrate, often broadening at base, blade mostly more or less cordate, sometimes almost hastate, less often elliptic to ovate with more or less cuneate base, mostly coarsely dentate-serrate; basal leaves often persisting until anthesis, often recurved; cauline leaves increasingly sessile toward apex, lower cauline leaves often with very broadly winged petiole, often larger than basal leaves, upper cauline leaves mostly lanceolate, entire, amplexicaul; petiole and major veins of leaves often with reddish/purplish tinge; lower leaves mostly glabrous, rarely sparsely arachnoid or somewhat floccose, lower surface distinctly lighter than upper surface, upper leaves increasingly white arachnoid to somewhat floccose. Capitula (2 or)3–12 in pseudoumbel; peduncle 1–7 cm long at anthesis, extending to 12 cm long at fruiting time; very commonly with single longpedunculate capitula or rarely 2- or 3-capitulate accessory pseudoumbels below terminal pseudoumbel. Involucral bracts 14–30, 8–15 mm long, often purple, purplish or with purple tip. Capitula mostly white arachnoid at base; involucral bracts mostly sparsely white arachnoid. Ray florets 15–21, 8–15 × 1.5–3 mm, mostly yellow, sometimes with reddish/purplish lines, spreading. Achenes 2.5–4.5 mm long, glabrous, very rarely pubescent, light brown; pappus 4–9 mm long, white.

Chromosome number — $2n = 48$ (Watanabe 2002).

Phenology — Flowering and fruiting from May to August.

Habitat — The species almost exclusively grows in very wet and mesotrophic to eutrophic localities, such as wet meadows, springs, marshes, peat bogs, alluvial *Alnus* forests and in tall-herb subalpine communities with neutral to slightly acid or basic soil, from 200 to 2000 m.

Distribution — For overall distribution see Meusel & Jäger (1992, sub *Senecio rivularis*) and Fig. 15. For more detailed distribution see: Snowarski (2000–2021, Poland, sub *S. rivularis*), Bartha & al. (2021, Hungary), Bundesamt für Naturschutz (BfN) (2021, Germany), Sârbu & al. (2005, Romania, sub *S. rivularis*), Pladias (2014–2021, Czech Republic); see also Kochjarová (1997).

Conservation status — The species has been assessed as not threatened but very rare and declining in Germany, as regionally endangered in Austria, as lower risk to near threatened in the Czech Republic and as potentially endangered or near threatened in Hungary. A detailed account of the ecology and population biology of *Tephroseris crispa* (as *Senecio rivularis*) in Poland was presented by Czarnecka (2008). The conservation status of the species in Poland has not been assessed.

Remarks — Of the species of the *Tephroseris longifolia* clade, *T. crispa* is easy to recognize by the shape and indumentum of its lower leaves, which mostly have blades with a distinctly cordate base, are almost glabrous to glabrous and have a distinctly lighter lower than upper leaf surface. A darker network of veins is very conspicuous on the lower leaf surface, at least in herbarium material. The species can be very similar to what has been called *T. pseudocrispa* (and partly classified as such within *T. crispa*) and what we include in *T. longifolia* (see above). As regards the mostly almost glabrous or glabrous lower leaves, these are glabrescent. In his account on trichomes in *Tephroseris* (as *Senecio* sect. *Tephroserides* DC.), Hayek (1915) showed that the trichomes of all species he investigated are essentially identical. They consist of a basal part of several cells and an upper, unicellular flagellum, responsible for the arachnoid appearance of the indumentum. This flagellum is shed during development. The basal part of the hairs is shorter in *T. crispa* than in most other species, and either the apical cells of this basal part are shed in addition to the terminal cell, leaving, according to Hayek (1915), a foot of two to four cells, or they are shed entirely.

Selected specimens seen — [Germany], Oberwiesenthal, montane Quellflur, 13 Jun 1963, *W. Hempel 6123* (B); [Germany], Erzgebirge, Crottendorf, Flachmoor, 31 May
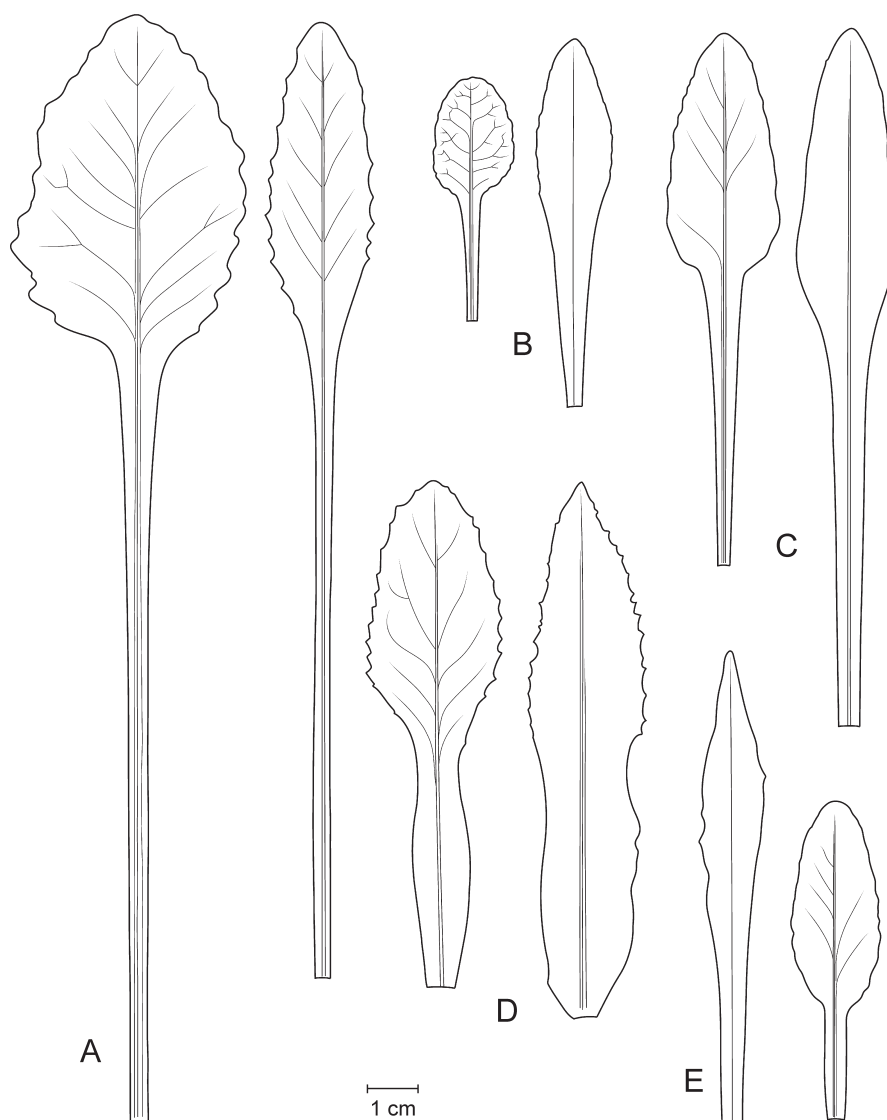
Fig. 21. *Tephroseris helenitis* – France, dép. Pyrénées-Atlantiques, La Corniche, 17 May 1993, *A. Salazar & P. Urrutia 15229* (B).

1963, *S. Fröhner s.n.* (B); [Austria], Feuchte Stelle mit Eschen im Fichtenforst unterhalb Köstinger, 31 May 1974, *M. A. Fischer s.n.* (WU); [Austria], Steiermark, Söchau, s.d., *H. Sabransky s.n.* (WU); Austria, Oberösterreich, nordöstliches Mühlviertel, südöstlich von Unterwald, 18 May 2012, *W. Till 120115* (WU); [Austria], Flora Vindobonensis, bei Purkersdorf(?), 5 May 1872, *R. & A. L. v. Reuss s.n.* (WU); [Poland], Laski near Olkusz, valley peat-bogs and wet meadows in Biała River Valley, c. 300 m, 20 May 2008, *W. Bartoszek & al. s.n.*(WU); [Poland], Riesengebirge, Karpacz, 1380 m, Quellsumpf, 21 Jun 1986, *R. Vogt 4425* (B); [Poland], Silesia Inferior, Montes Sudeti Occidentales, ad fluminem in lacum Mały Staw torrentem, 19 Jun 1959, *A. Krawiecowa s.n.* (B); [Czech Republic], Bohemia meridionalis, Montes Šumava, sub vico Dobrá, 700 m, 6 May 1949, *I. Klášterský s.n.* (H); Slovakia, Nationalpark Slovenský Raj, c. 5 km nördlich Dedinky, 900 m, 18 Jun 2004, *F. Schuhwerk 04/99* (B); Slovenia, Karavanke, in declivibus septemtrionalibus montis Golica, 1800 m, 7 Jul 1937, *F. Dolšak 27234* (B).

Fig. 22. Leaves of *Tephroseris helenitis* – A: France, dép. Pyrénées-Atlantiques, La Corniche, 17 May 1993, *A. Salazar & P. Urrutia 15229* (B); B: [Austria], Salzburg, Moorwiesen, s.d., *M. Eysn s.n.* (WU); C: [France], Lans (Isère), 28 May 1888, *A. Pellat s.n.* (S); D: [Germany], Klingenstein Kreis, Blaubeuren, 24 May 1935, *K. Müller s.n.* (B); E: [France], Laruns, vallée d'Ossau, 14 May 1990, *J. J. Lazare s.n.* (H).

6. *Tephroseris helenitis* (L.) B. Nord. in Opera Bot. 44: 44. 1978 ≡ *Othonna helenitis* L., Sp. Pl.: 925. 1753. – Type: not designated. – Protologue: "Habitat in Sibiria. D. Gmelin. Gallia". – Note: Following Brunerye (1969), the statement "Habitat in Sibiria" by Gmelin is an error. – Fig. 21, 22.

= *Senecio brachychaetus* var. *discoideus* DC., Prodr. 6: 362. 1838 ≡ *Tephroseris helenitis* var. *discoidea* (DC.) Kerguélen in Lejeunia 120: 173. 1987. – Holotype: France, 1814, *Coder s.n.* (G-DC 00468207).

= *Senecio spathulifolius* DC., Prodr. 6: 362. 1838. – **Lectotype (designated here):** Germany, 1834, *Wallroth s.n.* (G-DC 00468272).

= *Cineraria longifolia* var. *macrochaeta* Willk., Prodr. Fl. Hispan. 2: 111. 1865 ≡ *Tephroseris helenitis* subsp. *macrochaeta* (Willk.) B. Nord. in Opera Bot. 44: 44. 1978. – Type: not designated. – Protologue: "In regione fagorum montium Cantabriae raro (in cacumine Monte de la Haya pr. Yrun ad alt. 1500', Wk.)".

= *Cineraria lanceolata* var. *candida* Corb., Nouv. Fl. Normandie: 318. 1894 ≡ *Tephroseris helenitis* subsp. *candida* (Corb.) B. Nord. in Opera Bot. 44: 44. 1978. – Type: not designated. – Protologue: "Seine-Inférieure falaises crayeuses: Fécamp (Lacaille! Thériot!); Etretat, St-Valéry (Niel)".

= *Senecio arvernensis* Rouy, Fl. France 8: 316. 1903 ≡ *Tephroseris helenitis* subsp. *arvernensis* (Rouy) B. Nord. in Opera Bot. 44: 44. 1978. – Type: not designated. – Protologue: "Hab. — Cantal: de Ste-Anastasie à Allanche (Clisson in h. R.); éboulis au pied

Fig. 23. *Tephroseris papposa* – Greece, Nom. Kastoria, 1.3 km NO Pano Arena, 8 Jun 1989, *Willing 6045* (B).

du mamelon terminal du plomb, versant nord (A. Dumas); sous les rochers de Vacivières, en haut du ravin de la Croix (fr. Héribaud in h. R.): à rechercher".

= *Senecio helenitis* subsp. *salisburgensis* Cufod. in Repert. Spec. Nov. Regni Veg. Beih. 70: 129. 1933 ≡ *Tephroseris helenitis* subsp. *salisburgensis* (Cufod.) B. Nord. in Opera Bot. 44: 44. 1978. – Type: not designated. – Protologue: "Fl. exs. Austro-Hung., No. 1798 b (*Sen. prat.* f. *ligulata*). – Schultz, Herb. norm., cent. 7, No. 689; 1862 (*Sen. prat.*)".

Description — Plants perennial, 20–80 cm tall, erect, mostly unbranched below, very rarely branched from base. Rootstock short, erect or oblique. Axis mostly with reddish/purplish lines, sparsely to densely white arachnoid. Lower leaves 4.5–30 × 1.5–5 cm, distinctly petiolate, petiole as long as to much longer than blade, often more or less distinctly winged particularly in smaller leaves; blade elliptic to ovate, sometimes with truncate to almost cordate base, entire, undulate, undulate-serrate or less often more or less finely dentate to serrate; upper surface often somewhat rugose between veins, leaf margin very narrowly revolute at least in lower leaves; cauline leaves increasingly sessile and entire toward apex, upper leaves often somewhat amplexicaul; leaf indumentum more or less densely arachnoid to floccose, lower surface mostly much more densely arachnoid than upper surface, veins on upper surface less densely arachnoid than on lower surface and clearly visible. Capitula 3–15 in pseudoumbel, sometimes with single long-pedunculate capitula or 2- to 3-capitulate accessory pseudoumbels below terminal pseudoumbel. Involucral bracts 12–22, 5–10 mm long, often with purple or purplish tip. Capitula mostly white arachnoid at base; involucral bracts sparsely to densely white arachnoid. Ray florets 14–23, 8–15 × 2–3 mm, yellow, or ray flo-
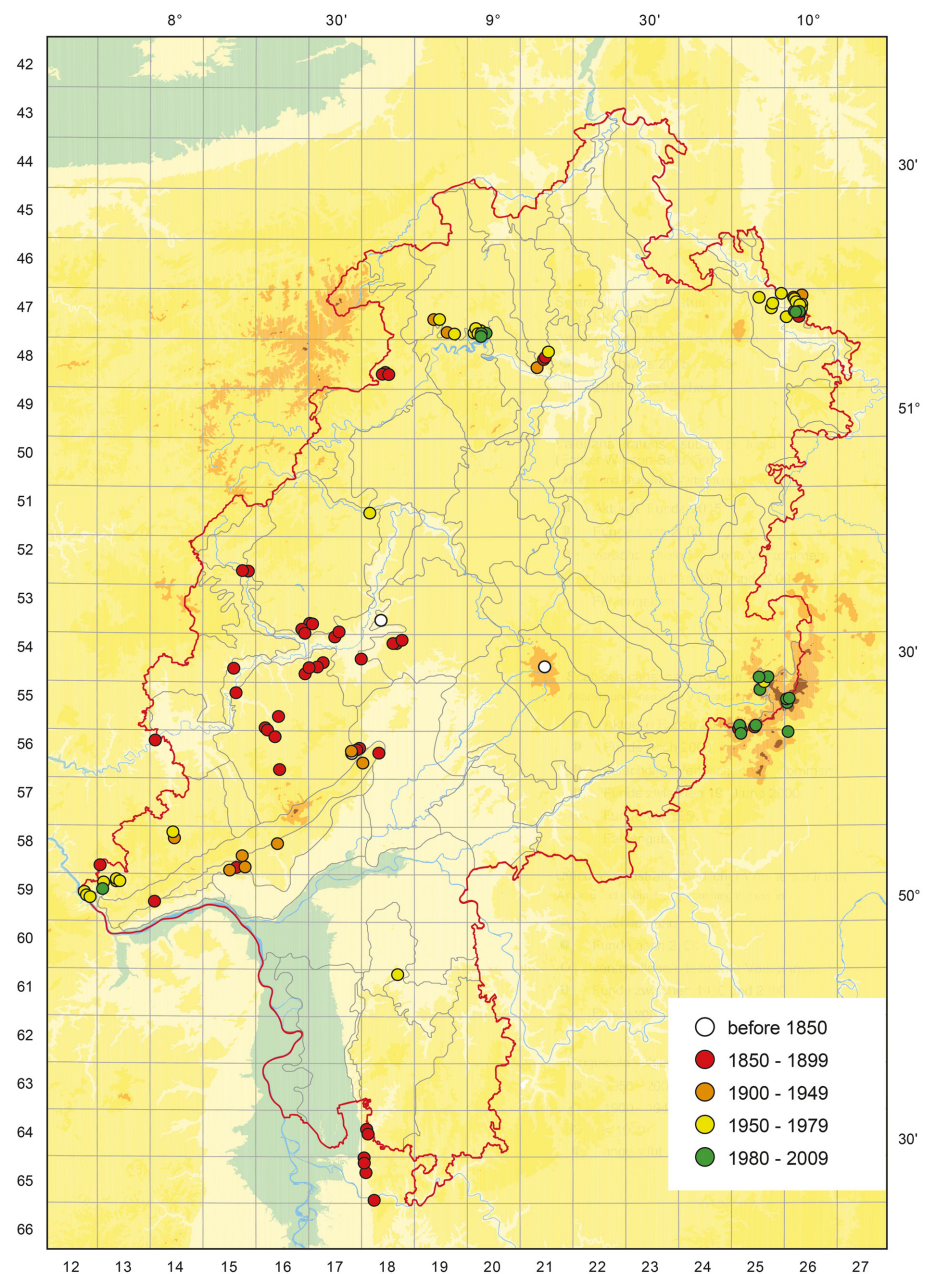

Fig. 24. Past and present distribution of *Tephroseris helenitis* in Hessen (Germany). Map prepared on 28 May 2019 by Sylvain Hodvina (Zwingenberg, Germany). In the latest survey (Bönsel & al. 2021), the species could be found in only one locality (Katzenstein near Waldeck).

rets absent. Achenes 3–4 mm long, mostly pubescent, more rarely glabrous; pappus 4–8 mm long.

Chromosome number — 2*n* = 48 (Watanabe 2002).

Phenology — Flowering and fruiting from March to July.

Habitat — The species mostly grows in humid to somewhat wet, neutral to somewhat acid (rarely basic) and more or less light places, such as wet meadows, blanket bogs or open broad-leaved forests.

Distribution — For overall distribution see Meusel &

Jäger (1992, sub *Senecio helenitis*) and Fig. 15. For more detailed distribution see: Bundesamt für Naturschutz (BfN) (2021, Germany), Tela Botanica (2021, France), Info flora (2021, Switzerland).

Conservation status — *Tephroseris helenitis* has been assessed as vulnerable to endangered in Switzerland, endangered in Austria and Germany, where regional accounts assess it as critically endangered or in danger of extinction, and near threatened (subsp. *candida*; if recognized) or vulnerable (subsp. *macrochaeta*; if recognized) in France.

Remarks — The most obvious character of this species, and the one used by most authors, is its leaf indumentum, which in typical material is much more densely arachnoid on the lower than on the upper surface. The upper leaf surface is often rugose. However, leaves also can be fairly glabrous. Often the margin of lower leaves is very narrowly revolute, recognizable as a narrow, dark margin.

Within *Tephroseris helenitis*, a number of subspecies have been recognized in the more recent literature (Chater & Walters 1976; Fischer & al. 2005; Jäger 2011; Tison & Foucault 2014). These are subsp. *candida* (Corb.) B. Nord., subsp. *macrochaeta* (Willk.) B. Nord., subsp. *salisburgensis* (Cufod.) B. Nord. and partly subsp. *arvernensis* (Rouy) B. Nord., the last recognized at subspecific rank by Greuter (2006+) and at varietal rank within subsp. *helenitis* by Tison & Foucault (2014). Recognition of these taxa is based mainly on the careful work by Brunerye (1969). Of all these subspecies, subsp. *salisburgensis* is the best known. The major character used by all authors to distinguish this from the type subspecies is its glabrous achenes. In addition to this, the following characters have been used to distinguish the two subspecies: smaller basal leaves and a sparser indumentum of stems and leaves in subsp. *salisburgensis* (Chater & Walters 1976) or a glabrescent lower leaf surface (Fischer & al. 2005), number of ligules (15–18 in subsp. *salisburgensis* vs mostly 13 in subsp. *helenitis*; Fischer & al. 2005), colour of involucral bracts (apex red in subsp. *salisburgensis* vs green throughout in subsp. *helenitis*; Fischer & al. 2005) and shape of leaf blade (gradually narrowing into petiole in subsp. *salisburgensis* vs abruptly narrowing in subsp. *helenitis*; Jäger 2011). In a thorough analysis of *T. helenitis* subsp. *helenitis* and subsp. *salisburgensis* including an analysis of AFLP variation, Pflugbeil (2012) reported that individuals with glabrous vs pubescent achenes cannot be separated by AFLPs, that populations of individuals with glabrous achenes always contain individuals with pubescent achenes in varying percentages, that no other morphological character is correlated with the genetic data and that individuals with glabrous or pubescent achenes are not different ecologically. Although populations with individuals with glabrous achenes occupy a distinct range, Pflugbeil (2012) concluded that subsp. *salisburgensis*

should not be recognized at subspecific rank. Recently, Pflugbeil & al. (2021) hypothesized that forms with glabrous achenes (referred to as subsp. *salisburgensis* by the authors) originated postglacially during eastward range expansion of subsp. *helenitis*. Subspecies *candida* is a somewhat succulent taxon of coastal distribution in Normandy (Brunerye 1969; Tela Botanica 2021) with rather short and wide ligules (6–8 mm vs 8–15 mm long unless absent in subsp. *helenitis* and subsp. *macrochaeta*; Chater & Walters 1976). Subspecies *macrochaeta*, distributed in the western Pyrenees and adjacent parts of northeastern Spain (Brunerye 1969), has been differentiated by the indumentum of its capitula, which are arachnoid at the base but have glabrous bracts (Brunerye 1969; Chater & Walters 1976; Tison & Foucault 2014). Within subsp. *helenitis*, Tison & Foucault (2014) distinguished var. *discoidea* (DC.) Kerguélen from the Pyrenees by the absence of ligules and var. *arvernensis* (Rouy) B. Bock from the Auvergne by its small size. The latter was treated as a subspecies by Greuter 2006+ (see above).

Brunerye (1969) demonstrated the large overlap in variation among the infraspecific taxa he and later authors recognized. However, *Tephroseris helenitis* subsp. *macrochaeta* occupies a distinct range in the very southwest of the overall range of *T. helenitis*, and more than 90% of specimens have involucral bracts that are glabrous in their upper ¾ according to Brunerye (1969), and this subspecies has been accepted by Aedo (2019). *Tephroseris helenitis* subsp. *helenitis* var. *discoidea*, recognized at varietal rank by Tison & Foucault (2014) and Brunerye (1969, as var. *pyrenaicus* (Nyman) Brunerye), and mentioned as *Senecio lapeyrousii* Rothm. by Chater & Walters (1976), is limited to the Hautes-Pyrénées and is consistently eligulate. These two subspecies may eventually deserve formal recognition. However, in view of the large overlap in variation among taxa (Brunerye 1969), this should await examination of additional material. As regards subsp. *candida*, this taxon differs from subsp. *helenitis* mainly by its succulent and more densely arachnoid leaves. As these characters might well be modifications at its coastal sites, we recommend not accepting this taxon until further investigation. In contrast to *T. integrifolia* subsp. *maritima* discussed above, which is disjunctly distributed with subsp. *integrifolia* in Britain, subsp. *helenitis* occurs in inland localities close to subsp. *candida* in Normandy, and even coastal populations of subsp. *helenitis* are known (Tela Botanica 2021), so that ecological distinction between the two taxa is not possible.

Selected specimens seen — [Spain], prov. Guipúzcoa, Aia, Laurgain, 375 m, 15 Apr 1985, *F. Garín s.n.* (H); [Spain], Provinz Navarra, Puerto de Ibaneta, 1100 m, Wiesenkuppe auf der Paßhöhe, 17 Jun 2001, *R. Chizzola s.n.* (WU); [France], Pâturages de Madril, vallée de Gèdre, 1600 m, 25 Jul 1871, *Bordère s.n.* (B); France, dep. Pyrénées-Atlantiques, La Corniche, 17 May 1993, *A. Salazar & P. Urrutia 15229* (B); [France], Laval-le-

Prieuré im Tal des Dessoubre, 500 m, 9 Jun 1962, *E. Berger 2684* (B); [France], Laruns, vallée d'Ossau, 14 May 1990, *J. J. Lazare s.n.* (B, H); [France], Lans (Isère), 28 May 1888, *A. Pellat s.n.* (S); France, Languedoc-Roussillon, Montaigne Noir, Cupserviès, 808 m, track embankment in forest, 31 May 2010, *R. Vogt 16676, C. Oberprieler 10631, K. Konowalik* (B); [Austria], Salzburg, Moorwiesen, s.d., *M. Eysn s.n.* (WU); [Germany], Klingenstein Kreis, Blaubeuren, 24 May 1935, *K. Müller s.n.* (B); [Germany], Moor an der Mindel SO Schöneberg, Pfaffenhausen–Schöneberg, 550 m, 31 May 1987, *R. Vogt 6275* (B); [Germany], im Schilf um den Deininger Weiher SO Dingharting, 2 Jun 1983, *R. Vogt 1533* (B); [Germany], Esperstedt b. Arnstadt, im naturnahen Traubeneichenmischwald, 24 May 1959, *W. Hempel 2245* (B).

7. *Tephroseris papposa* (Rchb.) Schur, Enum. Pl. Transsilv.: 344. 1866 ≡ *Cineraria papposa* Rchb., Iconogr. Bot. Pl. Crit. 2: 13. 1824. – Holotype: s.loc., s.d., *Besser s.n.* (W-Rchb. 1889-0285642). – Note: Cufodontis (1933: 188) cited this specimen as the original specimen from Besser in the Reichenbach herbarium, but other relevant protologue information cannot be found on the specimen. – Fig. 18A, B, 23.

Description — Plants perennial, 15–50 cm tall, erect, unbranched below. Rootstock short, erect or oblique. Axis mostly densely arachnoid at flowering time, sometimes floccose. Lower leaves 4.5–9 × 1–2.5 cm, more or less sessile, with short and broadly winged petiole or distinctly petiolate, petiole shorter than to as long as blade, blade broadly to narrowly ovate to elliptic, entire to sinuate-dentate; basal leaves sometimes persisting until anthesis and appressed to ground, more commonly withered at anthesis; lower cauline leaves 10–26 × 2–2.5 cm, narrowly ovate to lanceolate, sessile to long petiolate with petiole as long as blade; lower cauline leaves held conspicuously upright, almost parallel to axis; cauline leaves increasingly sessile toward apex; leaves densely persistent arachnoid to floccose, commonly more strongly so on lower than on upper surface. Capitula 2–6 in pseudoumbel; peduncle 1–2 cm long at anthesis, rarely longer. Involucral bracts 16–28, 7–12 mm long, green. Capitula mostly densely arachnoid at base; involucral bracts often more or less densely to sparsely arachnoid throughout, tips sometimes glabrous; capitula glabrescent. Ray florets 14–22, 9–14 × 2–4 mm, yellow, spreading. Achenes 3–4 mm long, glabrous or pubescent; pappus 5–8 mm long, white.

Phenology — Flowering and fruiting from June to August.

Habitat — The species mostly grows in dry meadows and on rocky slopes and ledges from 1000 to 2400 m.

Chromosome number — $2n = 48$ (Watanabe 2002; Sârbu & al. 2005).

Distribution — For overall distribution see Meusel & Jäger (1992, sub *Senecio papposus*) and Fig. 15. For more detailed distribution see: Snowarski (2000–2021, Poland, sub *S. papposus*), Sârbu & al. (2005, Romania, sub S. *papposus*).

Conservation status — *Tephroseris papposa* has been listed as endangered in Poland (Snowarski 2000–2021) but not in Greece (Phitos & al. 2009).

Remarks — Typical *Tephroseris papposa* has a dense and persistent arachnoid indumentum on both leaf surfaces, the leaves are often entire, or else distantly dentate or sinuate-dentate, and mostly very narrow. Some material particularly from the northern part of its overall range as illustrated by Meusel & Jäger (1992; see also Fig. 15) approaches *T. helenitis* in leaf indumentum (see above).

Greek material of *Tephroseris papposa* was treated as *T. integrifolia* subsp. *integrifolia* with pubescent achenes and as *T. integrifolia* subsp. *aucheri* with glabrous achenes by Kadereit (1991). Although plants with glabrous achenes appear to have a more northerly distribution than plants with pubescent achenes in Greece (A. Strid, Ørbæk, pers. comm.), they also grow sympatrically and in our opinion do not deserve formal recognition.

Selected specimens seen — Bosnia and Herzegovina, Šator E of Bosansko Grahovo, slopes S of Šatorsko Jezero, 1580 m, alpine meadows and *Pinus mugo* shrub, 7 Sep 2011, *R. Vogt 17011* (B); Serbia, Suva Planina, s.d., *S. Petrovic s.n.* (WU); Kosovo, Sar Planina, above ski center 5 km SE of Brecovica, 1900–2300 m, meadows and grassland on rocky slopes, schistes vert, 15 Aug 1982, *P. Hartvig & al. 10013* (B); [Serbia], Flora Serbica, in m. Bussara pr. Pirot, 10 Jun 1898, *L. Adamović s.n.* (WU); Bulgaria, Rila, Maljovika, 2400 m, 17 Jun 1964, *W. Hempel s.n.* (B); [North Macedonia], Makedonien, Tal der Mavrovska Beka zwischen Mavrovi Hanovi und Trnica, 28 May 1968, *M. Bäßler & I. Quasdorf 788* (B); Greece, Nom. Kastoria, 1.3 km NO Pano Arena, 8 Jun 1989, *Willing 6045* (B); [Greece], Nomos Florina, Mount Kajmakcalan, 1800–1850 m, subalpine pastures, on micaceous schist, 3 Jul 1999, *A. Schuler 99/803* (B); [Greece], Macedonia or., prov. Serres, distr. Sindiki, montis Kerkini, 1900–1970 m, in pratis, solo rupestri vel arenoso gneisico, 27 Aug 1978, *W. Greuter 16790* (B); [Greece], Nom. Serres, Menikion-Massiv, N-Hang des Spanakokorifi, felsige Bergwiesen u. Felsen, 17 Jun 1990, *Willing 10652* (B); [Greece], Nom. & Ep. Serron, Mt Vrondous, summit area, 1700–1840 m, 6 Jul 1985, *P. Uotila 33930* (H).

Decline of *Tephroseris* in Europe

The status of *Tephroseris* species in Europe as assessed in various red lists has been summarized in the species accounts above. With the exception of some assessments

of *T. crispa*, all species are at least vulnerable to extinction. This assessment is amply supported by mostly regional accounts. For *T. integrifolia*, Isaakson (2009) noted that of 42 populations known in southern Sweden in the 19th century only four still existed in the early 21st century, and that population size decreased dramatically between 1980 and 2009 despite far-reaching conservation measures. In the Augsburg area of Germany, the number of populations of this species decreased from 12 in 1951 to two in 2010 (Meindl 2010), and a constantly decreasing number of flowering individuals in these two populations between 1994 and 2009 was reported by Meindl (2011). In addition to a decrease in number of British vice counties with *T. integrifolia* from 23 to 15, Stroh (2016) noted considerable retraction in range in many vice counties. For *T. aurantiaca* (here included in *T. integrifolia*), Leban & Anderle (2012) noted for Slovenia that this taxon thrived around the end of the 19th and the beginning of the 20th century, but could not be confirmed in most localities since. These authors proposed to classify the species as rare in the red list of Slovenia. For *T. longifolia* (subsp. *longifolia*), Olšavská & al. (2015) described the extinction of 12 of 31 microlocalities in the Pannonian region and, for subsp. *moravica*, the extinction of nine of 16 localities in the Carpathians. For *T. crispa* and *T. palustris*, strong decline was noticed in Sachsen, Germany (Geoportal Sachsenatlas 2021).

The decline of *Tephroseris helenitis* in parts of Germany (Hessen) is well illustrated in Fig. 24, and a strong decline of the species in the Regensburg area of Germany was noted by Eichhorn (1955). Figure 24 also shows that much extinction took place before 1950 or even before 1900.

Possible causes of the decline of *Tephroseris* in Europe

Most authors considered habitat loss or habitat modification the major cause of decline (Isaakson 2009; Meindl 2010; Martínez-García & al. 2012; Meindl 2011; Pflugbeil 2012). For *Tephroseris integrifolia*, Stroh & al. (2017) identified modification of grazing management as a major cause of decline of the species in England; the same observations were made by Meindl (2011) for the Augsburg area in Germany, and Schratt-Ehrendorfer (2000) discussed the need of *T. integrifolia* for open habitats in Austria. As regards *T. balbisiana* in Spain (sub *T. coincyi*), Martínez-García & al. (2012) considered intensive livestock activity to represent the main factor threatening the species. Those studies looking at genetic variation found no evidence for inbreeding depression in small populations (Isaakson 2009; Meindl 2011), although seed set appears to be correlated with population size (Widén 1993), and all (*T. integrifolia*: Isaakson 2009; Meindl 2011; *T. helenitis*: Pflugbeil 2012) found that genetic differentiation among populations is low and provided no evidence for genetic isolation.

A possible role of rising temperatures?

As has been pointed out many times, the effects of land-use change and climate change on species interact and cannot be easily separated (de Chazal & Rounsevell 2009; Willis & Bhagwat 2009; Cahill & al. 2013; Oliver & Morecroft 2014; Zhang & al. 2017). However, efforts to quantify the effect of climate change have been made (Doxford & Freckleton 2012; Lunney & al. 2014; Hill & Preston 2015). We will not undertake any formal analysis of the possible role of climate change for *Tephroseris* here, but will only list some observations that may point that way.

First, *Tephroseris integrifolia* has been considered a glacial relic (vs recent immigrant) by Engler (1879), Böcher & al. (1946) and Pigott & Walters (1954). An occurrence of *T. integrifolia* in Yorkshire/Westmorland, which apparently went extinct between 1938 and 1963 (Smith 1964, 1979), lies near an area "which harbours the most famous Late Glacial relic assemblage in Britain and there are numerous other sites on the limestone in and near Westmorland which have arctic-montane or boreo-arctic montane species" (C. D. Preston, Cambridge, pers. comm.). Equally, *T. palustris* was considered a glacial relic by Engler (1879), and *T. helenitis* in Austria was postulated by Pflugbeil (2012) to have survived glacial periods near the Alpine glaciers. The interpretation of the species of *Tephroseris* in Europe as glacial relics may be supported by the ecology of most species which, with the exception of *T. integrifolia*, grow in humid to wet places. This may recall predominant summer conditions in periglacial environments (Godwin 1975) and is similar to the conditions in which arctic species of the genus grow today.

Second, dramatic decreases in population sizes between 1980 and 2009 (Isaakson 2009) and a steady decrease of flowering individuals between 1994 and 2009 (Meindl 2011) were recorded, irrespective of conservation measures, and Meindl (2011) suspected that in this period the lack of vernalization by low winter and early spring temperatures might be causal.

Third, it seems, although good data are rare, that decline gathered pace near the end of the 19th century. This is best documented for *Tephroseris integrifolia* in Sweden, where of 42 populations known in the 19th century only 15 persisted through the turn to the 20th century (Isaakson 2009). A steep decline between 1850 and 1899 can also be seen in *T. helenitis* in Hessen, Germany (Fig. 24), where it could be found in only one locality in 2019 (Katzenstein near Waldeck; Bönsel & al. 2021), and *T. palustris* went extinct in 1899 in the United Kingdom. However, *T. palustris* still can be found quite frequently in the Netherlands where, however, it is declining too (van der Slikke 1998). Also, fast southeast-northwest range expansion of *T. crispa* between 1881 and 1910 was reported by Rothe (1910) in the Polish Opolskie area to the east and southeast of Wrocław, where apparently the

species expanded into lowland areas from more mountainous areas to the south and east. Interestingly, the Little Ice Age is considered to have ended between 1850 and 1920 (Owens & al. 2017), which might imply that rising temperatures after this period may have accelerated the decline of *Tephroseris*. Also, much decrease in *T. helenitis* appears to have taken place before the onset of the Great Acceleration around 1950 (Fig. 24), when anthropogenic effects increased steeply (Steffen & al. 2015).

Fourth and finally, as far as we can see, the genus is doing well in the Arctic. Considering the widespread *Tephroseris palustris* alone, a species that is extinct, rare or declining in Europe, this has been described as frequent for all but one of the subareas used in the panarctic flora (Elven 2021).

Acknowledgements

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DNA alignments in NEXUS format for the five markers: ITS, ETS, *trnT-trnL*, *trnL-trnF* and *rpl32-ndhF*.