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

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

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**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. *serpentinii* 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*

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**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, Wohlff. & 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.
**Tephroseris**, first introduced as an unranked subgroup 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. Chatter & 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; Nordenstrom & al. 2009). Morphological characters in support of the placement of *Tephroseris* in subtr. *Tussilagininae*, far removed from *Senecio* of subtr. *Senecioneae*, 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-Cremothodium-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 pseudumbels (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* (Chatter & 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 pseudumbels, and those of *Jacobaea* have capitula not arranged in pseudumbels (*J. incana* (L.) Veld.) or large solitary capitula (*J. uniflora* (L.) Veld. = *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. coineyi* Rouy, *S. elodes* DC., *S. helenitis* (L.) Schinz & Thellung, *S. integrifolius* (L.) Clairy., *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 Chatter & 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), Chatter & Walters (1976) included *S. brachychaetus* in *S. ovirensis* and did not treat *S. coineyi* 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 Chatter & 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 Chatter & 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 Chatter & 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. Tephrosia coicocy was identified as supported sister to two larger clades, one containing only T. integriofila (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. integriofila subsp. aucheri (DC.) B. Nord., T. italic Holub, T. longifila (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 Tephrosia 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 Oliavská & 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 Tephrosia 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 Tephrosia 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 trnL-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 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 trnL-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 Ślask         | 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*   | Tep38   | France, Alpes-Maritimes    | Schönswetter & Tribsch 32564 | WU 0030837 |
| subsp. capitata              | 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*   | Tep6    | Germany, Thüringen         | Kader & Schwarzberg 2018-533 | protected population |
| subsp. integrifolia          | Tep9    | Germany, Thüringen         | Kader & Pasch 2018-534 | protected population |
| Tep11                        | United Kingdom, Bedfordshire | Preston & Stroh | protected population |
| Tep12                        | United Kingdom, Wiltshire   | Gurney & Preston | protected population |
| Tep18                        | Germany, Thüringen          | Kader & Schwarzberg 2018-532 | protected population |
| Tep19                        | Germany, Thüringen          | Kader & Pasch 2018-535 | protected population |
| Tep45                        | United Kingdom, Yorkshire   | Meinerthagen 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*   | Tep14   | United Kingdom, Anglesey   | Shaw s.n.   | protected population |
| subsp. maritima              | Tep16   | United Kingdom, Anglesey   | Shaw s.n.   | protected population |
| Tep21                        | United Kingdom, Anglesey    | Griffith & Bangor |                                   |
| *Tephroseris integrifolia*   | Tep37   | Austria, Burgenland        | Fischer & Fischer s.n. | WU 5214 |
| subsp. serpentinil           | Tep42   | Norway, Troms og Finnmark  | Arnstein Lye 12866 | O 9051 |
| Tephroseris integrifolia     | Tep43   | Italy, Emilia-Romagna      | Luccioli & Padovina s.n. | B 10 0630751 |
| subsp. ”tundricola”          | Tep36   | Italy, Veneto              | Schönswetter & Tribsch 5271 | WU 0040178 |
| Tephroseris longifolia       | Tep41   | United States, Alaska      | 2018-00641  | protected population |
| Tephroseris palustris        | Tep27   | Kosovo, Prizren            | Hartvig & al. 10013 | B 10 0630792 |
| Tephroseris papposa          | Tep29   | Greece, Ditiki Makedonía   | Schuler 99/803 | B 10 0162245 |
| Tep30                        | Greece, Kentrik Makedonía   | Greater s.n. | B 10 0630793 |
| Tep31                        | Greece, Ditiki Makedonía    | Willing 6045 | B 10 0525937 |

(5′-GGC TTG TAA AYT TTT GCC TAA TA-3′) and ndhF-118R (5′-TTA ACA 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 MgCl₂, 0.1 mM dNTPs, 0.8 µM of each primer, 1 U Taq DNA Polymerase (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 GTR+GAMMA model and the plastid dataset was 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 Akaake 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 1000⁸ 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 burn-in. 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. “trundrica”, 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. flammaea (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. balbiana 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. balbiana 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
| GenBank accession number | Taxon Country | ITS | ETS | rpl32 | ndhF | trnT | trnL | trnF |
|--------------------------|---------------|-----|-----|-------|------|------|------|------|
| KU696044                 | Nemosenecio formosanus China |    |     |       |      |      |      |      |
| GU818092                 | Nemosenecio formosanus China |    |     |       |      |      |      |      |
| KU696043                 | S. globiger |      |     |       |      |      |      |      |
| KU696223                 | Sinosenecio euosmus China |      |     |       |      |      |      |      |
| WM796253                 | Sinosenecio euosmus China |      |     |       |      |      |      |      |
| KU696279                 | Tephroseris atriplicifolia Spain |      |     |       |      |      |      |      |
| KU696272                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796234                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796235                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796236                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796237                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796238                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796239                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796240                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796241                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796242                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796243                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796244                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796245                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796246                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796247                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796248                 | T. balbisiana Spain |      |     |       |      |      |      |      |
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| MW796253                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796254                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796255                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796256                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796257                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796258                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796259                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796260                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796261                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796262                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796263                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796264                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796265                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796266                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796267                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796268                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796269                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796270                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796271                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796272                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796273                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796274                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796275                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796276                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796277                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796278                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796279                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| MW796280                 | T. balbisiana Spain |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
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| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |      |      |
| KU818092                 | T. crispa Czech Republic |      |     |       |      |      |  |
| 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. serpentina 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. kjellmani                  | 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. moravia) | 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        |

continued on next page
Table 2 (continued from previous page)

| GenBank accession number | Taxon | Country | ITS | ETS |
|-------------------------|-------|---------|-----|-----|
| MW79639*                | T. palustris | United States | MW79639* | MW79640* |
| GU181800               | T. papposa | Turkey | na | na |
| MW796375*               | T. papposa | Kosovo | na | na |
| MW796376*               | T. papposa | Greece | MW796378* | MW796379* |
| MW796342*               | T. papposa | unknown | na | na |
| EU195522               | T. papposa | China | K1992264 | K1992265 |
| KY197073               | T. papposa | unknown | K1992031 | K1992032 |
| AF961880               | T. papposa | Canada | na | na |
| MG218262               | T. subdentata | unknown | 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*).
Species identification

Except for our treatment of *Tephroseris balbisiana*, *T. cooincyi* 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 & Jüger 1992; Greuter 2006+). We hope, however, that our discussion and comparison of charac-

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.
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.

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.
(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; Meinl 2011) and *T. helenitis* (Pflugbeil 2012).

The molecular dating analysis of *Tephrosferis* by Skokanová & al. (2019) and us places diversification of the genus well in the Quaternary, confirming the long-held view that *Tephrosferis* 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 *Tephrosferis* 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 (Sana bria, 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) ........ 2c. *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) ........ 4
   - Leaves 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 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 densely and persistently arachnoid to floccose; plants from SE Europe (Fig. 18A, B, 23) ........ 7. *T. papposa*

1. *Tephrosferis 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).
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 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, noding 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.

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 pseudumbels, 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 (einzährig-überwintert) 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, Zuiderzee), 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. Davigneaud 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], Rathe, Graben nordwestlich vom Klefkener See, 1 Jul 1980, D. Benkert s.n. (B); [Belarus], in pratis ad ripas fluminis Struma prope vicum Szarkowszczynza, 6 Jul 1938, I. Dabrowska s.n. (B); [Latvia], Rézekne region, Ančupani hills, in a gravel pit, 15 Jun 1980, G. Klovina 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 Pyreniacis, 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-
aggregated 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, 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 — 2n = 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
Fig. 6. Tephroseris integrifolia subsp. integrifolia – [Austria], Pannonischer Bezirk, Ebreichsdorf, 25 May 1964, Schönbeck s.n. (WU).
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. integrifolia. 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); [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).

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).
Fig. 8. Tephroseris integrifolia subsp. aurantiaca – [Austria], Kärnten, Glantschach, s.d., s.coll. s.n. (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 of- ten 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 — 2n = 48, 96 (Watanabe 2002).

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

Habitat — The subspecies mostly grows in dry to hu- mid 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 en- dangered 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. 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 Gratza, 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, Baise Peyrefique, 8 Jul 1998, W. Gutermann, P. Schönswetter, A. Tribsch 32564 (WU).
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., C. 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 Gómör, 4 Jun 1906, Filarszky & Kümmerle s.n. (H); [Slovakia], 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: 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 pseudumbell; 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 discolored. 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), Sárub & 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 Wölzer Tauern, Klosterneuburgerhütte – Niederer Zin­ken–Hoher Zinken–Schieß fleck, 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).
There exist three very locally distributed taxa, which we recognize here as subspecies of Tephrosperis integrifolia.

2d. Tephrosperis 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. 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.

Fig. 12. Leaves of Tephrosperis 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, Vardo, Hestmannes, 1 km Ø f Austerelva i Persfjord, 28 Jul 1987, K. A. Lye 12866 (O).
Fig. 13. *Tephrosperm integrifolia* subsp. *serpentini* – [Austria], Burgenland, Bernsteiner Gebirge, zwischen Redlschlag und Bernstein, 14 May 2011, G. & M. A. Fischer s.n. (WU).
helenitis subsp. candidus (Corb.) Brunerye by Brunerye (1969), now data clearly place subsp. in may be supported by the ratio of petiole to blade – the est relative to each other (Fig. 1, 2). Such relationship 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 extent its morphology is the result of phenotypic plasticity.

Chromosome number — 2n = 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 spathialfolius), 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).

2c. Tephroseris integrifolia subsp. serpentinii (Gáyer) B. Nord. in Opera Bot. 44: 45. 1978 ≡ Senecio serpentinii Gáyer in Vasvárm. Szombathelyi Város Kultúregyes. Vasvárm. Múz. Évk. 1: 7. 1925. – Type: not designated. – Protologue: “S. Serpentinii (S. spathialfolius Waisb.) et mte Steinstückl ad Borostyánkő”. – 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. serpentinii. – Fig. 12A, B, 13.

An ecologically specialized population from serpentine has been treated as a subspecies of Tephroseris integrifolia, i.e. subsp. serpentinii by, e.g., Fischer & al. (2005; for illustration and description see also Fischer & al. 2015). This population is known only from Steinstük at 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. serpentinii 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: 16-5550). – isolectotype: S 16-55496). – Note: The name might not be applicable
Fig. 14. *Tephroseris integrifolia* subsp. “*tundricola*” – [Norway]. Finnmark, Vardo, Hestmannes, 1 km Ø f Austerelva i Persfjord, 28 Jul 1987, K. A. Lye 12866 (O).
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/lbo/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).
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, G00342263, G00342264, 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. – Protologue: “ESPAGNE: le « Pinar » de Hoyocasero, montagnes d’Avila (herbier Rouy, leg. de Coincy, 24 juin 1888)”.

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 pseudumbel. Involucral bracts 16–28, 7–11 mm long. Capitula mostly white arachnoid at base; involucral bracts 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 wet places in the Spanish Sierra Nevada, parts of central Spain (Sabanabra, 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. coineyi 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. coineyi as T. elodes subsp. coineyi (Rouy) Aedo. The leaf margin of T. coineyi 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. coineyi 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. coineyi 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 Trévezel, 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 1799, B. de Retz 79344 (H); [Spain], Ávila, inter Piedrahita et Puerto de Peña Negra, 1700 m, in humidis ad rivilum, 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 Rabouins, 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 brachychaetum DC., Prod. 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 Kärnten von Dr. Rohde gesammelt, lag in Mertens Sammlung unter C. campestris”.

= Cineraria tenuifolia Gaudin, Fl. Helv. 5: 307. 1829 = Senecio gaudini Gremli, Excursionsfl. Schweiz, ed. 8: 238. 1896 = Tephroseris tenuifolia (Gaudin) Holub in Folia Geobot. Phytotax. 8: 174. 1973 = Tephroseris longifolia subsp. gaudini (Gremli) Kerguélen in Bull. Assoc. Informat. Appl. Bot. 1: 184. 1994. – 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 var. pseudocrispus Fiori in Fiori & al., Fl. Italia 3: 220. 1903 = Senecio rivularis subsp. pseudocrispus (Fiori) E. Mayer, Annunt 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 longifolia subsp. moravica Holub in Folia Geobot. Phytotax. 8: 173. 1973. – [Senecio brachychaetum sensu Cufod. in Repert. Spec. Nov. Regni Veg. Beih. 70: 101. 1933, non Senecio brachychaetum DC., Prod. 6: 362. 1838]. – Holotype: Fl. Exciss. Ital., Fiori, Béguinot & Pamela 171 (F n.v.).

= Tephroseris longifolia subsp. pseudocrispus Holub 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 towards 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 pseudo-dumbbell; peduncle 2–6 cm long at anthesis, extending at fruiting time; commonly with single long-pedunculate dumbbell; peduncle 2–6 cm long, commonly with purple tip. Capitula 3–12 in pseudo-axillary; leaves 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 — n = 48 (Watanabe 2002; see also Ošavská & 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 (Janíšová & al. 2018) from 400 to 2500 m.

Distribution — For overall distribution see Meusel & Jäger (1992, sub Senecio brachychaetus, S. ovirensis, S. rivularis subsp. pseudocrispa) 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. italic, T. longifolia subsp. longifolia, subsp. gaudiniai, 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 indument 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 (Ošavská & al. 2015), ecological (Janíšová & al. 2018) and molecular (Skokanová & al. 2019) approaches. Whereas Ošavská & al. (2015) recognized five subspecies within T. longifolia, i.e. subsp. longifolia, subsp. moravica Holub, subsp. brachychaeta Greuter, subsp. gaudiniai (Gremli) Kerguelen and subsp. pseudocrispa (Fiori) Greuter (an intraspecific classification also used by Greuter [2006+]), Skokanová & al. (2019) treated subsp. brachychaeta, subsp. gaudiniai and subsp. pseudocrispa as T. italic 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 Ošavská & 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 Ošavská & 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. italic, T. papposa), and several taxa are polymorphic for ITS ribotypes (T. crispa, T. integrifolia subsp. aucheri, T. italic, 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. italic + T. tenuifolia, and the remaining taxa as the third group. Finally, ecological differentiation among taxa is weak. Although Janíšová & 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 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], Hungary merid.-orient., ad thermas Herkulis, s.d., Degen s.n. (WU); Austria, Steiermark, Schönau, 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).

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).
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. Tribisch 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; isolecotypes: 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 cuneate base, mostly coarsely dentate-serrate; basal leaves often persisting until anthesis, often recurved; cauline leaves often with reddish/purplish tinge; lower leaves with very broadly winged petiole, of the species in Poland has not been assessed.

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); [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); [Austria], Söchau, s.d., H. Sabransky 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 Malý 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 Slovensky Raj, c. 5 km nördlich Dedinky, 900 m, 18 Jun 2004, F. Schuhwerk 04/99 (B); Slovenia, Karavanke, in declivi-bus septemtrionalibus montis Golica, 1800 m, 7 Jul 1937, F. Doššak 27234 (B).

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 Brunerey (1969), the statement “Habitat in Siberia” 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-Anastatie à Allanche (Cisson 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 rechækcher”.

= Senecio helenitis subsp. salisburgensis Cufod. in Repert. Spec. Nov. Regni Veg. Beih. 70: 129. 1933
≡ Tephroseris helenitis subsp. salisburgenensis (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-capitalitate 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 florets absent. Achenes 3–4 mm long, mostly pubescent, more rarely glabrous; pappus 4–8 mm long.

Chromosome number — 2n = 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.) Kerguëlen 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 ¼ according to Brunerye (1969), and this subspecies has been accepted by Aedo (2019). *Tephroseris helenitis* subsp. *salisburgensis* 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 segregated. 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], Provínz Navarra, Puerto de Ibaneta, 1100 m, Wiesenkuppe auf der Paßhöhe, 17 Jun 2001, *R. Chiz­zola* s.n. (WU); [France], Pâtures 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 Weier SO Dingharting, 2 Jun 1983, R. Vogt 1533 (B); [Germany], Esperstedt b. Arnstadt, im naturnahen Trauben eichenmischwald, 24 May 1959, W. Hempel 2245 (B).

7. *Tephroseris papposa* (Rchb.) Scherb, Enum. Pl. Transilv.: 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 indumentum on both leaf surfaces, tips sometimes arachnoid at base; involucral bracts often more or less distinctly 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, Ørbeak, 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 Serbia, 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 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 (Geportal 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. coincyti*), 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; Cahlil & 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).

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**Supplemental content online**

See https://doi.org/10.3372/wi.51.51209

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

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