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## *Caucasoseris*, a new genus of subtribe *Chondrillinae* (*Asteraceae*: *Cichorieae*) for the enigmatic *Prenanthes abietina*

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**Abstract:** A new genus, *Caucasoseris*, is established to accommodate *Prenanthes abietina*, a species of hitherto uncertain systematic position distributed in the western Caucasus and northeasternmost Turkey in montane conifer and mixed forests. Agreement has existed that the species belongs somewhere in the *Crepidinae* or *Lactucinae* but its morphological features do not match any genus and previous molecular phylogenetic analyses could not establish its sister group. This study provides additional micro- and macromorphological, palynological and anatomical data, and used a molecular phylogenetic sampling designed to ascertain its relationship. A sister group relationship with the *Chondrillinae* is inferred from the phylogenetic tree based on nrITS. In the plastid DNA tree, where the *Chondrillinae* are resolved as a clade nested inside the *Crepidinae*, the species is resolved further remote from the *Chondrillinae* clade and in a rather early diverging position of the *Crepidinae*. In agreement also with the anatomical and micro- and macromorphological findings, it is considered an orphan lineage with affinities to the *Chondrillinae*, best treated as a genus of its own. A key to the genera of the *Chondrillinae* including *Caucasoseris* is provided.

**Keywords:** *Asteraceae*, Caucasia, *Chondrillinae*, *Cichorieae*, *Compositae*, molecular phylogenetics, new genus, *Prenanthes abietina*, taxonomy

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### Introduction

When the widely travelled French botanical explorer Benjamin Balansa (1825–1891) collected a yellow-flowered species in montane *Picea orientalis* (L.) Peterm. forests of NE Turkey in September 1866, he could not know that he presented a long-standing riddle to the botanical community, solved only 140 years later. The gathered plants of a doubtlessly new species, which he issued in his exsiccatae “Plantes d’Orient 1866” as “*Crepis abietina* n. sp.”, did not well match any of the genera recognized in the SW Asian *Cichorieae*. Boissier (1875: 802) formally published it in the third volume of his *Flora orientalis* as *Mulgedium abietinum* Boiss. & Balansa, and stated that the species actually holds an intermediate position

between *Crepis* L. and *Mulgedium* Cass. Subsequent botanical exploration of the Caucasus region, intensified in the first half of the 20<sup>th</sup> century, then revealed that the occurrence of the species in the Turkish province of Rize is only the southernmost occurrence of its main distribution area in the western Caucasus region (Grossheim 1934; Sennikov 2009). Noteworthy, the species grows mostly under the cover of montane forests (Kirpicznikov 1964), as alluded by Balansa’s epithet “*abietina*” (growing with conifers) and its distribution area corresponds to a larger extent with that of *Picea orientalis* (Farjon & Filer 2013: 176, map MAJ 5). Whereas *Cichorieae* are known to grow mostly in open habitats, there are, however, a good number of species of the tribe that grow like *Prenanthes abietina* (Boiss. & Balansa) Kirp. under forest canopy.

Author sequence determines credit.

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The taxonomic position of the species has remained unsettled throughout its history. Bornmüller (1905) transferred it to *Lactuca* L., Beauverd (1910) to *Crepis*, a conclusion not accepted by Babcock (1947), and Grossheim (1934) to *Cicerbita* Wallr., a view affirmed by Stebbins (1937). Kirpicznikov (1964), however, placed it then with some reservation in *Prenanthes* L. under “species of doubtful taxonomic position”. Sennikov (1997) maintained the placement in *Prenanthes* but erected a section of its own for this species. Hence, except Beauverd (1910), all authors placed the species in the subtribe *Lactucinae* in its current narrow sense going back to Bremer (1994). When Kilian & al. (2017) for the first time included *P. abietina* in a molecular phylogenetic analysis, performed to reconstruct the phylogeny of the *Lactucinae* globally, the species was not resolved in any of the clades corresponding to the genera so far suggested as its home. Instead, it turned out to represent an orphan lineage, with a position in the nrITS tree outside any of the subtribes included, and as an isolated member of the *Crepidinae* in the plastid DNA trees. Güzel & al. (2021), including three additional samples of *P. abietina*, corroborated these results.

Molecular phylogenetics have so far confirmed that the uncertainties pervading the taxonomic history of *Prenanthes abietina* are fully justified but the phylogenetic placement of the species is still unresolved. This urged us to undertake another approach. Therefore, the current study aims to (1) reassess the morphology of *P. abietina* on the micro- and macromorphological and anatomical level; (2) ascertain its sister group relationship based on a further diversified sampling for molecular phylogenetic analysis; and (3) draw the taxonomic conclusions.

## Material and methods

**Plant material and sampling** — The plant samples of *Prenanthes abietina* used in this study were collected in Turkey on field trips during the years 2013–2015 and are preserved at the herbarium of Karadeniz Technical University Department of Biology (KTUB) with a duplicate at the Botanischer Garten und Botanisches Museum Berlin (B). The nrITS and cpDNA sequences of *P. abietina* used in the molecular phylogenetic analysis were retrieved from Kilian & al. (2017) and Güzel & al. (2021). Based on these previous studies, further taxa were included to diversify the sampling in iterative analyses, with the aim to establish sister group relationships for *P. abietina* in the nrITS and plastid DNA trees. The voucher data are given in the Appendix.

**Achene anatomy** — Mature achene samples were selected from herbarium specimens. Preparation of the achenes for anatomical studies followed Zhu & al. (2006). The selected samples were boiled in water 30 min, subsequently

dehydrated through an alcohol series, then embedded in paraffin (melting points 65°C) before sectioning by a rotary microtome. Sections with a thickness of 5–15 µm were stained in a safranin-fast green combination before being mounted in entellan. The slides were examined and photographed under the light microscope. The terminology of Sennikov & Illarionova (2001) and Zhu & al. (2006) is adopted for describing achene anatomical features.

**Micromorphology** — Achene and pollen grain samples obtained from herbarium specimens were prepared for investigation with the scanning electron microscope (SEM). Pollen grains were pretreated with the acetolysis method (Erdtman 1952), then suspended in 90% ethanol. The mature achenes and pretreated pollen grains were mounted onto aluminium stubs with double-sided adhesive tape, and sputter coated with gold to a maximum thickness of 20 µm. SEM examinations were carried out using a Jeol JSM-6510LV SEM at 10 kV. The terminology of Barthlott (1981), Zhu & al. (2006) and Zhang & al. (2013) is adopted for describing achene epidermal micromorphology. Surface sculpturing of the achene was observed based on four characters proposed by Barthlott (1981): cellular arrangement; shape of the epidermal cells; ornamentation of the outer cell walls; and development degree of epicuticular wax. Descriptive terminology of pollen characters follows Punt & al. (2007).

**DNA isolation, amplification and sequencing** — Total genomic DNA was extracted from herbarium material or c. 20 mg of silica-dried leaf sample following the modified CTAB extraction procedure of Doyle & Doyle (1987) or Plant Kit Rev. 03 (Macherey-Nagel GmbH & Co. KG, Germany) following the manufacturer’s protocols. Amplification of the studied markers followed the protocols described by Wang & al. (2013). Sequences of one nuclear (nrDNA ITS) and five plastid genome regions (*petD* region, *psbA-trnH* spacer, 5'*trnL*<sup>(UAA)</sup>-*trnF* spacer, *rpl32-trnL*<sup>(UAG)</sup> spacer and *trnQ*<sup>(UUG)</sup>-5'*rps16* spacer) were used as phylogenetic markers. The markers were amplified by the same primer pairs as in Wang & al. (2013), Kilian & al. (2017) and Güzel & al. (2021).

**Sequence alignment, coding of length mutational events, and phylogenetic analyses** — The boundaries of the studied markers were defined according to Wang & al. (2013), Kilian & al. (2017) and Güzel & al. (2021). The nrITS and plastid sequences were automatically aligned using the L-INS-i algorithm implemented in MAFFT (v.7.407) (Kato & Standley 2013). The alignment of the non-coding plastid DNA markers was subsequently subjected in PhyDE v.0.9971 (Müller & al. 2010) to a motif-based homology assessment following the criteria outlined by Kelchner (2000), Borsch & al. (2003) and Löhne & Borsch (2005) and adjusted

manually where necessary. A few sections were excluded because of homology uncertainties, and inversions were re-inverted. Two separate datasets were built for the nrDNA ITS region and the five concatenated non-coding plastid DNA regions. Indels and inversions were coded as binary characters according to the simple indel coding (SIC) method (Simmons & Ochoterena 2000) implemented in the program SeqState v.1.40 (Müller 2005a).

For the phylogenetic analysis, newly generated sequences and selected sequences from Kilian & al. (2017) and Güzel & al. (2021) were used. The newly generated sequences with INSDC (International Nucleotide Sequence Database Collaboration) accession numbers are provided in the Appendix. The final nrITS and plastid DNA matrices are available in the Supplemental content online.

Phylogenetic relationships were reconstructed using Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI), using the same software and parameters as described by Güzel & al. (2021): the MP analyses were carried out using the Parsimony Ratchet (Nixon 1999) with PRAP (Müller 2004), and run in PAUP\* version 4.0b10 (Swofford 2003) applying the optimal jackknife parameters according to Müller (2005b); the BI analyses were done with the high-performance computing system of the Freie Universität Berlin (Bennett & al. 2020); the ML analyses were performed on the Cipres Gateway (Miller & al. 2010). The tree topologies were assessed and visualized with TreeGraph v.2 (Stöver & Müller 2010).

## Results

**Molecular datasets and phylogenetic analysis** — The final nrITS alignment comprises 82 accessions belonging to 73 taxa across the tribe *Cichorieae*; five sequences belonging to four taxa were newly generated in this study. The aligned nrITS sequences are 686 nucleotides in length and the coded indels added 114 binary characters to the nrITS matrix; of these, 375 were parsimony informative. The MP analysis resulted in 240 most parsimonious trees ( $L = 2175$ ,  $CI = 0.3913$ ,  $RI = 0.6990$ ,  $RC = 0.2735$ ,  $HI = 0.6087$ ).

The final concatenated plastid DNA alignment comprises 324 accessions belonging to 62 taxa across the tribe *Cichorieae*; 30 sequences belonging to six taxa were newly generated in this study. The aligned plastid DNA sequences were 4995 nucleotides in length and the coded indels and inversions added 438 binary characters; of these, 826 were parsimony informative. The MP analysis resulted in 626 most parsimonious trees ( $L = 2983$ ,  $CI = 0.7037$ ,  $RI = 0.7935$ ,  $RC = 0.5584$ ,  $HI = 0.2963$ ).

The BI majority consensus phylograms, which are mostly congruent in topology with the trees of the MP and ML analyses, were supplemented with the BI pos-

terior probabilities (PP) and ML bootstrap (BS) support values and the MP jackknife (JK) support values, and are presented in Fig 1 and 2 for the nrITS and plastid DNA dataset, respectively.

Three accessions of *Prenanthes abietina* were resolved as a clade of their own presumably in a sister group relationship to the members of subtribe *Chondrillinae* in the nrITS tree (Fig. 1; PP = 1, JK = –, BS = 72). In the plastid DNA tree (Fig. 2), where the *Chondrillinae* clade is deeply nested within *Crepidinae*, the *P. abietina* clade was found nested in the *Crepidinae* in a rather early diverging position.

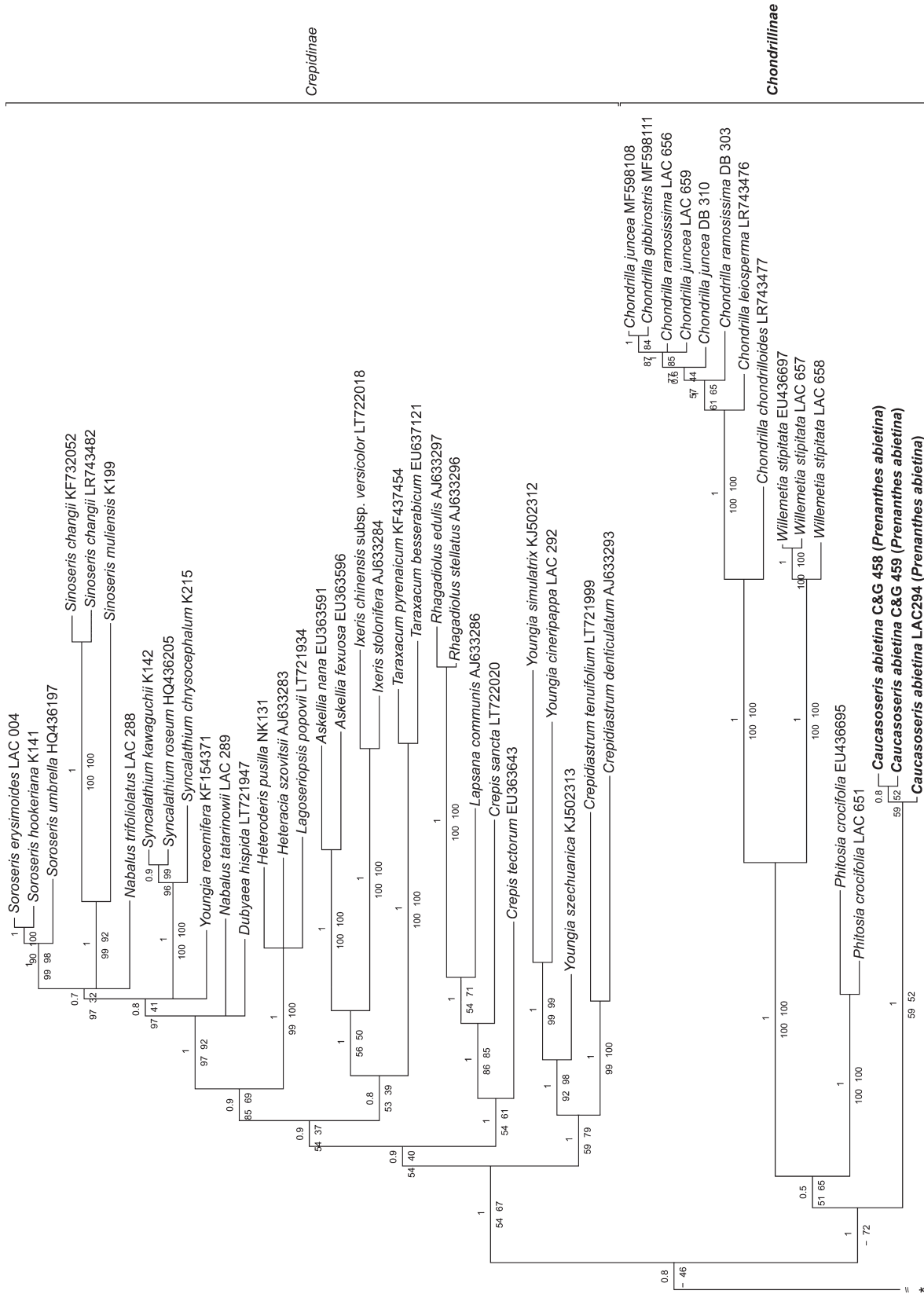
**Achene and pappus features** — The pappus is homomorphic of snow-white, very thin, scabrid bristles, similar to each other in shape and size (Fig. 3B).

The achenes have an epidermis of longitudinally elongated cells and are covered with epicuticular wax. The epidermal cells are oblong-shaped with hooded to conic antrorse apical prolongation and tiny globular ornamentation (Fig. 3D, E). Cross-section in the middle third of the corpus shows that the achenes (Fig. 3A) are clearly five-ribbed (Fig. 4: m, lm). Secondary ribs are absent. Corresponding to the ribbing pattern, all main ribs contribute equally to the five-lobed carpodium (Fig. 3C).

The cross-section shape is weakly five-angular, corresponding to the five well-defined main ribs, and subisodiametric, according to the weakly bilaterally compressed corpus; also the lateral main ribs are somewhat more pronounced than the others (Fig. 3A, 4: m, lm). The achene wall (pericarp) comprises in the middle third a continuous, mostly three or four cells-thick inner layer (sheath) of sclerenchyma tissue, which breaks close to the carpodium by parenchyma into five large lobes (Sennikov & Illarionova 2001), and a two to several (in the ribs) cells-thick outer layer of parenchyma tissue (Fig. 4: pa), whose cells are large-pitted (Sennikov & Illarionova 2001); the embryo is enclosed by the one-layered testa (Fig. 4: t) and two-layered endosperm (Fig. 4: en). The epidermis is covered with a tiny layer of cuticle.

**Pollen characters** — The pollen grains of *Prenanthes abietina* (Fig. 5) are of the common *Cichorium* type (Blackmore 1986): echinolophate, tricolpate with 15 lacunae; they are oblate-spheroidal, the equatorial plane measures 32.2–35.74 ( $x = 34.38$ )  $\mu\text{m}$  in diameter and the polar axis measures 29.15–32.53 ( $x = 31.23$ )  $\mu\text{m}$  (both measured in equatorial view); the polar areas are moderately extensive and each has c. 15 spines.

**Morphological characterization** — The main morphological features of *Prenanthes abietina* (Fig 6) and other genera of the subtribe *Chondrillinae* are presented in Table 1. Particularly, beakless and apically truncate achenes, ovate-cordate leaves and a thick rhizome are key features to separate *P. abietina* from the rest of the subtribe.



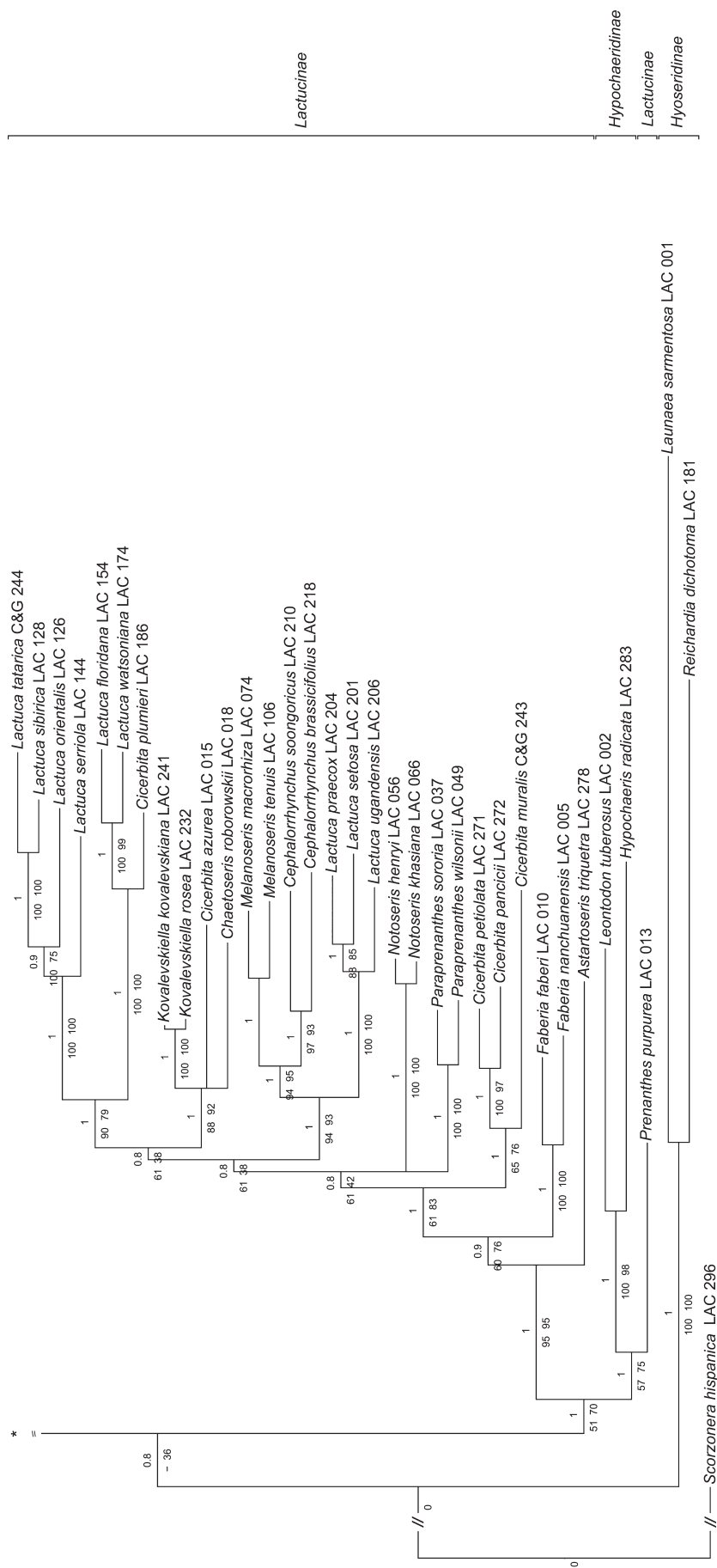


Fig. 1. Majority consensus phylogram of the tribe *Cichorieae* p.p. backbone from the BI analysis based on the nrITS dataset (support values: first line: BI posterior probability, second line: MP jackknife, and ML bootstrap).

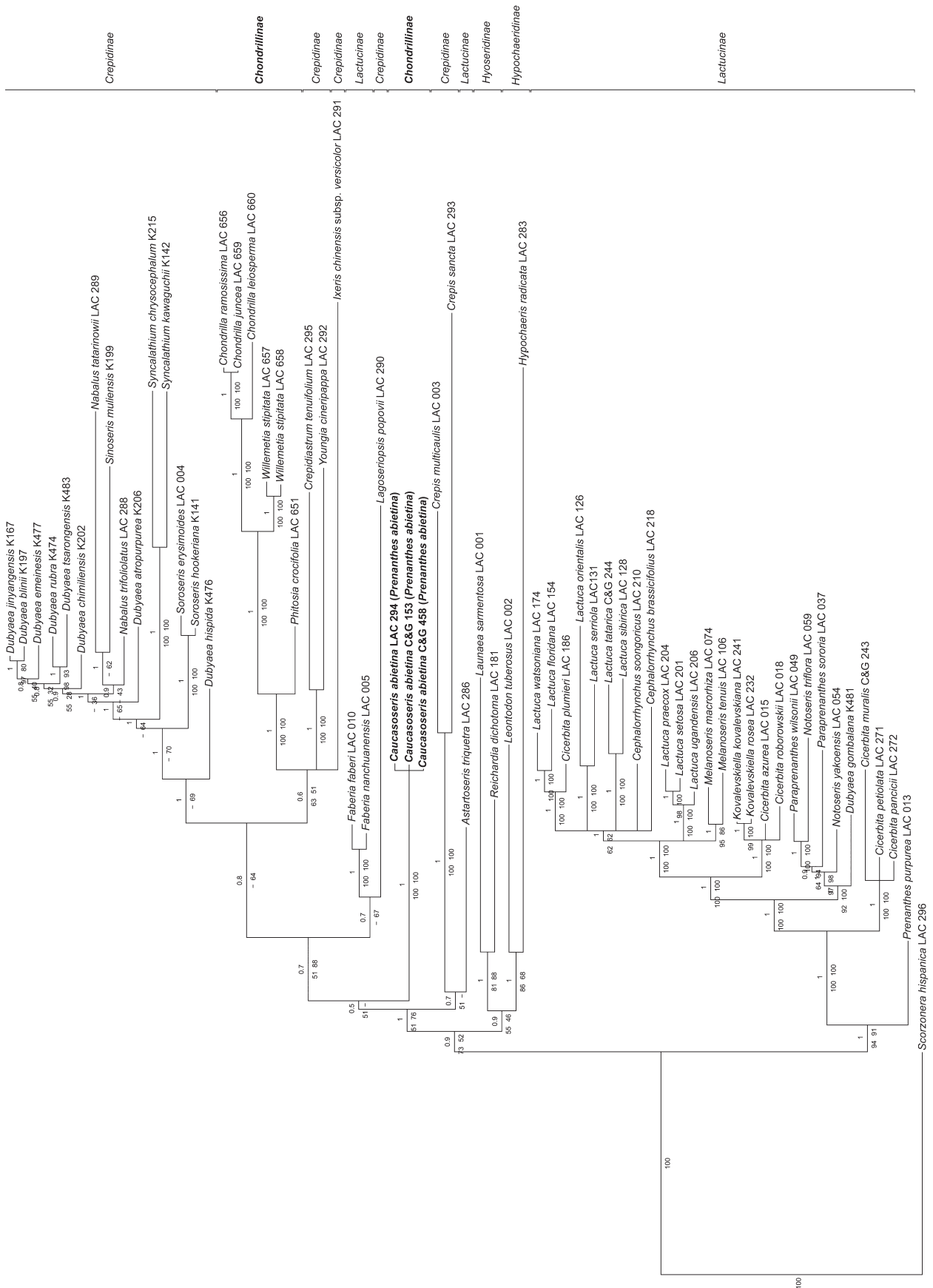


Fig. 2. Majority consensus phylogram of the tribe *Cichorieae* p.p. backbone from the BI analysis based on the concatenated plastid DNA dataset (support values: first line: BI posterior probability, second line: MP jackknife, and ML bootstrap).

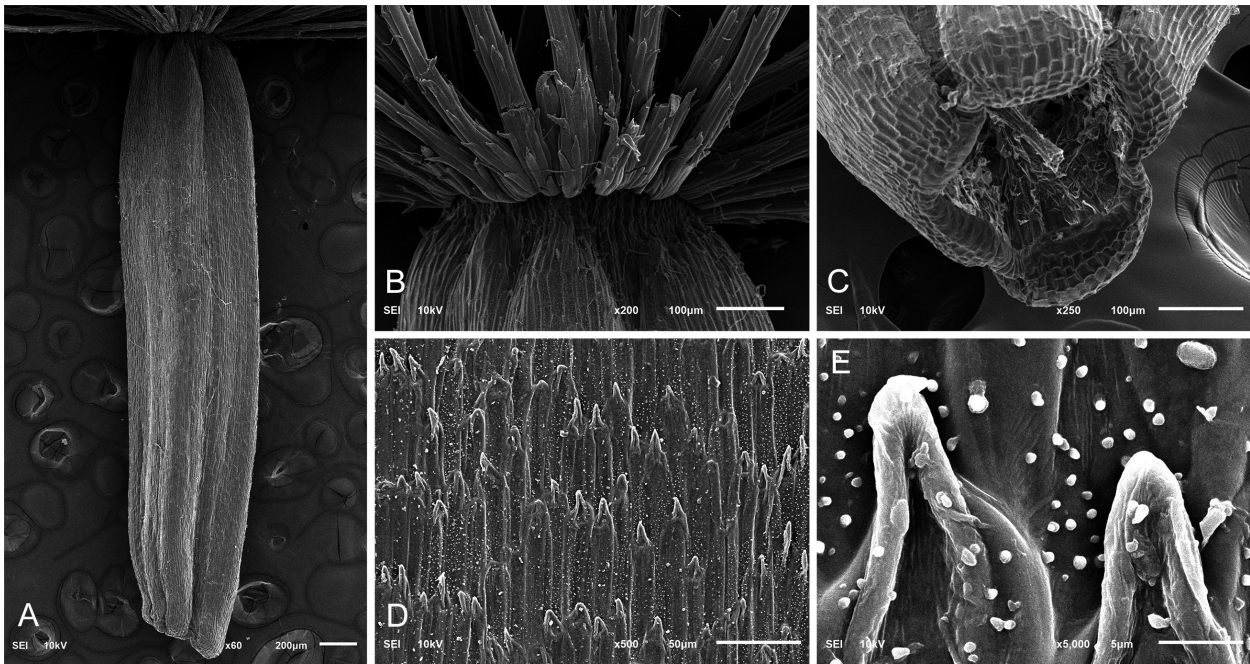


Fig. 3. Achene and pappus structures of *Caucasoseris abietina* (*Prenanthes abietina*) – A: achene; B: pappus disk; C: carpopodium; D: general view of middle third of the achene; E: close view of middle third of the achene. – From Coşkunçelebi & Güzel 458. – Scale bars: A = 200 µm; B, C = 100 µm; D = 50 µm; E = 5 µm.

## Discussion

The subtribe *Chondrillinae* (W. D. J. Koch) Lamotte has recently been reinstated by Kilian & al. (2009a) to accommodate the genera *Chondrilla* L., *Phitosia* Kamari & Greuter and *Willemetia* Neck., which were found to form a clade separate from the *Crepidinae* Dumort. in the nrITS

phylogeny, but had been formerly treated as members of the subtribe *Crepidinae* (Bremer 1994; Lack 2007). While *Chondrilla* comprises 25–30 species (Lack 2007; Kilian & al. 2009b+), *Willemetia* and *Phitosia* include two and one species, respectively (Kilian & al. 2009b+). The subtribe is naturally distributed from Europe (except N Europe) and NW Africa across SW to Central Asia,

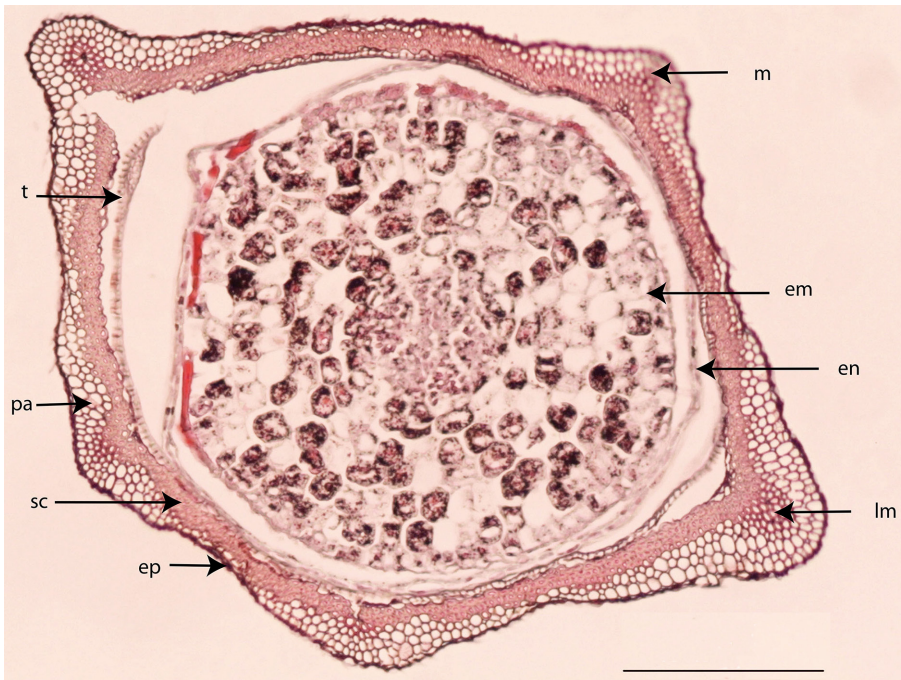


Fig. 4. Achene cross-section (middle third) of *Caucasoseris abietina* (*Prenanthes abietina*) – m = main rib; lm = lateral main rib; ep = epidermis; pa = parenchyma; sc = sclerenchyma; t = testa; en = endosperm; em = embryo. – From Coşkunçelebi & Güzel 460. – Scale bar = 200 µm.

and introduced with one species to America and Australia (Kilian & al. 2009b+). *Prenanthes abietina* is now found to form the earliest diverging branch of the *Chondrillinae* in the nrITS phylogeny (Fig. 1). However, incongruent with the nrITS tree, the *Chondrillinae* are deeply nested in the *Crepidinae* in the plastid DNA tree (Fig. 2). This holds true also for the *P. abietina* clade, which is resolved as a member of the *Crepidinae* clade too, but in a rather early diverging position distant from the *Chondrillinae* clade. The plastid DNA phylogeny corroborates *P. abietina* as an orphan lineage but its affinity to the *Chondrillinae* due to its sister group relationship in the nrITS phylogeny may justify its classification



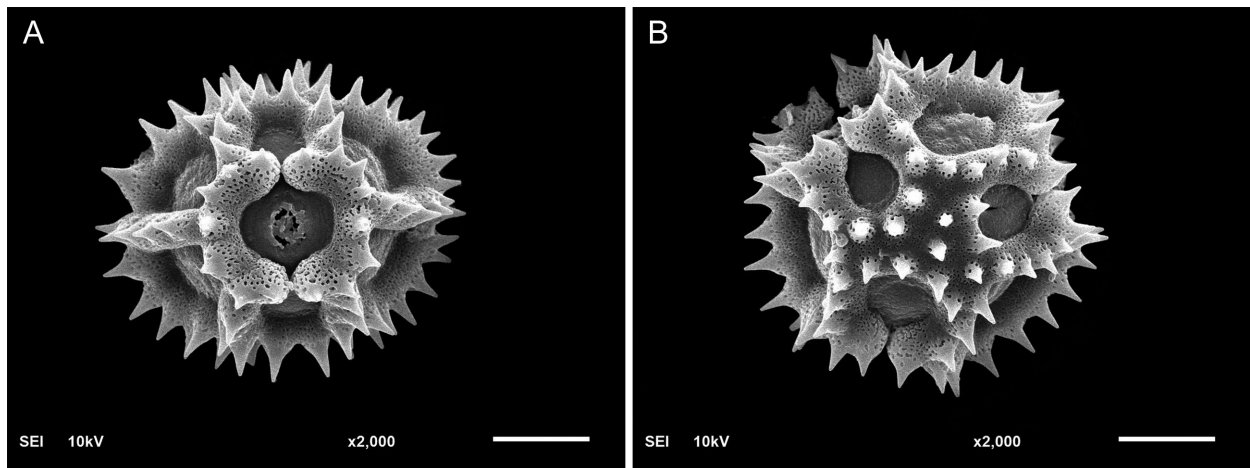


Fig. 5. Pollen grain of *Caucososeris abietina* (*Prenanthes abietina*) – A: equatorial view; B: polar view. – From Coşkunçelebi & Güzel 153. – Scale bars = 10 µm.



Fig. 6. *Caucososeris abietina* (*Prenanthes abietina*) – A: habit; B: flowering capitula; C: fruiting capitula; D: lower cauline leaf; E: upper cauline leaf. – From Coşkunçelebi & Güzel 458; photographs by Coşkunçelebi & Güzel from province Rize, Turkey. – Scale bars = 1 cm.

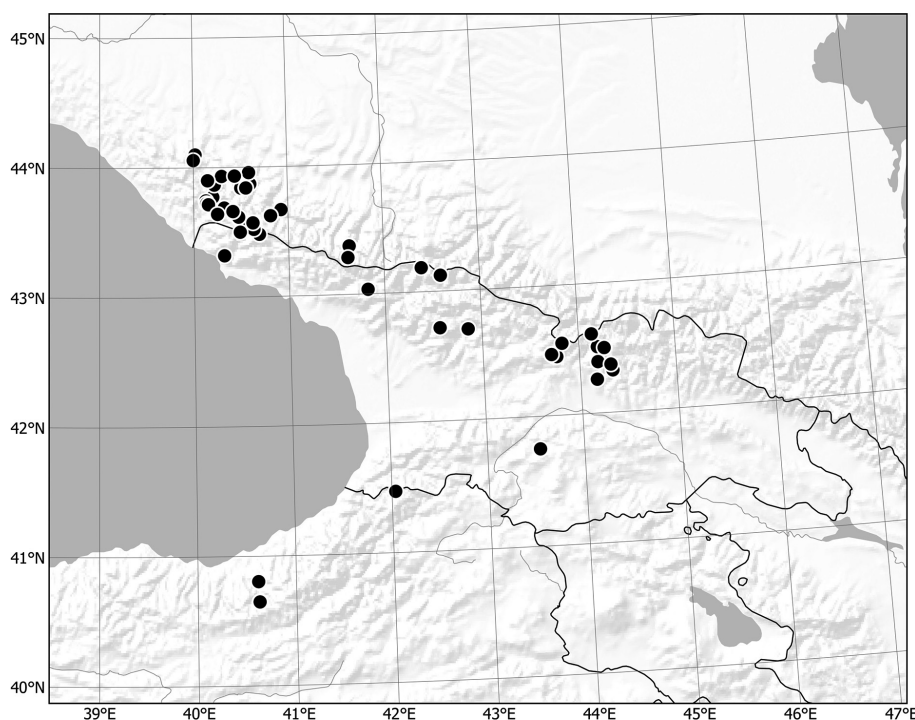


Fig. 7. Distribution area of *Caucososeris abietina* (*Prenanthes abietina*) in the Caucasus region, based on herbarium specimens and documented observations (Sennikov 2022).

as a member of this subtribe. Incongruences between plastid DNA and nuclear ribosomal phylogenies as revealed for the *P. abietina* clade are not uncommon in the *Cichorieae*. Wang & al. (2013), e.g., reported a number of cases at different evolutionary levels for the *Lactucinae*, and discussed the likely reasons (in particular chloroplast capture and reticulate evolution). A recent study by Stull & al. (2020) provided evidence that such cytonuclear discordance is, moreover, not restricted to shallow evolutionary levels but a phenomenon also present in deep levels of phylogeny in the *Asteridae*.

*Etymology* — The generic name is composed of the classical Greek names, “Kaukasos” (Καύκασος) for the Caucasus and “seris” (σέρης) for salad (more precisely, for *Cichorium* species; Liddell & al. 1940).

*Caucososeris abietina* (Boiss. & Balansa) M. Güzel, N. Kilian, Sennikov & Coşkunç., **comb. nov.** ≡ *Mulgedium abietinum* Boiss. & Balansa in Boissier, Fl. Orient. 3: 802. 1875 ≡ *Lactuca abietina* (Boiss. & Balansa) Bornm. in Mitt. Thüring. Bot. Vereins 20: 29. 1904–1905 ≡ *Crepis abietina* (Boiss. & Balansa) Beauverd in Bull. Soc. Bot.

## Taxonomic conclusion

*Caucososeris* M. Güzel, N. Kilian, Sennikov & Coşkunç., **gen. nov.** ≡ *Prenanthes* sect. *Abietinae* Sennikov in Bot. Zhurn. (Moscow & Lenin-grad) 82(2): 113. 1997. – Type: *Caucososeris abietina* (Boiss. & Balansa) M. Güzel, N. Kilian, Sennikov & Coşkunç.

*Diagnosis* — Rhizomatous perennial herb, with erect leafy stem and paniculiform synflorescence; leaves ovate-cordate, long petiolate; capitula with 37–41 yellow florets, involucre subglabrous with inconspicuous simple blackish hairs; achene subtruncate, columnar, with five main and no secondary ribs; pappus of white scabrid bristles.

Table 1. Comparison of genera of the subtribe *Chondrillinae*. <sup>1</sup>Shi & Kilian (2011), <sup>2</sup>Leonova (1964), <sup>3</sup>Lack 2007, <sup>4</sup>Babcock (1947), <sup>5</sup>Kamari & Greuter (2000), <sup>6</sup>Kirschnerová & Kirschner (1996), \*present study.

	<i>Chondrilla</i> <sup>1,2,3</sup>	<i>Phitosia</i> <sup>4,5</sup>	<i>Willemetia</i> <sup>6</sup>	<i>Prenanthes abietina</i> *
<b>Habit</b>	herbs with cauline leaves and with or without basal leaf rosette <sup>1</sup>	caespitose with mostly basal leaf rosette <sup>4,5</sup>	herbs with basal leaf rosette <sup>6</sup>	herbs with cauline leaves*
<b>Subterranean structure</b>	slender taproot*	slender taproot <sup>4</sup>	creeping to ± vertical rootstock <sup>6</sup>	thick rhizome*
<b>Leaves</b>	linear	linear	lanceolate or oblanceolate	ovate-cordate, long petiolate
<b>Capitula</b>	numerous <sup>2</sup>	numerous*	solitary or few to several <sup>6</sup>	numerous*
<b>Phyllaries</b>	2 series <sup>3</sup>	2 or 3 series*	2 series <sup>6</sup>	3 or 4 series*
<b>Phyllaries indumentum</b>	glabrous, arachnoid hairy, or with simple bristles <sup>1</sup>	sparsely canescent-tomentulose <sup>4</sup>	densely covered with simple blackish hairs <sup>6</sup>	subglabrous with inconspicuous simple blackish hairs*
<b>Floret number per capitulum</b>	5–12 <sup>1,2</sup>	9–15 <sup>5</sup>	47–60*	37–41*
<b>Floret colour</b>	yellow <sup>1,2</sup>	yellow <sup>4,5</sup>	yellow <sup>6</sup>	yellow*
<b>Achene apex</b>	usually beaked <sup>1</sup>	strongly attenuate <sup>4</sup>	beaked <sup>6</sup>	subtruncate*
<b>Pappus</b>	white <sup>1</sup>	pale yellowish <sup>4</sup>	white <sup>6</sup>	white*

Genève 2: 115. 1910 ≡ *Cicerbita abietina* (Boiss. & Balansa) Grossh., Fl. Kavk. 4: 252. 1934 ≡ *Prenanthes abietina* (Boiss. & Balansa) Kirp. in Komarov, Fl. URSS 29: 270. 1964. – **Lectotype (designated here):** [Turkey, prov. Rize,], forêts d'*Abies orientalis* [actually *Picea orientalis*] situées au-dessus de Khabakhor (Lazistan) [= Kabahor = Kabakçur; current name: Gölyayla], vers 2200 metr. d'alt., 3 Sep 1866, B. Balansa, *Plantes d'Orient s.n.* (G-BOIS: G00781484; isolectotypes: GOET001920, K000815062). – Fig. 6.

**Description** — Perennial herb with thick rhizome. Stem 100–190 cm high, erect, leafy, striate, unbranched or rarely branched from base, glabrous or subglabrous with eglandular hairs. Leaves sparsely covered with setulose hairs at veins, margin sinuate, apex more or less acuminate, base cordate-hastate; lower cauline leaves ovate-cordate in outline, rarely 2–5-lobed, 11.5–23 × 6–11 cm; petiole 3.5–10 cm long, semiamplexicaul at base; middle cauline leaves similar to others in shape, 4–15 × 3–9 cm; petiole 1–4.5 cm long, slightly expanded at base. Synflorescence corymbiform or paniculiform-corymbiform with fewer than 50 heads, peduncles glabrous. Capitula with 37–41 florets, ovoid-campanulate, 17–20 mm long in flower, 12–14 mm long in fruit; peduncle 2–5 cm long. Phyllaries c. 30 in 3 or 4 series, dark to blackish green; outer phyllaries less than 1/4 as long as inner phyllaries, ovate-lanceolate, acute, subglabrous with inconspicuous simple blackish hairs; inner phyllaries c. 10, slightly prolonged at fruiting, lanceolate, acute, subglabrous with inconspicuous simple blackish hairs. Florets bright to pale yellow, corolla tube 3.4–3.6 mm long, hairy in upper part; ligule 12.6–13.6 × c. 2 mm; anther tube brownish, c. 3.7 mm long; fertile part 2.8–3.2 mm long, apical appendages 0.3–0.5 mm long, basal appendages c. 0.3 mm long. Style 8.7–10 mm long; branches 1.5–1.8 mm long. Achenes cylindric, 2.6–5 × 0.6–0.9 mm, brownish, with 5 ribs, corpus slightly narrowed toward apex and near base, carpopodium 5-lobed, epidermis cells with very short, light-coloured antrorse apical prolongation (under high magnification). Pappus 5–6.3 mm long, of scabridulous bristles of equal size and shape in 1 series, persistent, snow-white.

**Distribution, ecology and phenology** — The species is distributed in the Greater Caucasus (common and locally abundant in its western and central parts) and the Lesser Caucasus (sporadically found from the Pontic Range in the west to the Trialeti Range in the east). It occurs in Russia (Krasnodar Krai, Adygea, Karachay-Cherkessia, North Ossetia and possibly Kabardino-Balkaria), Georgia (incl. Abkhazia and South Ossetia) and northeastern-most Turkey (Artvin and Rize) (Sennikov 2009, 2022). A point distribution map is provided in Fig. 7. In that area, the species occurs in the high-humidity montane forests to their upper limit or slightly above it, generally under the shade of *Picea orientalis* or *Fagus* L., or less often in mixed *Fagus*, *Abies* Mill., *Pinus* L. and elfin forest and

in *Rhododendron ponticum* L. thickets (Kirpicznikov 1964), at altitudes of (1500–)1800–2200(–2500) m in the western Caucasus and (1600–)1900–2400(–2800) m in Georgia. In Turkey, where the species is referred to as “Sarı eğişçiçek” (Ekim 2012), it occurs at altitudes of 1400–2200 m. The species flowers from July to early September, and fruits in September.

#### Key to genera of subtribe *Chondrillinae*

1. Capitula with more than 20 florets and simple blackish hairs present on involucre ..... **2**
- Capitula with fewer than 20 florets and involucre glabrous, arachnoid hairy, with simple bristles, or sparsely canescent-tomentulose ..... **3**
2. Involucral bracts in 3 or 4 series; achenes truncate; leaves ovate-cordate ..... ***Caucasoseris***
- Involucral bracts in 2 or 3 series; achenes beaked; leaves lanceolate or oblanceolate ..... ***Willemetia***
3. Pappus pale yellowish; achene apically smooth and distinctly attenuate; capitula with 9–15 florets .... ***Phitosia***
- Pappus white; achenes apically with tubercles or scales and usually beaked; capitula with 5–12 florets ..... ***Chondrilla***

#### Author contributions

MEG and NK designed the study, wrote the paper (with contributions by ANS and KC), analysed the molecular data and (together with ANS) analysed the morphological and anatomical data; MEG (with participation by KC, SM and MG) did the field work and the molecular, morphological and anatomical studies; ANS (with contributions by MEG) elaborated the distributional and habitat data; all authors read and approved the paper.

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## Appendix

Specimen data and INSDC accession numbers for the studied taxa. INSDC accession numbers appear in the following sequence: nrITS / *petD* / *psbA-trnH* / *5'trnL<sup>(UAA)</sup>-trnF* / *rpl32-trnL<sup>(UAG)</sup>* / *5'rps16-trnQ<sup>(UUG)</sup>*; missing sequences are designated by a dash (—).

***Caucososeris abietina*** (Boiss. & Balansa) M. Güzel & al. LAC-294 [DB26502]: Caucasus, 7 Aug 1977, *Dolukhanov s.n.* (LE), LT721995 / LT722538 / LT722069 / LT722192 / LT722307 / LT722422

C&G 153: Turkey, A8 Rize, from İkizdere to Çağrankaya, *Fagus* sp.-*Picea* sp. forest, 1864 m, 12 Sep 2013, *Coşkunçelebi & Güzel 153* (KTUB), — / MT953198 / MT953325 / MT985634 / MT985753 / —

C&G 458: Turkey, A9 Artvin, Borçka, from Uğurköy to Meydancık, 1665 m, 22 Aug 2015, *Coşkunçelebi & Güzel 458* (B 10 1014270, KTUB), MT952208 / MT953199 / MT953326 / MT985635 / MT985754 / MT985872

C&G 460: Turkey, A9 Artvin, Borçka, from Uğurköy to Meydancık, 2209 m, 22 Jul 2015, *Coşkunçelebi & Güzel 460* (KTUB), MT952209 / — / — / — / — / —

### ***Chondrilla juncea*** L.

[DB 310/2005] LR743478 sub synonym *C. canescens*: ITS; LAC-659 [DB 7933], from wild source Berlin, Staaken, Hahneberg, Aug 1998, *T. Dürbye & al.* 585, cultivated in BG Berlin, 20 Aug 2010, *M. Cubr 47386* (B 10 0346424), — / OV304771 / OV304849 / OV305400 / OV304777 / OV305605

### ***Chondrilla leiosperma*** Kar. & Kir.

LAC-660 [DB 306/2005], Kyrgyzstan, Tien-Shan, Issyk-Kul-Gebiet, Issyk-Kul-See, Ak-Sakji, *Artemisia-Ephedra*-Steppe, 1620 m, 25 Jul 2002, *T. Dürbye DÜR 1754* (B 10 0096856), — / OV304772 / OV304850 / OV305401 / OV304778 / OV305606

### ***Chondrilla ramosissima*** Sm.

[DB 303/2005] LR743475 ITS; LAC-656 [DB 8004], from wild source Greece, Kea island, cultivated in BG Berlin, 26 Aug 2008, *M. Cubr 45780* (B 10 0292628), — / OV304768 / OV304846 / OV305397 / OV304774 / OV305602

***Phitosia crocifolia*** (Boiss. & Heldr.) Kamari & Greuter LAC-651 [DB 18820]: Nom. Messinias, Ep. Kalamon: Mt. Taygetos, S part, NE of Mavrovouna, above place called Ag. Dimitrios, along valley leading to the summit ridge, 1600–1950 m, 30 Jun 1979, *Strid & Papanicolaou 15261* (B 10 0517779), OV304853 / OV304767 / OV304845 / OV305396 / OV304773 / OV305601

### ***Willemetia stipitata*** (Jacq.) Dalla Torre

LAC-657 [DB 462]: Greece, Nom. Kastoria, Grammos-Massiv, Pijes Arenes, 40°19'30"N, 20°53'E,

1600 m, 25 Jun 1990, *E. Willing 11335* (B 10 0209153),  
OV304855 / OV304769 / OV304847 / OV305398 /  
OV304775 / OV305603

LAC-658 [DB 463]: Switzerland, Canton d'Appenzell,  
Rhodes intérieures, 1120–1150 m, 26 Jun 1981, *A.*  
*Charpin & P. Geissler AC 16330* (B 10 0209154),  
OV304856 / OV304770 / OV304848 / OV305399 /  
OV304776 / OV305604

### Supplemental content online

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Matrices in Nexus format for nrITS and plastid DNA datasets.

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