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 exsiccate “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 Caucasian region, intensified in the first half of the 20th 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 Lactucae 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 Lactucaeae 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 prevailing 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(UAA)-trnF spacer, rpl32-trnL(UAA) spacer, and trnQ(UUG)-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) (Katoh & 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 = 2983, 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 are 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 posterior 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 antorse 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 carpododium (Fig. 3C).

The cross-section shape is weakly five-angular, corresponding to the five well-defined main ribs, and subsidametric, 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 carpododium 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) µm in diameter and the polar axis measures 29.15–32.53 (x = 31.23) µm (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).
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, 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 *Caucasoseris abietina* (*Prenanthes abietina*) – A: equatorial view; B: polar view. – From Coşkunçelebi & Güzel 153. – Scale bars = 10 µm.

Fig. 6. *Caucasoseris 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.
Taxonomic conclusion

**Caucasoseris** M. Güzel, N. Kilian, Sennikov & Coşkunç., **gen. nov.** ≡ **Prenanthes** sect. **Abietinae** Sennikov in Bot. Zhurn. (Moscow & Leningrad) 82(2): 113. 1997. – Type: *Caucasoseris 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.

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

**Caucasoseris 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.

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

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

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*.

Fig. 7. Distribution area of *Caucasoseris abietina* (*Prenanthes abietina*) in the Caucasus region, based on herbarium specimens and documented observations (Sennikov 2022).
Abies orientalis, forêts d’Balansa) Grossh., Fl. Kavk. 4: 252. 1934

...for performance of anatomical studies; ANS (with contributions by ANS and KC), analysed the molecular, morphological and anatomical data; ANS 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 and NK designed the study, wrote the paper (with contributions by MEG) elaborated the distributional and habitat data; all authors read and approved the paper.

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\'rnlL(IRA-T)/trnF / rpl32-trnL(UAG) / 5\'rps16-trnQ(UUG); missing sequences are designated by a dash (—).

### Caucasoseris 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 İzikdere to Çağrınkaya, 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, 1655 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. Messinians, 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, Gramnos-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

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