

5-14-2024

## The Sect. *Tricheroides* in the genus *Knautia* (Caprifoliaceae) is more complex than known: an unusual new species from Türkiye

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### Recommended Citation

AYKURT, CANDAN; GÜLBEN, Mertcan; GÜNAYDIN, Sinem; SARI, Duygu; GÖKTÜRK, Ramazan Süleyman; BERBEROĞLU, Emirhan; and GÜLSOY, Serkan (2024) "The Sect. *Tricheroides* in the genus *Knautia* (Caprifoliaceae) is more complex than known: an unusual new species from Türkiye," *Turkish Journal of Botany*. Vol. 48: No. 3, Article 2. <https://doi.org/10.55730/1300-008X.2802>  
Available at: <https://journals.tubitak.gov.tr/botany/vol48/iss3/2>

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## The sect. *Tricherooides* in the genus *Knautia* (Caprifoliaceae) is more complex than known: an unusual new species from Türkiye

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Received: 24.11.2023

Accepted/Published Online: 24.03.2024

Final Version: 14.05.2024

**Abstract:** During a biodiversity survey in the Western Taurus Mountains (Antalya, Türkiye), a new species of the genus *Knautia* (Dipsacoideae, Caprifoliaceae), named *K. sivridaghense*, was discovered. This new species, characterized by its dwarf caespitose perennial habit, is found in rocky areas under mixed forests at elevations of 1400–1450 m. *Knautia sivridaghense* is distinguished from its morphologically similar species, *K. goecmenii*, especially by its dwarf caespitose perennial habit, unbranched stems, length of involucre bracts, and other floral characteristics. Our phylogenetic analyses based on the nuclear ITS and chloroplast petN(ycf6)-psbM regions confirm its placement within sect. *Tricherooides*, contributing to the understanding of the complexity of the genus. In addition to introducing the new species, this study also underscores the need for further research to unravel the evolutionary history and speciation mechanisms within the genus *Knautia*.

**Key words:** *Knautia*, *Tricherooides*, new species, phylogeny, taxonomy, Türkiye

### 1. Introduction

The genus *Knautia* L. (Dipsacoideae, Caprifoliaceae), commonly known as the “widow flower” (Botanical Society of America, n.d.), comprises a diverse group of plants renowned for their unique adaptation: a soft, lipid-rich elaiosome at the base of its fruits, which attracts ants for seed dispersal (Sernander, 1906; Mayer and Svoma, 1998; Mayer, 2016). Moreover, unlike other members of the subfamily Dipsacoideae, the receptacle in *Knautia* lacks scales, being hairy instead (Mayer, 2016). This genus comprises approximately 40–60 species distributed in the west of Eurasia and the northwesternmost part of Africa (Ehrendorfer, 1976; Mayer, 2016; Yıldırım et al., 2022), and its presence significantly enriches the botanical diversity of southern and southeastern Europe (Rešetnik et al., 2014; Frajman et al., 2016; Mayer, 2016).

During a biodiversity monitoring project in Antalya (Türkiye), we discovered a population of *Knautia* that are distinguished from all other species known from Türkiye. *Knautia sivridaghense*, which is described as a new species in the present study, grows in rocky areas under the

mixed forest on the north face of the Sivri Dağ, a part of the Western Taurus Mountains. This mountainous area is among the richest and most important areas in Türkiye in terms of plant diversity (Eren et al., 2004; Parolly, 2015; Noroozi et al., 2019) and falls within the putative refuge areas in Mediterranean Basin identified by Médail and Diadema (2009). The genus *Knautia* is represented by 12 species in Türkiye, including the new species described here, (Matthews, 1972; Davis et al., 1988; Göktürk, 2012; Tunçkol et al., 2021; Yıldırım et al., 2022) and is traditionally divided into three sections, which are sect. *Knautia*, sect. *Trichera* Schrad. ex Schultes & Schultes f., and sect. *Tricherooides* K. Candolle (Mayer, 2016). Section *Trichera* is particularly complex, both in terms of species diversity and the challenges it presents for taxonomic study (Rešetnik et al., 2014; Frajman et al., 2016). This complexity arises from the frequent occurrence of polyploidy and the high incidence of hybridization, which blur species boundaries (Ehrendorfer, 1962, 1981; Rešetnik et al., 2014). Additionally, within this section, it is noteworthy that there is a consistent presence of intermediate

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forms, even between species with clear morphological distinctions and ecological separations, such as *K. arvensis* (L.) Coult. and *K. drymeja* Heuff. (Szabó, 1911; Hayek, 1914; Ehrendorfer, 1962; Štěpánek, 1997; Rešetnik et al., 2014). Section *Tricherooides* and sect. *Knautia* are primarily found in the eastern Mediterranean region (Frajman et al., 2016). In these two sections, species are represented mostly by the annual life form (Rešetnik et al., 2014; Frajman et al., 2016). However, a recent discovery from western Türkiye has introduced *K. goecmenii* Yıldırım as a unique perennial member in sect. *Tricherooides*, resembling those in sect. *Trichera* (Yıldırım et al., 2022). Recent studies (e.g., Yıldırım et al., 2022) and our results indicate that species resembling those in sect. *Trichera* in terms of habitus are also present in sect. *Tricherooides*. Recognizing the potential for in some individuals (Rešetnik et al., 2014) indicates that sect. *Tricherooides* is more complex than previously thought. These findings enhance our understanding of the taxonomy and distribution of the genus *Knautia*, while also emphasizing the significant influence of Türkiye's geographical location on the evolutionary processes within this genus. The discovery of the new species also serves as a compelling example of the botanical richness of the region, warranting further comprehensive studies.

## 2. Materials and methods

### 2.1. Plant specimens and morphological studies

The specimens of the new species were collected from rocky areas under the mixed forest of Sivri Dağ (Konyaaltı, Antalya). The overall morphology of the newly discovered species was carefully examined under a stereo-binocular microscope, and accurate measurements of these specimens were conducted using a millimeter ruler. Detailed morphological characteristics such as flower parts and indumentum type were meticulously documented both in the field and within the controlled laboratory. The collected specimens were comprehensively evaluated using the relevant literature (Boissier, 1875; Bobrov, 1957; Matthews, 1972; Ehrendorfer 1976; Kokkini, 1991; Rechinger and Lack, 1991; Szabó, 1911; Mayer, 2016) and the specimens present in Akdeniz University (AKDU). The distribution maps of *Knautia* species occurring in Türkiye were prepared considering both the relevant literature (e.g., Matthews, 1972; Yıldırım et al., 2022) and the records in AKDU.

### 2.2. Isolation of DNA, PCR amplification, and sequencing

Total genomic DNA was extracted from dried tissues using the CTAB method as described by Doyle and Doyle (1990) with minor adjustments such as extra chloroform-isoamyl alcohol and 70% ethanol cleaning steps. DNA quality and quantity were estimated by electrophoresis on 1% agarose gel, and the amount was fixed at 100 ng/μL using lambda DNA as a reference.

Amplification of the nuclear ribosomal ITS region (ITS-1, 5.8S rDNA subunit, ITS-2) and the chloroplast *petN(ycf6)*-*psbM* region was conducted with the primers ITS5/ITS4 (White et al., 1990) and *ycf6F/psbM-R* (Shaw et al., 2005), respectively. Polymerase chain reaction (PCR) for both the ITS and *petN(ycf6)*-*psbM* regions was performed in 15 mL of reaction mixture containing 2 mM of MgCl<sub>2</sub>, 200 mM of each dNTP, 0.4 μM of each primer, and 1 U of Taq DNA polymerase (Fermentas Life Sciences, Burlington, Canada) with supplied reaction buffer at 10X concentration, and 40 ng of template DNA. PCR was carried out with the following protocol: initial denaturation step for 5 min at 95 °C, 35 cycles of denaturation for 1 min at 95 °C, annealing for 30 s at 52 °C for the ITS region and 1 min at 68 °C for the *petN(ycf6)*-*psbM* region, and then a final extension of 5 min at 72 °C. PCR products were loaded onto 1.5% agarose gel and visualized under UV light after staining with ethidium bromide. The products of each sample were purified using the GeneJET Gel Extraction Kit (Thermo Scientific Fermentas, Vilnius, Lithuania). Sequencing was carried out at Macrogen Inc., Europe via BM Laboratories Ltd., as direct sequencing in two directions using the amplification primers. The sequences were submitted to GenBank (see Appendix).

### 2.3. Phylogenetic analyses

For molecular analysis, we chose 40 accessions from 30 Caprifoliaceae species. (*K. goecmenii* data were missing for the *petN(ycf6)*-*psbM* region). This selection encompassed samples from the three broadly recognized sections of *Knautia*, in addition to two *Dipsacoid* species and two other genera that are distantly related, serving as outgroups. To ascertain the phylogenetic placement of the new species, maximum likelihood and Bayesian analyses were conducted based on the nuclear ITS and chloroplast *petN(ycf6)*-*psbM* regions. Our initial analysis yielded different topological results for the nuclear and chloroplast data sets of species found in sect. *Tricherooides*. We combined the aligned ITS and PetN datasets using the Biopython library (Cock et al., 2009) to create a comprehensive alignment for phylogenetic analysis, thereby enhancing the robustness of our study. Sequence data for phylogenetic analysis of the newly discovered *K. sivridaghense* were obtained and prepared from plant specimens, while sequences from the other plant species were retrieved from GenBank. The raw ITS and *petN(ycf6)*-*psbM* sequences of the new species were meticulously edited using Unipro UGENE software version 37.0 (Okonechnikov et al., 2012). Reference sequences KF993470 and KJ025975 were consulted for ITS and *petN(ycf6)*-*psbM*, respectively. We aligned the ITS and *petN(ycf6)*-*psbM* sequences separately using MAFFT software (Kato and Standley, 2013) at default settings for both.

Phylogenetic analysis was performed with raxmlGUI 2.0 (Edler et al., 2020) for maximum likelihood-based tree construction and MrBayes v3.2.6 (Ronquist et al., 2012) for Bayesian phylogenetic inference. We chose the models guided by the Akaike information criterion (AIC), corrected Akaike information criterion (AICc) for maximum likelihood analysis, and Bayesian information criterion (BIC) for Bayesian analysis, all with ModelTest-NG v0.1.5 (Darriba et al., 2020). For the ITS region, the TrN+G4 model was employed based on the BIC scores, while the TIM3+G4 model was selected based on AIC and AICc values. Similarly, for the petN region, the TVM+G4 model was utilized based on the values of all three criteria: BIC, AIC, and AICc. In the case of the combined dataset, the GTR+G4 model was chosen based on AIC and AICc values, whereas the TVM+G4 model was applied for BIC. Due to the specificity of the parameters, models such as TrN+G4, TIM3+G4, or TVM+G4 may not directly correspond to the nomenclature within these software tools. Hence, these models were configured using a combination of automated settings in raxMLGUI and manual parameterization in MrBayes. At the end, in RAxML (Stamatakis, 2014), we chose the rapid bootstrapping option with 1000 bootstrap iterations and in MrBayes, the analysis involved 1,000,000 generations, with one tree sampled every 1000 generations. The first 25% of trees were discarded as “burn-in” to ensure stable estimation, and the final trees were visualized using FigTree v.1.4.4.

### 3. Results

#### 3.1. Molecular results

The ITS dataset comprised 40 sequences from 30 species, measuring 940 bp with 318 variable sites and 235 parsimony informative sites. The petN(ycf6)-psbM dataset included 39 sequences from 29 species, with a length of 1452 bp, 268 variable sites, and 196 parsimony informative sites, and the combined (ITS + petN(ycf6)-psbM) dataset encompassed the aggregate of both datasets. According to our ITS, petN(ycf6)-psbM, and combined trees, sect. *Knautia*, including only *K. orientalis* (>85% bs; 1 pp), is separated from other sections with a different branch. In all three obtained trees, *K. sivridaghense* is found to be within sect. *Tricheroides*. In the ITS tree, the new species is clearly separated from the clade containing *K. integrifolia*, *K. degenii*, and *K. goecmenii*, while *K. byzantina* is in a different branch from these two clades. Since only the ITS sequence of *K. goecmenii* is available, this species is not included in our petN(ycf6)-psbM tree. In the tree obtained from the chloroplast dataset, *K. sivridaghense* is also separated from all other species within sect. *Tricheroides*. Moreover, in our combined tree, the new species is observed to be distinct from all other species within this section (Figure 1).

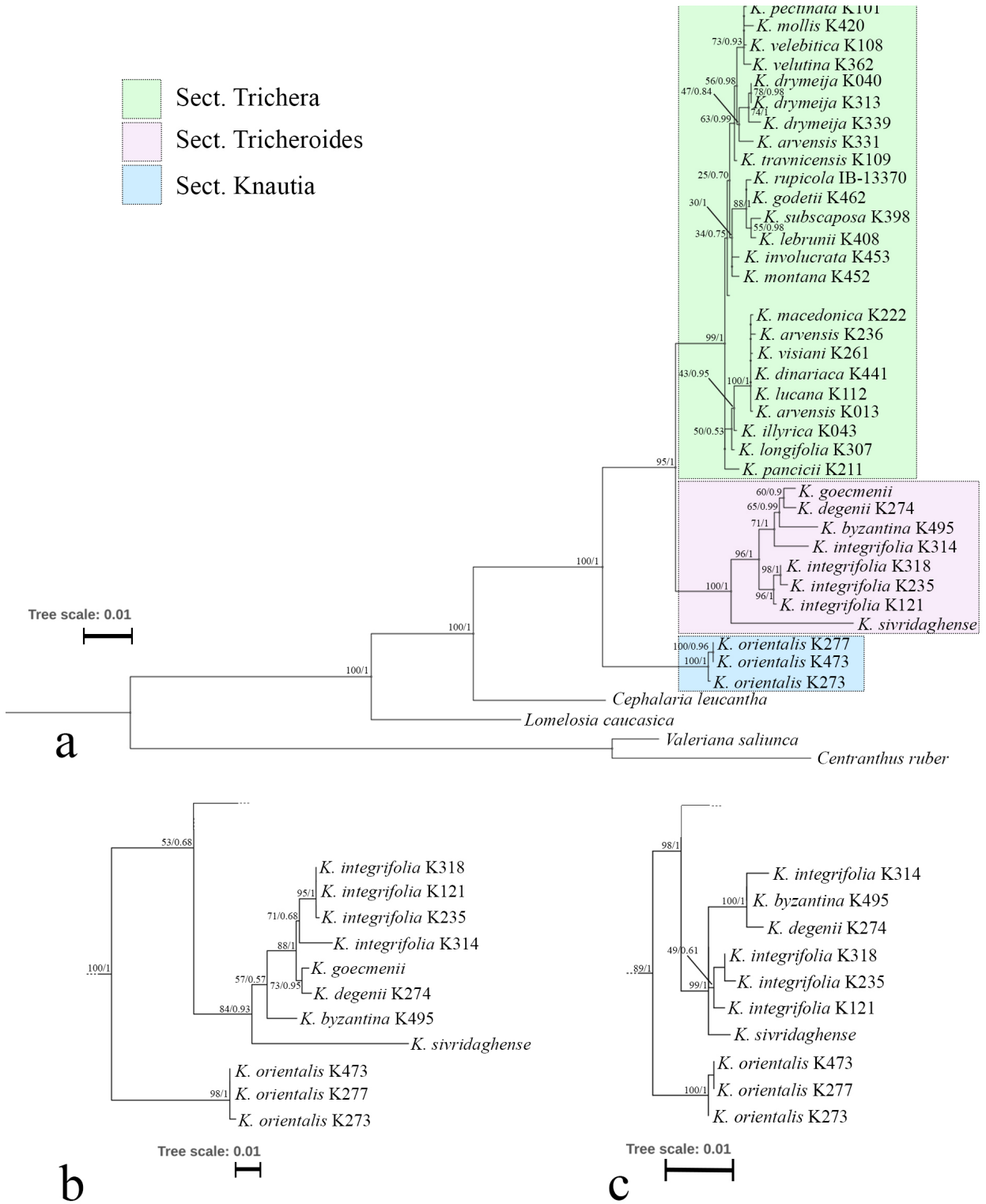
#### 3.2. Taxonomic treatment

*Knautia sivridaghense* Aykurt & M. Gülben sp. nova (Figures 2–3)

**Type:** TÜRKİYE, Antalya, Konyaaltı, Sivri Dağ Wildlife Development Area, 1400–1450 m, S of Karabel Pass Camping Area, 10 June 2023, C. Aykurt 6001, M. Gülben, E. Berberoğlu, S. Günaydın, S. Gülsoy (holotype: AKDU 6447).

**Diagnosis:** *Knautia sivridaghense* differs from *K. goecmenii* by its dwarf caespitose perennial habit (vs. suffrutescent), unbranched stems (vs. many-stemmed at base), and 10 involucre bracts, 4.5–6 mm long (vs. 8–16 involucre bracts, 2–5 mm long).

**Description:** Dwarf caespitose perennial herb with tortuous taproot. Stems up to 40 cm, erect to ascending, slender, fragile, slightly striate, unbranched, old remains generally present, covered with crisped hairs with stipitate glandular hairs and fewer unicellular long spreading hairs up to 2 mm. Leaves lyrate-pinnatisect to lyrate-pinnatifid, flat or margins slightly recurved, crowded towards the base through short internodes, covered with soft and dense indumentum of short-crisped, adpressed setose and long spreading setose hairs together, glandular hairs absent; lower leaves 4.5–10.6 × 0.8–2.8 cm (including petiole), with 3–5(–6) lateral lobes on each side, lobes generally rounded or with 1–2 small obtuse teeth; terminal segments conspicuously larger than the laterals with 3–5 teeth on each side, lanceolate, obtuse; uppermost leaves 9–29 × 0.5–7 mm, linear to lanceolate or pinnatisect with 1–2 linear lateral segments on each side, entire, obtuse. Inflorescence solitary on each branch. Bracts 10 (in all investigated specimens), in 3 rows, 4.5–6 mm long, bracts on the outer two rows (involucre bracts) ovate-lanceolate; inner bracts (receptacular bracts) linear or linear-lanceolate; outer surface covered with white crisped hairs, long setose on margins and midvein; inner surface glabrescent with dense crisped hairs towards apex and near margins. Capitula 15–20 mm in diameter in flower, 20–24 flowered, ±radiant. Involucre approximately 2–2.5 mm long at flowering time; tube approximately 1.5–1.75 mm long, covered with sessile glands and densely long hirsute; crown 0.75–1 mm long, denticulate-ciliate, often purplish. Calyx cupuliform, 0.6–1 mm in diameter, long hirsute and with few glands, with 8 setae; setae 1.5–2 mm long, scabridulous. Corolla 0.7–1.5 cm long, very pale whitish-lilac, with punctate pellucid glands, loose ciliate both on tube and at throat, lobes 1.5–3 mm long, loosely ciliate on dorsal side, glabrescent towards apex. Stamens 7–10 mm long; anthers approximately 1–2 mm long; filaments 6–8 mm long; pollen grains yellow. Style 0.5–1.1 cm long. Fruit 5.5–8 × 1.5–2 mm, dorsally compressed, linear, irregularly toothed, long and short ciliate at apex, mostly 2-horned, straw-colored. Seed 4–5 mm long, sericeous.



**Figure 1.** Phylogenetic placement of *Knautia sivridaghense* based on; combined dataset both of ITS and petN(ycf6)-psbM regions (a); ITS region (b); petN(ycf6)-psbM region (c). Bayesian posterior probabilities and ML bootstrap values are shown on the main nodes. Members of sect. *Knautia*, sect. *Tricheroides*, and sect. *Trichera* were highlighted by different colors.



**Figure 2.** *Knautia sivridaghense* from holotype C. Aykurt 6001, a- Habit, b- Upper cauline leaves, c- Lower cauline leaves, d- Lowest cauline leaves, e- Capitula, f- Involucral bracts, g- Flower, h- Calyx, i- Calyx setae, j- Achene, k- Seed.

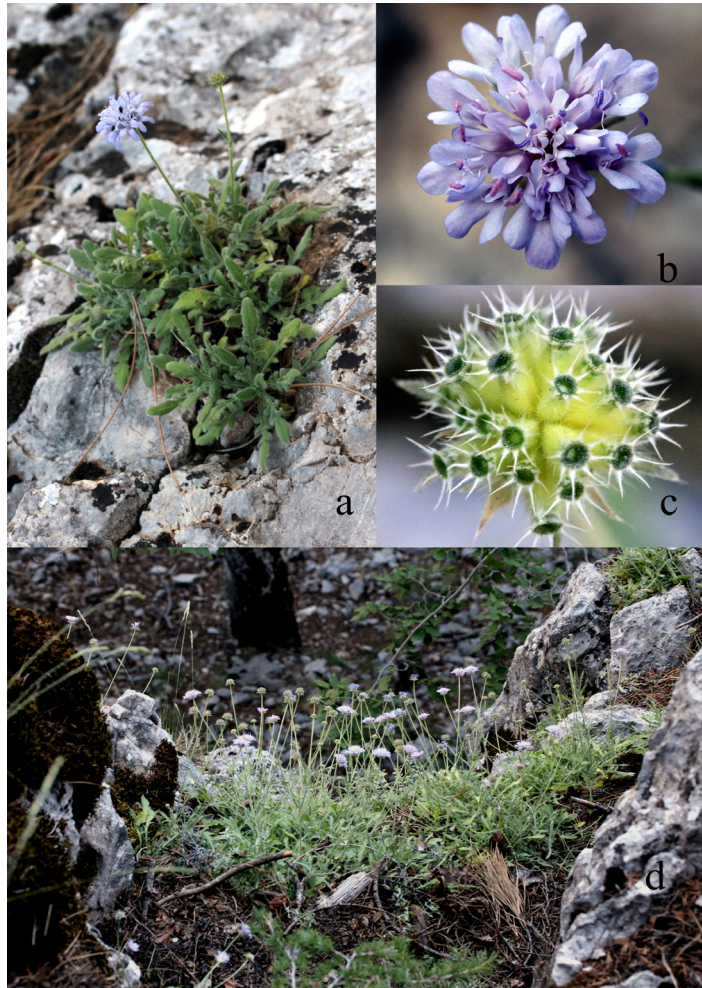
**Distribution, habitat, and ecology:** *Knautia sivridaghense* is distributed in rocky areas under montane coniferous forest mixed with *Pinus brutia* Ten. var. *brutia*, *P. nigra* J.F.Arnold subsp. *pallasiana* (Lamb.) Holmboe var. *pallasiana* and *Cedrus libani* A.Rich. var. *libani* ranging from 1400 to 1450 m. It grows both on limestone rocks and in soil. The new species is associated with plants such as *Styrax officinalis* L., *Juniperus oxycedrus* L. subsp. *oxycedrus*, *Quercus infectoria* G. Oliver subsp. *Infectoria*, *Celtis australis* L., *Astragalus pinetorum* Boiss., *Doronicum orientale* D. Bieb., *Hippocrepis emerus* (L.) Lassen subsp. *emeroides* (Boiss. & Spruner) Greuter & Burdet ex Lassen, and *Vinca herbacea* Waldst. & Kit. The distribution areas of all *Knautia* species in Türkiye are given in Figure 4.

**Eponymy:** The specific epithet ‘sivridaghense’ refers to Sivri Dağ where the new species was discovered. Sivri Dağ was established as a Wildlife Development Area to protect the wild goat (*Capra aegagrus* Erxleben) in 1985. This

mountainous area is notable for its proximity to the city center and its rugged rocky peak that rises steeply.

#### 4. Discussion

Traditionally, the genus *Knautia* is delineated into three distinct sections: sect. *Knautia*, sect. *Trichera*, and sect. *Tricheroides*, with each section being conspicuously represented by a diverse array of species within Türkiye. While characteristics such as life form (annuals vs. perennials), ploidy level, and habitat type are included in the definition of these three sections, they are not sharply separated from each other with respect to their morphology and karyology (Ehrendorfer, 1962, 1981; Rešetnik et al., 2014). Section *Knautia* is uniquely characterized by *K. orientalis*, whereas sect. *Trichera* encompasses species like *K. drymeja*, *K. involucrata* Sommier & Levier, *K. macedonica* Griseb., *K. montana* (Roem. & Schult.) DC., and *K. arvensis*, all of which have a notable presence in



**Figure 3.** Field photographs of *Knautia sivridaghense* from type location, a-d- Habitus, b- Flowering capitula, c- Mature (fruiting) capitula.

Türkiye (Göktürk, 2012, Tunçkol et al., 2021). Contrary to the assertions of Göktürk (2012) and Yıldırım et al. (2022), only the recently described *K. goecmenii* stands out as an endemic species in Türkiye. Meanwhile, *K. byzantina* has its distribution rooted in Bulgaria (Ehrendorfer, 1976), and *K. shepardii* extends its presence to Lebanon and Syria<sup>1</sup>.

The phylogenetic backbone of the nuclear ITS and plastid petN(ycf6)-psbM and also the combined dataset trees coincide with previous phylogenetic studies dealing with the genus *Knautia* (Rešetnik et al., 2014; Frajman et al., 2016; Yıldırım et al., 2022). Our phylogenetic analyses, as shown in Figure 1, support the monophyly of the genus with maximum posterior probabilities (pp) and bootstrap support (bs) (pp = 1; bs = 100%), and *K. orientalis* in sect. *Knautia* is sister to the remaining two sections (pp = 1; bs = 88%, except for the chloroplast

ML tree, bs = 89%). All of the studied members of sect. *Trichera* formed a clade with 53% bs and 0.68 pp for ITS; 98% bs and 1 pp for petN(ycf6)-psbM; and 95% bs and 1 pp for combined dataset trees, and *K. sivridaghense* fell into the highly supported clade (84% bs and 0.93 pp for ITS; 99% bs and 1 pp for petN(ycf6)-psbM; and 100% bs and 1 pp for combined dataset trees) with the members of sect. *Tricherooides*. Rešetnik et al. (2014) stated that the exclusively annual and diploid sections “*Tricherooides*” and “*Knautia*” are restricted to the eastern Balkan Peninsula and northwestern Anatolia, and only *K. integrifolia* extends to the central and western Mediterranean. Yıldırım et al. (2022) noted that although *K. goecmenii* has a suffrutescent caespitose habit and a multistemmed structure resembling the perennial species in sect. *Trichera*, it is actually placed within a well-supported clade

<sup>1</sup> Musselman LJ (2011). Checklist of Plants of Lebanon and Syria [online]. Website <http://www.odu.edu/~lmusselm/plant/lebsyria/Checklist of Lebanon Plants.pdf> [accessed 15 September 2023].



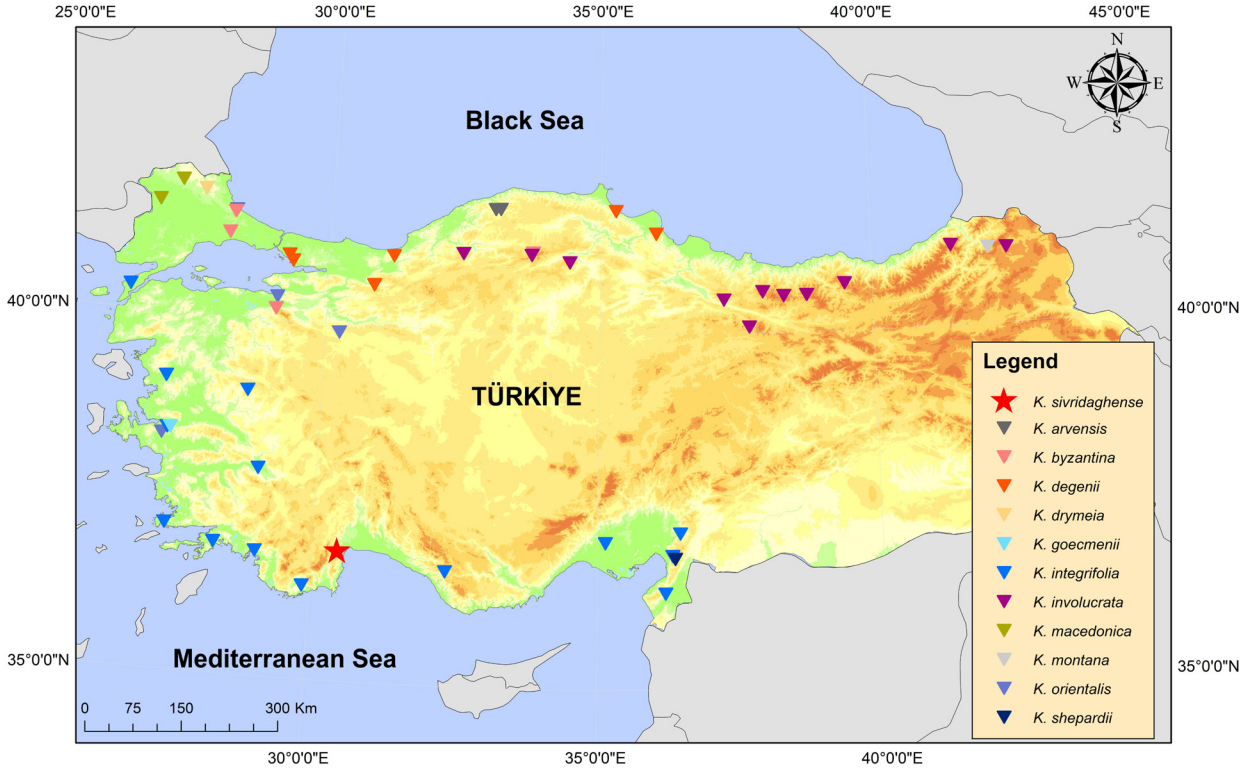


Figure 4. Distribution areas of all *Knautia* species in Türkiye.

with members of sect. *Knautia* and sect. *Tricherooides*. The species within sect. *Tricherooides*, except for *K. goecmenii*, are usually annuals, and the new species described here also shows differences with its caespitose habit and clonal structure. Although *K. sivridaghense* and *K. goecmenii* have similar perennial caespitose structures, *K. sivridaghense* is not suffrutescens, is not multistemmed, and has a tortuous taproot. Moreover, the preferred habitats of the two species are quite different; the new species is found in moist forest understory rocky areas, while *K. goecmenii* is found on the slopes below the summit. The detailed comparison of diagnostic morphological characters of the new species and its close relatives are shown in Table. Two species start flowering in July, which is different from the annual species in the same section that usually flower in spring and early summer. Furthermore, it has been suggested that this species may have evolved from the annual members of the genus. The inclusion of *K. sivridaghense* within sect. *Tricherooides* alongside *K. goecmenii* strengthens this possibility. However, as Yıldırım et al. (2022) have indicated, future studies need to incorporate plastid markers to clarify the phylogenetic position of the species. The species resembling the new species with respect to the habitus and habitat preferences, which are *K. rupicola* (Willk.) Font Quer, *K. subscaposa* Boiss. & Reut., and *K.*

*lucana* Lacaita & Szabó (S Italy; forest), *K. drymeja* (Central & SE Europe, N Italy and European part of Türkiye; forests and forest margins), *K. lebrunii* J. Prudhomme (tall herb communities, open forests; Western Europe) respectively, are in a different clade from it.

Another notable morphological feature of the new species is the short internodes between lower leaves instead of true basal leaf rosettes, whereas all annual species within sect. *Tricherooides* and *K. arvensis* (in sect. *Trichera*) possess basal rosettes. *Knautia sivridaghense* is identified as a new and distinct species based on both our morphological and molecular results. These findings suggest that the species within sect. *Tricherooides* in Anatolia have quite complex speciation mechanisms. Further molecular studies are necessary to clarify both the phylogenetic relationships and evolutionary processes of the species within this section.

#### Additional specimens examined:

**Paratype of *Knautia sivridaghense*:** Türkiye, Antalya, Konyaaltı, Sivri Dağ Wildlife Development Area, S of Karabel Pass Camping Area, 1400–1450 m, 06.07.2023, C. Aykurt 6005, M. Gülben, E. Berberoğlu, S. Günaydın, R.S. Göktürk (AKDU 6448). ***K. involucrata*:** Türkiye, Sivas, Şerefiye, east of Çamkale, hills, steppe, meadows, 19.07.2006, E. Hamzaoğlu, A. Aksoy, Ü. Budak (AKDU

**Table.** Morphological differences among *Knautia sivridaghense*, *K. goecmenii*, *K. integrifolia*, *K. byzantina*, and *K. arvensis*.

	<i>K. sivridaghense</i>	<i>K. goecmenii</i>	<i>K. integrifolia</i>	<i>K. byzantina</i>	<i>K. arvensis</i>
Habitus	Caespitose, perennials with tortuous taproot	Suffrutescent, caespitose perennials with thick cylindrical taproot	Erect annuals	Erect annuals	Stoloniferous perennials
Stem length	19–40 cm	20–60 cm	15–60 cm	15–60 cm	80–100(– 150) cm
Stem indumentum	Crisped hairs with stipitate glandular hairs and fewer unicellular long spreading hairs up to 2 mm	Intermixed with pubescent, hirsute, crisped and glandular hairs	Reflexed-setose and below spreading setose	Puberulent and reflexed or spreading-setose	More or less hirsute or setose and puberulent
Basal leaf rosettes	Lower leaves crowded towards the base through short internodes; like basal leaves	Basal rosettes absent	Basal leaves in rosettes	Basal leaves in rosettes	Basal leaves in rosettes
Lower cauline leaves	Lyrate-pinnatisect to lyrate-pinnatifid	Lyrate- pinnatisect, rarely oblanceolate spatulate or linear	Elliptic to lyrate	Linear, sometimes lyrate	Lanceolate to narrowly ovate, usually lyrate-pinnate
Upper leaves	Usually undivided, linear-lanceolate	Linear to oblanceolate, sometimes spatulate, rarely with one lateral segment	Usually pinnatisect with linear to elliptic lobes	Linear	The upper ones linear-lanceolate, lyrate-pinnatisect, with 2–3 pairs of linear lobes towards the base
Capitula	1–1.5 × 1.5–2 cm, 20–24 flowered, ± radiant	1–1.8 × 0.7–1.2 cm, 12–30 flowered, radiant	1.5–3 cm in diameter, ± radiant	1.5–3 cm in diameter, slightly radiant	Hermaphrodite capitula 2.5–3 cm in diameter; female capitula 2 cm in diameter
Involucral bracts	10, in 2 rows, 4.5–6 mm long, ovate-lanceolate	8–16, in 2 rows, 2–5 mm long, ovate to lanceolate, sometimes linear-lanceolate	10–15(–20), in 2–3 rows, ovate to lanceolate	12–15, lanceolate	12–14, in 2(–3) rows, ovate-lanceolate or oblong-lanceolate
Calyx	Cupuliform, long hirsute and with few glands, with 8 setae	Cupuliform, pubescent-tomentose, with 8 setae	Cupuliform, with numerous fine hair-like setae	Patelliform, with 8–10 setae	Cupuliform, scabrid, ciliate toward base, with (6–)8(–10) setae
Corolla	Pale lavender-blue	Very pale whitish-lilac	Lavender-blue, sometimes pinkish	Bluish-violet	Violet or blue
Achene	5.5–8 × 1.5–2 mm, dorsally compressed, linear, irregularly toothed, long and short ciliate at apex, mostly 2-horned	5–8 × 1–2 mm, dorsally compressed, linear, oblanceolate, mostly 2-, rarely 4-horned	With equal involucl-teeth, or those on 2 angles much longer and distinctly 2-horned	With unequal involucl-teeth	Ovate-oblong, 5–6 mm long, hairy
Habitat	Rocky places under mixed forests, 1400–1450 m elevation	Mountain slopes on calcareous substrates, 1420–1505 m elevation	Rocky slopes, fields, 0–1500 m elevation	Fields, slopes, 0–1300 m elevation	Meadows and open forest habitats in Küre Mountains (for Türkiye), 600–950 m elevation
Flowering time	July–August	July–September	April–June	May–June	April–June

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## Acknowledgments

We would like to thank the General Directorate of Forestry of the Ministry of Agriculture and Forestry of the Republic of Türkiye for their financial support for this study. English language editing was done by Philip Smith.

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