ACTA BOTANICA CROATICA

CODEN: ABCRA 25
ISSN 0365-0588
eISSN 1847-8476

ACCEPTED AUTHOR'S VERSION OF THE MANUSCRIPT

A detailed anatomical characterisation of 17 *Satureja* species (Lamiaceae) from Türkiye

DOI 10.37427/botcro-2027-001

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Please cite this article as: Öztekin, M., Doğan, C., Doğru-Koca, A., Zare, G.: A detailed anatomical characterization of 17 *Satureja* species (Lamiaceae) from Türkiye. Acta Botanica Croatica, DOI: 10.37427/botcro-2027-001.

This is a PDF file of a manuscript that has been language edited and accepted for publication. The manuscript will be technically edited, formatted and checked by the author before publication in its final form.

A detailed anatomical characterisation of 17 *Satureja* species (Lamiaceae) from Türkiye

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Running title: ANATOMICAL STUDY OF THE *SATUREJA*

Abstract – *Satureja* species, commonly known as savory herbs, are a diverse group of plants belonging to the family Lamiaceae and are widely distributed throughout Türkiye. These aromatic herbs play an important role in both culinary and medicinal practices, contributing to local traditions and customs. Understanding their anatomy is essential for identifying species variations, ecological adaptations, and potential uses in agriculture and pharmacology. This study provides comprehensive details of the anatomical characteristics of different *Satureja* species found in Türkiye. The anatomical characteristics of 17 *Satureja* species, including their leaf structure, stem, and roots, provided important insights into their identification and classification. For the taxa studied, the root and stem cross-sectional structure, such as the vascular bundles, collenchyma type, and presence and density of the sclerenchyma, was important. In particular, the leaf, trichome type density, and mesophyll characteristics also provided more reliable tools for identifying the taxa. Understanding these anatomical characteristics will not only aid in the classification of *Satureja* species but also enhance our knowledge of their ecological roles and their potential applications in improving crop resilience and medicinal applications.

Keywords: anatomy, collenchyma, Lamiaceae, *Satureja*, savory, Türkiye

Introduction

The genus *Satureja* L. s.l., commonly known as savory, comprises approximately 44 species of herbaceous aromatic herbs in the family Lamiaceae. The natural range of the genus includes the countries north of the Mediterranean Basin, Morocco, Libya, and Western, Southern, and Central Asia (POWO 2025). *Satureja* is comprised of mostly perennial and subshrub species, with only a few annuals such as *S. hortensis* and *S. laxiflora*. The taxonomic complexity and uncertainty within the genus *Satureja* are explicitly attributed to morphological similarities among its species. Some taxonomists have treated it broadly, combining related genera like *Clinopodium* L. and *Micromeria* Benth., while others have restricted it to fewer species (Bentham 1832–1876, Briquet 1895–1897, Kuntze 1891, Doroszenko 1985). Cantino and Wagstaff (1998) contributed significantly to clarifying *Satureja* taxonomy by using chloroplast DNA restriction site analysis and morphological data to demonstrate that the historically broad *Satureja* s.l. complex was non-

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monophyletic, especially due to the inclusion of genera like *Satureja* s.str., *Micromeria*, and *Piloblephis* Raf. This phylogenetic evidence supported a major revision that excluded these disparate elements, ultimately reclassifying the remaining complex, including most North American representatives, under the priority name *Clinopodium*. Previous studies frequently highlighted the existence of intermediate species and taxa that intergrade, which often suggests complex relationship patterns or potentially past hybridisation/introgression that have blurred taxonomic boundaries (Wagstaff et al. 1995, Cantino and Wagstaff 1998). Additionally, chromosomal studies have revealed variations in the chromosome number among Turkish *Satureja* species, providing insights into their evolutionary relationships, with dysploidy and polyploidy playing key roles in their speciation (Kavcı et al. 2023). Although there have been some studies on the phylogeny of the genus by Bräuchler et al. (2005), Bräuchler et al. (2010), and Moaied et al. (2021), the evolutionary relationships within the genus have not yet been fully elucidated.

Its diversity and the percentage of endemism in Türkiye and Iran are remarkable. Of the 18 *Satureja* species found in Türkiye, 6 taxa are endemic, with an endemism rate of 35% of taxa (Davis 1982, Tümen et al. 2000, Öztekin 2012, Fırat 2015, Duman et al. 2023). The concentration of species in this mountainous, climatically defined region may indicate that the area offers ecological, and possibly geographic, conditions conducive to speciation and isolation, thereby giving rise to a high number of unique taxa (Satıl et al. 2008, Duman et al. 2023, Bordbar and Mirtadzadini 2024).

Satureja species are commonly known among Turkish locals as "kekik, kayakekiği, sivri kekik, and kılıç kekik" (Baytop 1994, Satıl et al. 2008, Öztekin 2012, Sadıkoğlu and Özhatay 2019). *Satureja* is a traditionally valued medicinal plant, widely utilised by local communities for various therapeutic purposes due to its essential oils and phenolic and flavonoid constituents, and it is also commonly used in both traditional medicine and culinary applications. (Kürkçüoğlu et al. 2001, Edeoga et al. 2005, Satıl et al. 2006, Eminağaoğlu et al. 2007, García-Rellán et al. 2015, Baytop 1999, Sefidkon and Bistgani 2021). Commercially significant species include *S. thymbra* L., *S. cuneifolia* Ten., and *S. hortensis* L., which are an integral part of Turkish cuisine and have considerable potential in pharmaceuticals and cosmetics due to their antimicrobial properties (Satıl et al. 2008, Çarıkçı et al. 2020). In addition, *Satureja* species have a robust root structure that plays a crucial role in mitigating soil erosion by reducing the impact of rain and surface runoff (Satıl et al. 2008, Jamzad 2009, Malmir et al. 2014).

Mainly due to the essential oil content, the secretory hairs, and especially the leaf anatomy of the genus *Satureja*, have been the focus of research interest. The most comprehensive anatomical study of the genus was carried out by Satıl and Kaya (2007) on the leaf anatomy and hairs of taxa distributed in Türkiye. According to them, all the species have amphistomatous leaves with diacytic stomata. In all the species, except for the bifacial *S. spicigera*, the leaves are equifacial and the mesophyll is differentiated into a 1–3-seriate palisade parenchyma and 2–5-seriate spongy parenchyma. They also revealed that all the *Satureja* species have non-glandular hairs and two types of glandular hairs - peltate and capitate. In addition, the stem and leaf anatomical characteristics of *S. coerulea*, *S. parnassica* subsp. *sipylea* from Turkey have been investigated (Satıl et al. 2002; 2003). Bordbar et al. (2025) investigated the pollen, nutlet, and trichome micromorphology of 12 *Satureja* species growing in Iran, of which three species overlap with our study: *S. avromanica* Maroofi, *S. hortensis* L., and *S. macrantha* C.A. Mey. The leaf anatomy of *S. khuzestanica*, an endemic and traditional medicinal herb in Iran, was studied by Malmir et al. (2014). The leaf and stem anatomy of the species *S. montana* and *S. subspicata* from Croatia has been analyzed in detail, especially with regard to hairs (Stanić et al. 2004). Mosquero

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et al. (2006) concluded that the anatomical differences in the nutlet anatomy, especially the epicarp, mesocarp, and endocarp of *Satureja* species distributed in Spain, are taxonomically important. Shanaida et al. (2016) emphasised that the morphological and anatomical characterisation of *S. hortensis* is crucial for its reliable identification and quality evaluation as a medicinal herb. More recently, the anatomical structures of *S. spicigera* were studied by Akçin and Karadeniz (2023) using cross-sections of the aerial and subterranean organs. However, the root, stem, and leaf anatomy of the genus has not yet been elucidated with a holistic approach.

The aim of the study was to provide a comprehensive review of the anatomical characteristics of the *Satureja* species occurring in Türkiye, emphasising their distinctive structural features and diagnostic characteristics relevant for taxonomic identification. All *Satureja* species found in Türkiye were examined, with the exception of the newly described species *Satureja hasturkii* H. Duman and Dirmenci (Duman et al. 2023).

Material and methods

Plant samples belonging to seventeen species were gathered from various regions of Türkiye during the *Satureja* revision study from 1997 to 2024 (On-line Suppl. Tab. 1 and On-line Suppl. Fig. 1). The gathered materials, which included roots, stems, and leaves, were stored in 70% ethanol for anatomical examination. The identified voucher specimens (On-line Suppl. Tab. 1) were kept in Hacettepe University Herbarium (HUB).

For anatomical analysis, peridermal and transverse sections of the leaves (median), stems, and roots were obtained through freehand cutting with razor blades. All the slides were stained using a double staining technique with Astra Blue and Safranin. The sections were treated with a 9:1 Astra Blue:Safranin ratio (Çakırlar et al. 2010).

The slides were examined using an Olympus CX41 light microscope (Olympus Scientific Solutions, Shinjuku, Tokyo, Japan) and photographed with a Nikon Digital Sight camera (DS)-L1 with a DS-5M microscope connected to a Nikon Eclipse E600 camera (Nikon Corp., Minato City, Tokyo, Japan). The data for all the anatomical characteristics were derived from the measurements of all parts of the plant, in total 30 sections for each taxon. In general, three different individuals were evaluated for each specimen. The resulting images and data provided a comprehensive overview of the anatomical features, allowing for comparisons across different taxa, as well as enhancing our understanding of their morphological adaptations.

Results

The anatomical features of the root, stem, and leaf of 17 *Satureja* species growing in Türkiye were comprehensively investigated. Cross-sectional images were included for all species, and the examined anatomical characteristics are presented in Tables 1 and 2.

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Tab. 1. Stem characteristics of the *Satureja* taxa from Türkiye.

Taxon	Trichomes	Cortex layers	Collenchyma	Sclerenchyma	Vascular bundle
S. aintabensis	Dense	6–10	Annular	Absent	Continuous
S. amani	Sparse	4–9	Annular	Present	Continuous
S. avromanica	Dense	4–10	Lamellar	Present	Separated
S. boissieri	Dense	6–11	Lamellar	Present	Continuous
S. cilicica	Sparse	5–10	Lamellar	Present	Continuous
S. coerulea	Sparse	5–9	Lamellar	Present	Continuous
S. cuneifolia	Sparse	5–9	Lamellar	Absent	Continuous
S. hortensis	Sparse	5–9	Lamellar	Absent	Continuous
S. icarica	Sparse	6–12	Lamellar	Present	Continuous
S. macrantha	Sparse	5–9	Lamellar	Present	Continuous
S. metastasiantha	Sparse	5–10	Lamellar	Present	Continuous
S. parnassica subsp. *sipylea*	Sparse	4–9	Lamellar	Present	Continuous
S. pilosa	Sparse	5–9	Annular	Present	Continuous
S. spicigera	Sparse	6–12	Lamellar	Present	Continuous
S. spinosa	Dense	4–8	Lamellar	Present	Continuous
S. thymbra	Sparse	4–10	Lamellar	Absent	Continuous
S. wiedemanniana	Rare	5–10	Lamellar	Absent	Continuous

Tab. 2. Leaf characteristics of the *Satureja* taxa from Türkiye.

Taxon	Leaf shape	Non-glandular hair	Glandular hair	Mesophyll type	Sclerenchymatous	Palisade parenchyma	Spongy parenchyma
S. aintabensis	Not folded	Dense 1–5 cells	Capitate/ peltate	Isobilateral	Absent	2+2 layers	2–3 middle
S. amani	Folded	Sparse 1–5 cells	Capitate/ peltate	Isobilateral	Absent	1+1 layer	1–2 middle
S. avromanica	Not folded	Sparse 1–5 cells	Capitate/ peltate	Dorsiventral	Absent	2 Adaxial	2–3 Abaxial
S. boissieri	Folded	Sparse 1–5 cells	Capitate/ peltate	Isobilateral	Absent	2+2 layers	2–4 middle
S. cilicica	Folded	Sparse 1–5 cells	Capitate/ peltate	Isobilateral	Absent	1+1 layer	2–3 middle
S. coerulea	Not folded	Sparse 1–5 cells	Capitate/ peltate	Isobilateral	Absent	2+2 layers	Absent
S. cuneifolia	Folded	Sparse 1–5 cells	Capitate/ peltate	Isobilateral	Present	2+2 layers	Absent
S. hortensis	Folded	Dense 1–5 cells	Capitate/ peltate	Isobilateral	Present	2+2 layers	Absent
S. icarica	Folded	Moderate 1–5 cells	Capitate/ peltate	Isobilateral	Absent	1+1 layer	2–4 middle
S. macrantha	Folded	Sparse 1–5 cells	Capitate/ peltate	Isobilateral	Absent	1+1 layer	1–2 middle
S. metastasiantha	Folded	Sparse 1–4 cells	Capitate/ peltate	Isobilateral	Absent	2+2 layers	1–2 middle
S. parnassica subsp. *sipylea*	Folded	Moderate 1–5 cells	Capitate/ peltate	Dorsiventral	Absent	1-2 adaxial	3–5 abaxial
S. pilosa	Folded	Sparse 1–5 cells	Capitate/ peltate	Dorsiventral	Absent	2 adaxial	2–3 abaxial

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Tab. 2 continued

S. spicigera	Folded	Sparse 1–3 cells	Capitate/ peltate	Isobilateral	Absent	1+1 layer	2–3 middle
S. spinosa	Folded	Dense 1–5 cells	Capitate/ peltate	Isobilateral	Present	1+1 layer	2–3 middle
S. thymbra	Folded	Sparse 1–3 cells	Capitate/ peltate	Isobilateral	Absent	1+1 layer	2–3 middle
S. wiedemanniana	Folded	Sparse 1–5 cells	Capitate/ peltate	Isobilateral	Present	2+2 layers	2–3 middle

Cross-sectional structure of the roots

The periderm layer, located on the outermost surface, is particularly thick and its cells show signs of compression or fragmentation. The periderm consists of a cork layer of varying thickness among species, ranging from 4 to 15 cellular layers. Beneath the periderm, the cortex is composed of 4 to 7 layers of parenchymatous tissue organised in a regular pattern. The single-layered endodermis is characterised by rectangular or square cells, while the pericycle consists of a single layer of cells. The vascular structures vary among the taxa studied and show different configurations. In general, the vascular system follows a tetrarch pattern like in *Satureja aintabensis, S. cilicica, S. icarica*, *S. parnassica* subsp. s*ipylea* and *S. spinosa* (Fig. 1A, F, J, N and Q), whereas in *S. amani* (Fig. 1B) and *S. spicigera* (Fig. 1P), it follows a hexarch pattern.

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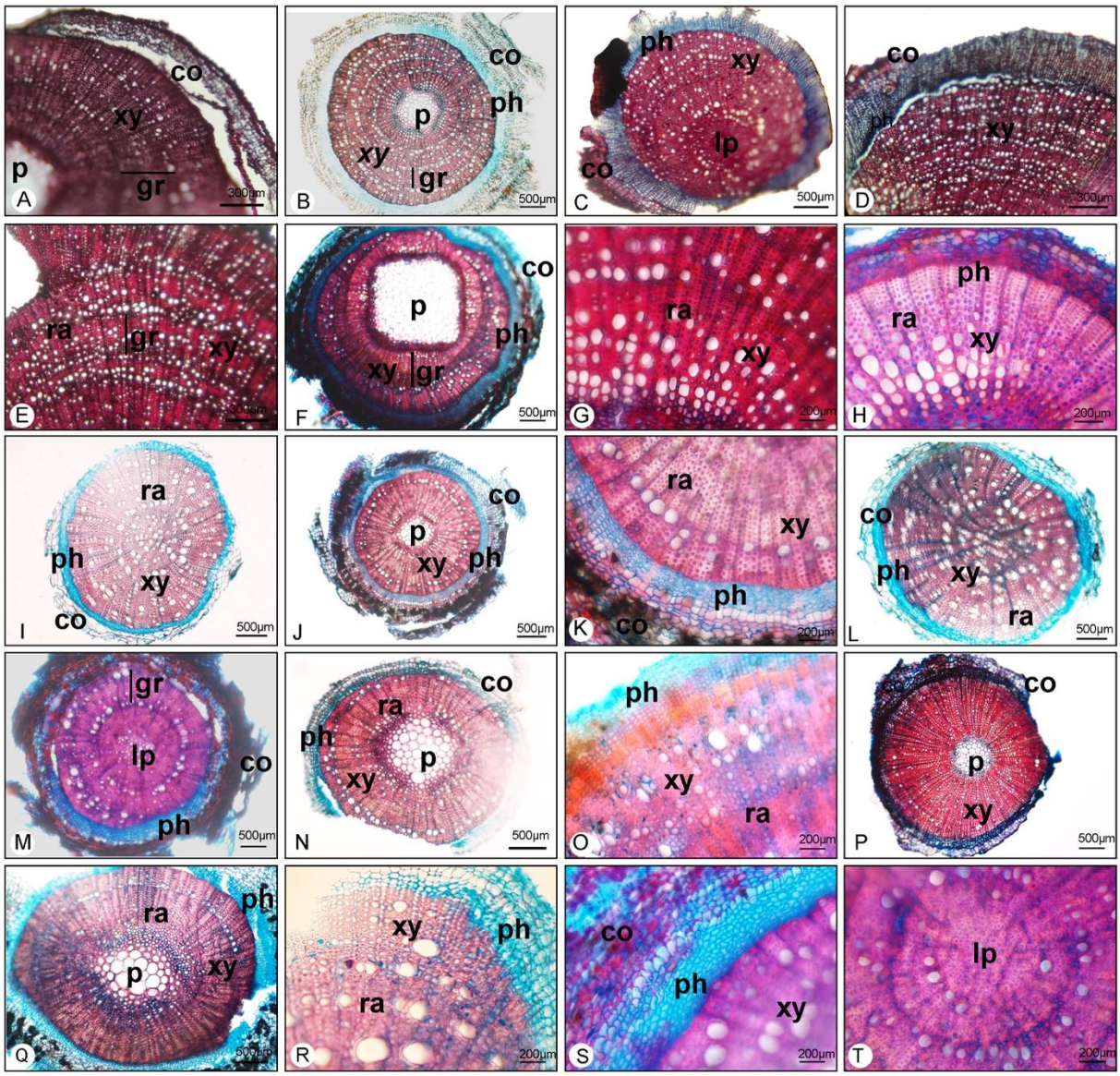


Fig. 1. Root cross-sections of the *Satureja* taxa from Türkiye: A – *S. aintabensis*, B – *S. amani*, C – *S. avromanica*, D-E – *S. boissieri*, F – *S. cilicica*, G – *S. coerulea*, H – *S. cuneifolia*, I – *S. hortensis*, J-K – *S. icarica*, L – *S. macrantha*, M – *S. metastasiantha*, N – *S. parnassica* subsp. *sipylea*, O – *S. pilosa*, P – *S. spicigera*, Q – *S. spinosa*, R – *S. thymbra*, S-T – *S. wiedemanniana*. co – cork; gr – growth ring; lp – lignified parenchyma; p – parenchyma; ph – phloem; ra – ray; xy – xylem.

The secondary phloem, consisting of 5 to 12 layers, is located under the cortex. It is composed of regular, thin, rectangular cells arranged in a ring. The cambium layer, located between the phloem and xylem, is present but not clearly identifiable. The secondary xylem occupies a considerable area and is composed primarily of lignified cells. The tracheary elements appear orbicular or ovoid in transverse sections, suggesting that they may be vessels rather than tracheids. The rays are typically composed of thin, polygonal cells. The root structures of the

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studied taxa exhibit three distinct configurations. In the first group (*S. amani*, *S. cilicica*, *S. icarica*, *S. parnassica* subsp. *sipylea*, and *S. spicigera*), the central part of the root consists of large, rounded parenchymatous cells surrounded by either secondary xylem or parenchyma cells (Fig. 1B, F, J, N and P). In the second group (*S. aintabensis*, *S. hortensis*, *S. macrantha*, *S. pilosa*, *S. spinosa*, and *S. thymbra*), the entire central region of the root is occupied by metaxylem cells (Fig. 1A, I, L, O, Q and R). In the third group (*S. avromanica*, *S. boissieri*, *S. coerulea*, *S. cuneifolia*, *S. metastasiantha* and *S. wiedemanniana*), the central part of the root is composed of lignified parenchyma cells (Fig. 1C, E, G, H, M and T). The xylem consists of vascular elements and tracheids, with the vascular elements being either circular or hexagonal in cross section.

Fluted stem structures

Fluted stem structures were identified in certain species of the genus, including *S. aintabensis S. cuneifolia*, *S. spinosa* and *S. wiedemanniana* (Fig. 2). These structures exhibit a thick woody composition, and consist of a cortex, parenchymatous tissue, secondary phloem, and xylem. The configuration of these structures is irregular. Annual rings are prominent in some species, such as *S. cuneifolia* (Fig. 2D).

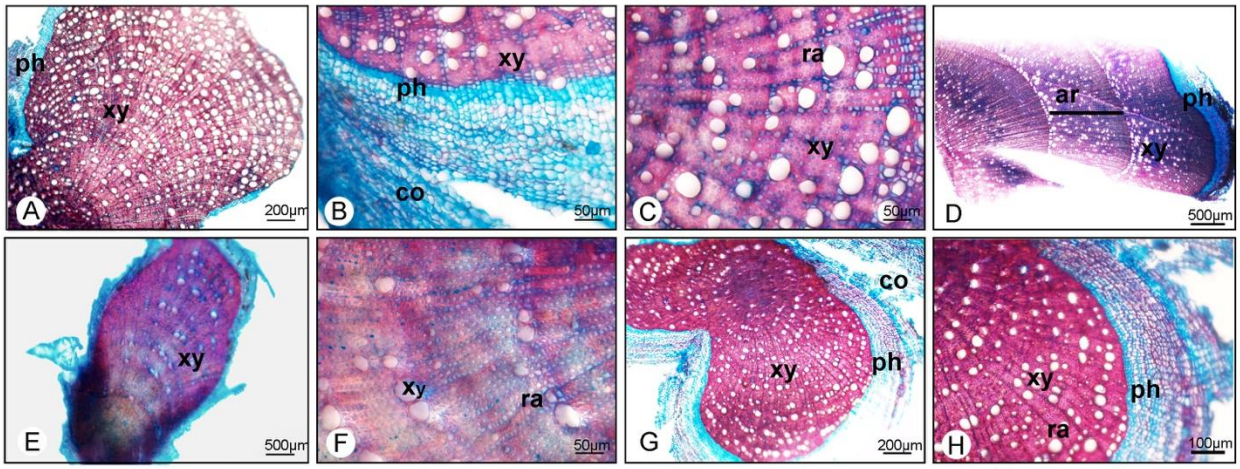


Fig. 2. Fluted stem structures of the *Satureja* taxa from Türkiye: A-C – *S. aintabensis*, D – *S. cuneifolia*, E-F – *S. spinosa*, G-H – *S. wiedemanniana*. ar – annual rings; co – cork; ph – phloem; pr – priderm; ra – ray; xy – xylem.

Cross-sectional structure of stems

The important anatomical characteristics of the stem are given in Tab. 1. The stem is almost square or rounded in shape, with four corners, which may be either rounded or sharp, and four faces between them. Just below the epidermis, within each corner, there is a region of lamellar or annular collenchyma cells. It is difficult to distinguish between these two types. The lamellar collenchyma consists of longitudinally elongated cells. The pattern of cell wall thickening is restricted to the tangential walls.

The annular collenchyma, on the other hand, consists of rounded cells with uniformly thickened cell walls. The parenchyma cells are compact and there are no intercellular spaces between them. In *S. cuneifolia*, *S. icarica* and *S. wiedemanniana*, the collenchyma is

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underdeveloped and not distinct. Scattered single sclerenchyma cells are present near the endodermis (Tab. 1, Fig. 3F, I and Fig. 4A, B).

The secondary phloem is delimited externally by a zone of phloem fibres and consists predominantly of sieve elements, companion cells, and phloem parenchyma. This region is succeeded internally by the fascicular and interfascicular cambial zones, which give rise to the secondary xylem. The secondary xylem is typically lignified and composed of vessel elements, tracheids, xylem fibres, and both axial and ray parenchyma. These tissues form the principal conducting and supporting components of the stem. Toward the centre, the pith (medulla) is composed mainly of thin-walled parenchyma cells, occasionally containing unlignified tracheary elements in the peripheral region adjacent to the xylem. The innermost part of the phloem consists of unlignified tracheary elements and peripheral pith cells. The vascular zone varies between species. In *S. avromanica*, the vascular bundles are separated and arranged in a ring (Fig. 3G, H), whereas in the remaining taxa of the genus, the vascular tissue is continuous throughout the stem. Rays are present in the xylem tissue and consist of thin, polygonal cells (Fig. 3A-R).

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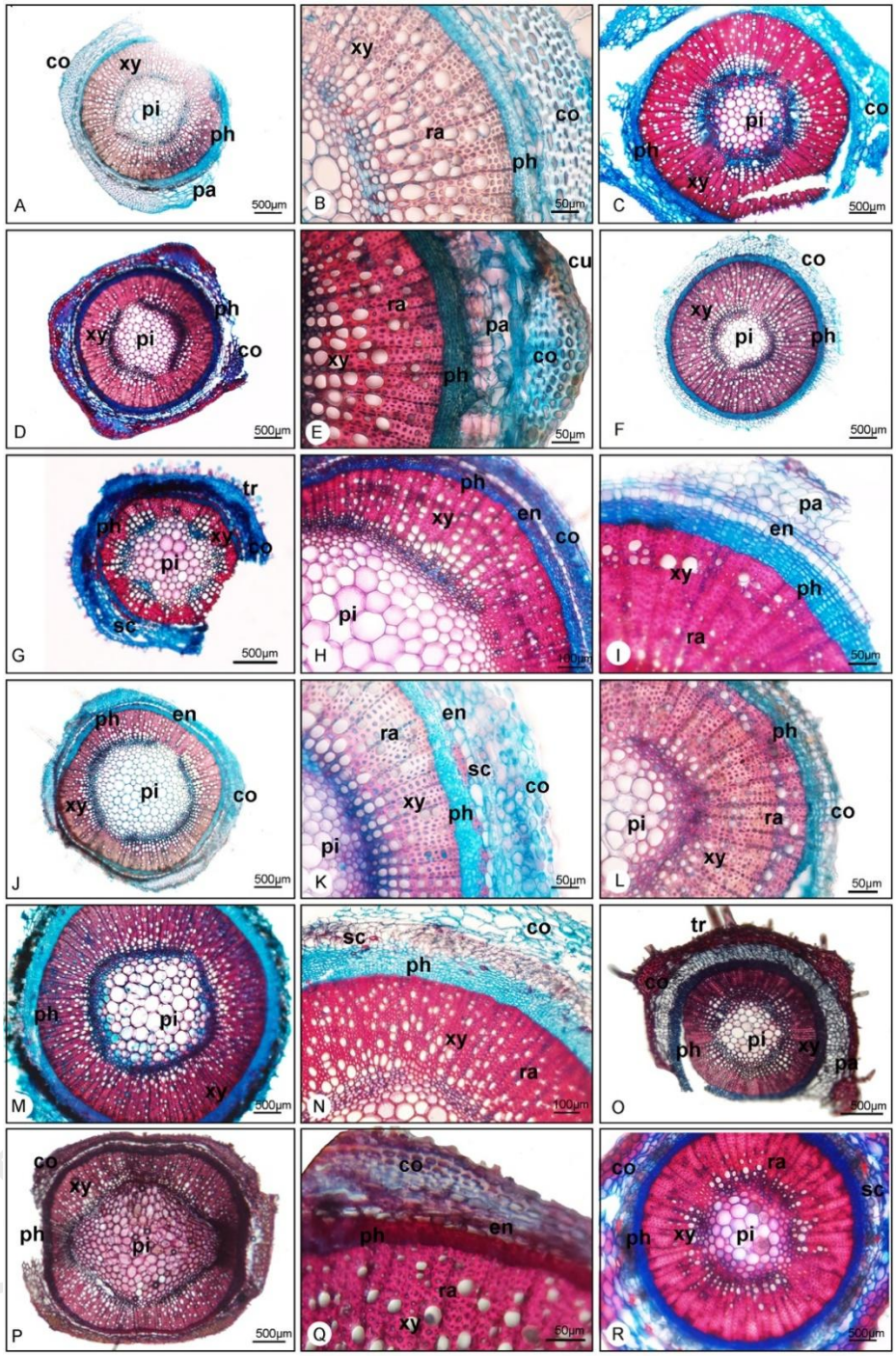


Fig. 3. Stem cross-sections of the *Satureja* taxa from Türkiye: A-B – *S. aintabensis*, C – *S. cilicica*, D-E – *S. amani*, F – *S. cuneifolia*, G-H – *S. avromanica*, I – *S. icarica*, J-K – *S. boissieri*, L – *S. parnassica* subsp. *sipylea*, M-N – *S. macrantha*, O – *S. metastasiantha*, P-Q – *S. spicigera*, R – *S. spinosa*. en – endodermis; co – chollenchyma; cu – cuticula; pi – pith; ph – phloem; ra – ray; sc – sclerenchyma; tr – trichome; xy – xylem.

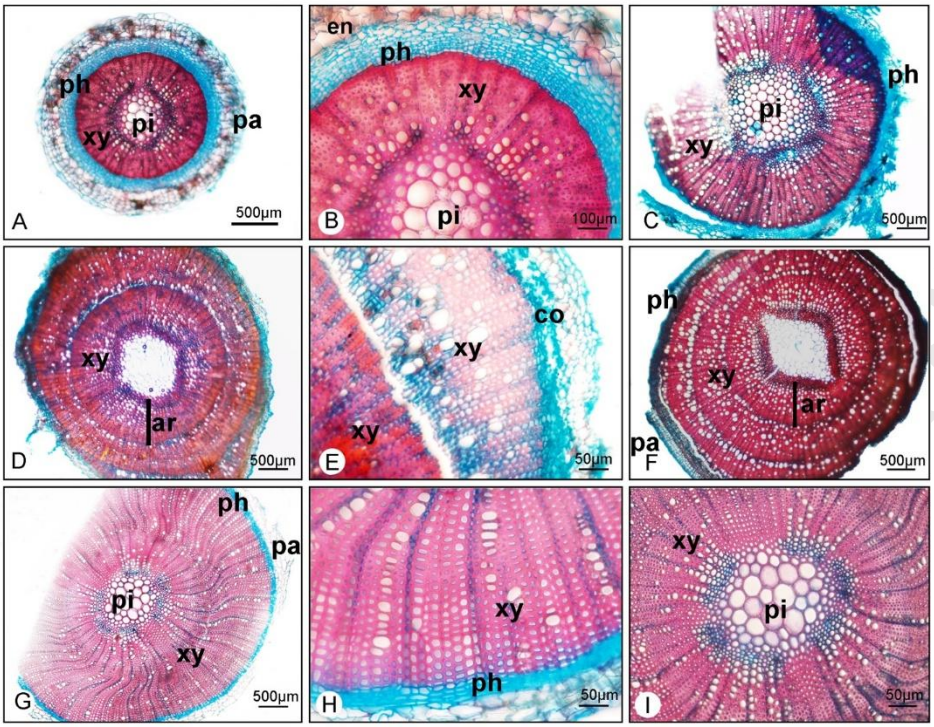


Fig. 4. Stem cross-sections of the *Satureja* taxa from Türkiye: A-B – *S. wiedemanniana*, C – *S. thymbra*, D-E – *S. pilosa*, F – *S. coerulea*, G-H – *S. hortensis*. ar – annual rings; en – endodermis; pa – parnchima; pi – pith; ph – phloem; xy – xylem.

Cross-sectional structure of leaves

Detailed leaf characteristics are documented in Tab. 2. The studied taxa can be divided into two groups on the basis of the leaf shape: non-midrib-folded leaves (Type I) – observed in *S. aintabensis*, *S. avromanica*, and *S. coerulea* (Fig. 5A-D, M, N) - and midrib-folded leaves (Type II) – found in all the other *Satureja* species (Fig. 5E-ZF).

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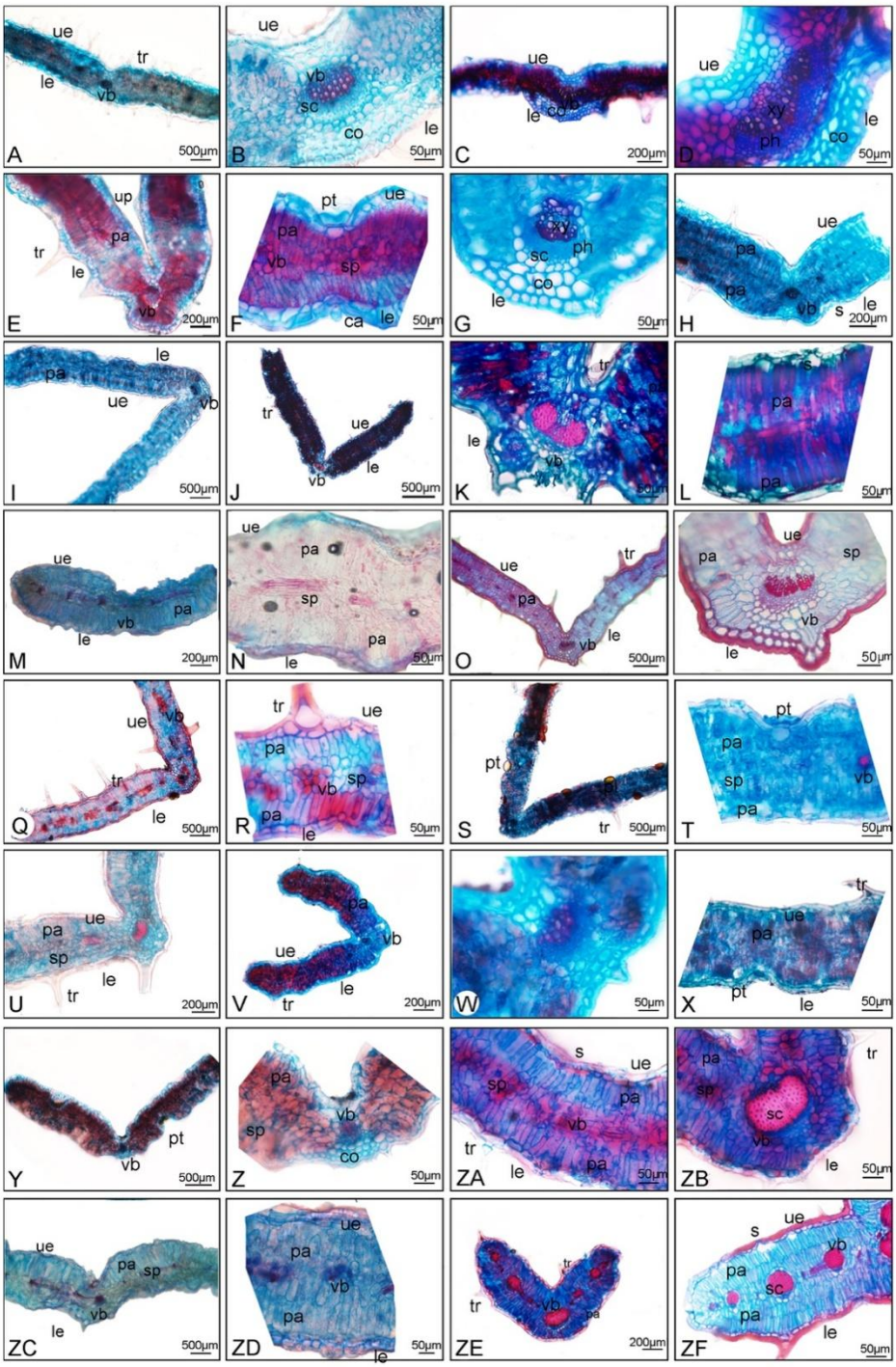


Fig. 5. Leaf cross-sections of the *Satureja* taxa from Türkiye: A-B – *S. aintabensis*, C-D – *S. avromanica*, E-G – *S. amani*, H – *S. boissieri*, I – *S. cilicica*, J-L – *S. cuneifolia*, M-N – *S. coerulea*, O-P – *S. hortensis*, Q-R – *S. icarica*, S-T – *S. pilosa*, U – *S. parnassica* ssp. *sipylea*, V – *S. metastasiantha*, W-X – *S. macrantha*, Y-Z – *S. spicigera*, ZA-ZB – *S. spinosa*, ZC-ZD – *S. thymbra*, ZE-ZF – *S. wiedemanniana*. ue – upper epidermis; le – lower epidermis; s – stoma; pa – palisade parenchyma; sp – spongy parenchyma; vb – vascular bundle; sc – schlerenchyma; tr – covering trichome, pt – peltate trichome; ca – capitate trichome; co – collenchyma.

Cross-sections of the leaf blades of the *Satureja* taxa show an epidermis that is uniseriate on both surfaces and lies beneath the cuticle (Fig. 5). Both epidermal layers are covered by a cuticle. All the taxa have amphistomatous leaves with stomata on one or both surfaces, predominantly of the diacytic type. The stomata are located at the same level as the epidermal cells, with stomatal cavities present on both surfaces (Fig. 5L). The mesophyll shows either isobilateral or dorsiventral (bifacial leaf) structures with multilayered palisade parenchyma cells. The mesophyll is differentiated into palisade and spongy parenchyma. Palisade parenchyma cells are cylindrical, whereas spongy parenchyma cells appear circular or ovoid (Tab. 2).

Typically, the mesophyll consists of 1- or 2-layered palisade parenchyma (rarely 2 to 3 layers in *S. aintabensis* and *S. macrantha*; Fig. 5A, B, W, X) and 1- to 4-layered spongy parenchyma (rarely 1 to 4 layers in *S. cilicica* and *S. icarica*; 2 to 5 layers in *S. spicigera* and *S. boissieri*) (Tab. 1). Spongy parenchyma layers consist of a minimum of 1 or 2 layers in the middle part of the leaf, between the palisade layers or on the abaxial surface.

The vascular bundles are collateral and surrounded by a vascular bundle sheath. This sheath is usually composed of parenchyma or sclerenchyma cells, which may have thick or thin cellulose-containing walls. In some cases, these cells contain chloroplasts, which contribute to photosynthesis. The vascular bundles of the veins are sometimes accompanied by sclerenchyma, especially in species with xerophytic characteristics such as *S. coerulea*, *S. parnassica* subsp. *sipylea*, and *S. wiedemanniana*, and the sclerenchymatous tissue is either larger or more prominent in the midrib region (Fig. 5M, N, U, ZE, ZF).

The xylem is oriented toward the adaxial surface of the leaf, while the phloem is oriented toward the abaxial surface. In the samples examined, collenchyma is present below the epidermis, both above and below the midvein. The cell walls of the collenchyma cells show an annular thickening.

Trichomes

In general, all investigated *Satureja* species possess non-glandular trichomes (eglandular) along with the two main glandular forms: sub-sessile (peltate) and capitate hairs. The glands vary in the number of cells in the head and the stalk. Several types of glands are often found together on a single leaf. The peltate trichomes consist of a basal cell, a short unicellular stalk, and a secretory head, usually consisting of 8 cells (Fig. 6A-B). They secrete pleasantly scented oils. The density of the peltate trichomes varies from species to species. The capitate trichomes have a short unicellular stalk, rarely bicellular, and a head (Fig. 6C).

The non-glandular hairs are uni- or multicellular, unbranched, and consist of elongated cells (Fig. 6D-H). The density of the non-glandular trichomes on the *Satureja* leaves varies. In some species, they are sparse, while in others, they form a dense covering (Tab. 2).

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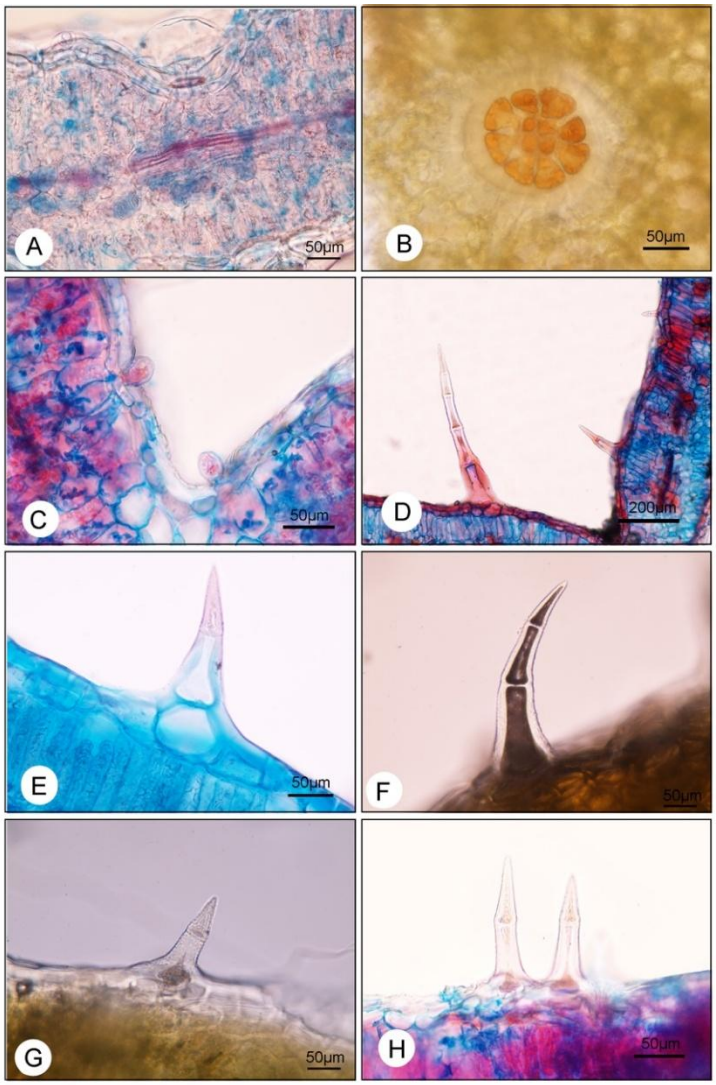


Fig. 6. Trichomes of the *Satureja* from Türkiye: A-B – peltate trichome, head 12 cells, C – capitate trichome, 1 cell, D – non-glandular 2 cellular trichomes, E-H – non-glandular 2 cellular trichome.

Discussion

Anatomical characteristics have often been used to identify relationships between species in the family Lamiaceae, which includes many species that are adapted to arid environments and exhibit pronounced xerophytic adaptations (Metcalfe and Chalk 1950, Garner 2017). An anatomical examination of *Satureja* roots, stems, and leaves reveals conserved traits of the Lamiaceae family, alongside significant interspecific variability, which enables the identification of co-occurring characteristic patterns associated primarily with ecological and systematic groupings.

The roots of *Satureja* species exhibit secondary growth, a characteristic feature of dicotyledonous plants (Simpson 2019). Our results revealed interspecific variation in root structure among the studied taxa, particularly with respect to periderm thickness, vascular arrangement (tetrarch vs. hexarch), and the composition of the central tissue. While most taxa displayed a tetrarch vascular pattern, *S. amani* and *S. spicigera* were distinguished by a hexarch configuration,

and three distinct anatomical groups were recognized based on the nature of the central root tissue (parenchymatous, metaxylem-dominated, or lignified parenchyma). These structural differences reflect a species-specific anatomical structure and underscore the taxonomic significance of root anatomical characteristics in discriminating closely related *Satureja* species. The presence of sclerenchyma in the pericycle likely contributes to mechanical support, particularly in species adapted to xeric environments. These findings are consistent with previous anatomical studies on members of the family Lamiaceae (Metcalfe and Chalk 1950, Satıl et al. 2002, 2003, Akçin and Karadeniz 2023). These observations suggest that the organisation of vascular tissues is important for the overall growth and adaptability of root systems in this family, likely affecting the efficiency of water and nutrient transport. In addition, this characteristic may be influenced by environmental factors or age-related changes in perennial plants (Tarshis and Tarshis 2012). Therefore, more anatomical research is needed to obtain conclusive results. Such research should focus on a wider range of species and environments to assess the variability and consistency of these vascular patterns in different populations.

The stem anatomy of *Satureja*, consistent with the subfamily Nepetoideae and the broader Lamiaceae family, generally adheres to the classic quadrangular stem blueprint, characterised by a single-layered epidermis covered by a cuticle (Metcalfe and Chalk 1950, Garner 2017, Akçın and Karadeniz 2023). Transverse sections reveal a cortex where collenchyma tissue is prominently developed in the corners, typically organised in multiple layers, supporting the angles immediately beneath the epidermis (Duarte and Lopes 2007, Pınar et. al. 2018). The central region features a pith composed of large parenchymatous cells, which may remain solid or become hollow/ruptured upon maturity (e.g., observed in *S. parnassica* subsp. *sipylea* and *S. hortensis*). For taxonomic clarification, internal anatomical features are highly diagnostic: the presence or absence of sclerenchymatous tissue in the vascular bundles is a marker, being present in species like *S. coerulea* and *S. parnassica* subsp. *sipylea*, yet absent in related taxa such as *S. cuneifolia* and *S. spicigera*. These results are also in agreement with those of Satıl et al. (2002, 2003). The only notable difference concerns the presence of clearly developed annual growth rings in our stem cross-sections (Fig. 4F), indicating a perennial structure, whereas the earlier studies did not explicitly describe the sections as perennial. In *S. spicigera*, the anatomical structures also show agreement with our findings, especially in terms of vascular bundle arrangement and the development of collenchymatous tissue (Akçin and Karadeniz 2023). Scattered sclerenchyma cells near the endodermis in the cortex form an important supportive tissue that enhances mechanical strength. These cells possess thick, lignified walls and are non-living at maturity, providing rigidity to the surrounding tissues. Their position indicates a role in reinforcing regions requiring additional support, particularly around vascular tissues. The increase in stem flexural and torsional stiffness during ontogeny is therefore mainly related to changes in the mechanical properties of these tissues rather than to their proportional distribution (Garner 2017, Kaminski et al. 2017, Akbar 2020). The occurrence of fluted stem structures in *S. aintabensis*, *S. cuneifolia*, *S. spinosa*, and *S. wiedemanniana* is characterised by a thick, woody organisation and well-developed annual rings, which are particularly prominent in *S. cuneifolia*, indicating species-specific patterns of secondary growth. Although the exact functional role of stem fluting is not yet fully understood, this anatomical feature has been reported in several members of the Lamiaceae family and is thought to be associated with structural adaptations that enhance mechanical stability and functional efficiency (Akbar 2020). Prior to the present study, fluted stem structures were also documented in *S. montana* and in several chamaephyte species, supporting the view that this trait may represent an adaptive growth form related to ecological or life-form strategies (Schweingruber et al. 2011).

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The leaf anatomical characteristics observed in the present study are generally consistent with those reported in previous investigations, particularly with respect to stomatal type, and isobilateral leaf patterns. The mesophyll is generally divided into palisade and spongy parenchyma. While some species have a dorsiventral leaf (bifacial leaf) structure, others have an isobilateral mesophyll organisation (Satıl et al. 2002, 2003, Satıl and Kaya 2007, Akçin and Karadeniz 2023). The main differences in the results were related to the number of parenchyma layers such as in *S. coerulea*. In certain species, the palisade parenchyma consists of two or more layers, contributing to increased photosynthetic efficiency. The vascular bundles in the leaf veins are often accompanied by sclerenchyma, especially in xerophytic species, whereas in others, they are surrounded by a parenchymatous sheath. The leaf structures, as considered by Satıl and Kaya (2007), provide reliable characteristics for diagnostic purposes due to their variable response to environmental conditions.

Trichomes are one of the most distinctive anatomical features of *Satureja*. These structures are very diverse and include both glandular and non-glandular types (Metcalfe and Chalk 1950, Fahn 2000, Jabeen et al. 2024, Bordbar et al. 2025). Glandular trichomes, such as the peltate and capitate types, play an important role in essential oil secretion and contribute to their aromatic properties, which is characteristic of the genus and related taxa (García-Rellán et al. 2015). Non-glandular trichomes serve as a protective barrier against herbivory and excessive water loss. Trichomes of the genus *Satureja* have been studied in detail by Satıl and Kaya (2007). Additionally, three species of *Satureja*, including the Turkish taxa *S. avromanica*, *S. hortensis*, and *S. macrantha*, were investigated via SEM by Bordbar et al. (2025). The results of the present study are generally consistent with theirs; however, while Bordbar et al. (2025) reported only peltate trichomes for *S. avromanica*, our cross-sectional analyses clearly reveal the presence of both glandular capitate and peltate trichomes. However, as Bordbar et al. (2025) did not provide corresponding micrographs, direct visual comparison is not possible.

Conclusion

The anatomical characterisation of the 17 *Satureja* species native to Türkiye provided some diagnostic features for clarifying the taxonomic complexities inherent to the genus, which are explicitly attributed to species' morphological similarities. The study confirmed that while the genus generally adheres to the classic Lamiaceae framework, variability across all organs provides reliable identification tools. Critical differentiating characteristics were found in the root structure, which exhibits distinct configurations regarding the central parenchymatous tissue or metaxylem cell occupancy, occurrence of fluted stem structures and stem morphology, where the presence or absence of sclerenchymatous tissue in vascular bundles serves as an important taxonomic marker distinguishing species. Furthermore, leaf structures provided reliable characteristics, including the variation in the mesophyll structure (isobilateral versus dorsiventral types), the leaf folding pattern, and the prominence of sclerenchyma in the midrib region of xerophytic taxa. Finally, the universal presence of both glandular (peltate and capitate) and non-glandular trichomes, with their variable densities and specific morphologies, provides systematic criteria, confirming that detailed anatomical and micromorphological analysis is indispensable for accurate species classification within the *Satureja* genus.

Acknowledgements
The authors dedicated this study to the memory of the late co-author Cahit Doğan.

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Author Contributions

MÖ: Conceived and designed the study, performed all stages of the experimental procedures, collected and analyzed the data, and drafted the manuscript. CD: Contributed to the laboratory experiments and anatomical sectioning. ADK: Supervised the project planning, monitored the study design, and critically revised the manuscript. GZ: Contributed to the anatomical laboratory work, sectioning, data interpretation, and writing of the manuscript.

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