



Comparative morpho-anatomical study of the native *Fritillaria* species from Romania and its taxonomic significance

Anca Sârbu^a, Alina Georgiana Cişlariu^{a,*}, Adrian Oprea^{b,c}, Culiţă Sîrbu^d,
Anca-Monica Paraschiv^e, Mioara Dumitraşcu^a

^a Faculty of Biology, Department of Botany and Microbiology, University of Bucharest, Bucharest, Romania

^b Faculty of Biology, „Alexandru Ioan Cuza” University of Iaşi, Iaşi, Romania

^c „Anastase Fătu” Botanic Garden, „Alexandru Ioan Cuza” University of Iaşi, Iaşi, Romania

^d “Ion Ionescu de la Brad” Iaşi University of Life Sciences, Iaşi, Romania

^e Botanical Garden „D. Brandza”, University of Bucharest, Bucharest, Romania

ARTICLE INFO

Edited by Teresa Terrazas

Keywords:

Liliaceae

Morphology

Anatomy

Diagnostic features

Taxonomic relevance

ABSTRACT

This study investigated the native *Fritillaria* species of Romania, *Fritillaria montana* Hoppe ex W.D.J. Koch (mesophilous), *Fritillaria meleagris* L. (meso-hygrophilous), and *Fritillaria meleagroides* Schult. & Schult. fil. (halo-hygrophilous). *Fritillaria montana* and *Fritillaria meleagris* are protected in Romania, whereas *Fritillaria meleagroides* is newly recorded in the national flora. Field identification of these taxa relied on morphological traits visible during the reproductive period.

The study examines the vegetative organs (roots, bulbs, stems, and leaves) to provide a detailed understanding of species morpho-anatomy and to aid taxonomic identification outside the flowering phase. Given their differing ecological requirements, particular focus was on structural variation related to soil moisture conditions. Morphological measurements were complemented by anatomical analyses of cross-sections and paradermal sections (leaf) examined under optical microscopy.

Morphological differences among taxa were minor, whereas anatomical analyses revealed distinct histological features in all vegetative organs. Key traits include the presence or absence of aeriferous cavities in the root cortex and bulb storage parenchyma; variation in aeriferous formations in the stem medullary parenchyma; dimensional variation in stem parenchyma; numerical and dimensional differences in conductive bundles; presence or absence of perifascicular sheaths in the lamina; and differences in lamina cross-section outline.

Anatomical traits linked to moisture preference, particularly the occurrence of aeriferous formations, proved most informative for distinguishing species outside the reproductive period. These features formed the basis of a dichotomous identification key, designed for use under optical microscopy. The key enables reliable identification of *Fritillaria* taxa during the vegetative stage or from vegetative fragments.

1. Introduction

The genus *Fritillaria* L. (Liliaceae) comprises 100–160 species distributed across the temperate regions of the Northern Hemisphere (Metin et al., 2013; Ronsted et al., 2005; Tomović et al., 2007; Turktas et al., 2012; Zahariadi, 1966). The most recent molecular phylogenetic classification recognizes eight subgenera (Ronsted et al., 2005). The largest, subgenus *Fritillaria*, is characterized by subglobose bulbs composed of two fleshy scales, partially tunicated by remnants of previous scales, and occurs from Western Europe and the Mediterranean

region to Eastern Asia (Peruzzi et al., 2008; Ronsted et al., 2005). This subgenus is further divided by style morphology into section *Fritillaria* (trifid style) and section *Olostylea* Boiss (undivided style) (Ronsted et al., 2005).

Fritillaria species are spring-flowering, bulbous perennials with fleshy, tunicate bulbs. Leaves are commonly opposite or whorled, and flowers are usually solitary, pendent, and campanulate, with six tepals bearing a basal nectarial pit, groove, or pouch. Anthers are generally pseudobasifixed, and seeds are flattened and winged (WFO, 2019).

Many *Fritillaria* species have economic and medicinal value. Several

* Corresponding author.

E-mail address: alina.cislariu@unibuc.ro (A.G. Cişlariu).

<https://doi.org/10.1016/j.flora.2025.152826>

Received 23 May 2025; Received in revised form 17 August 2025; Accepted 24 August 2025

Available online 26 August 2025

0367-2530/© 2025 The Author(s).

Published by Elsevier GmbH. This is an open access article under the CC BY license

(<http://creativecommons.org/licenses/by/4.0/>).

Table 1
Comparative overview of the ecological and distributional features of the three native *Fritillaria* species from Romania.

Characteristic	<i>Fritillaria montana</i>	<i>Fritillaria meleagris</i>	<i>Fritillaria meleagroides</i>
Geographic distribution	Southeastern Europe (Mancuso et al., 2012; Peruzzi et al., 2008; Zahariadi, 1966), Pontic-Mediterranean area (Oprea et al., 2015; Sârbu et al., 2013).	Central and Eastern Europe (Lozina-Lozinskaya, 1935; Rix, 1980; Sârbu et al., 2013; Zahariadi, 1966), Western Siberia, Altai (Vlasova, 1987).	Northwest China (Xinjiang), Central Asia (Altai, Kazakhstan, Western Siberia), Northwest Caucasus, Eastern Europe (Chen and Mordak, 2000; Korotchenko and Orlov, 2009; Yanev, 1964). Also in Ukraine (Korotchenko and Orlov, 2009; Lozina-Lozinskaya, 1935; Prokudin et al., 1987) and Bulgaria (Andreev, 1993; Assyov and Petrova, 2006; Ivanova, 2015; Oprea et al., 2015; Petrova and Vladimirov, 2009; Rix, 1980; Yanev, 1964).
Habitat type	Mesophilous habitats, shrubs and deciduous forests, forest steppe to beech forest belt (Sârbu et al., 2013; Zahariadi, 1966); plant communities: <i>Quercetalia pubescentis</i> Klika 1933, <i>Orno-Cotinetalia</i> Jakucs 1960 (Chifu et al., 2006; Sârbu et al., 2013), <i>Alnion incanae</i> Pawl. 1928, <i>Lathyro hallersteinii-Carpinion</i> (Soó 1964) Boşcaiu 1979 (Chifu et al., 2006; Oprea et al., 2015)	(Meso)-hygrophilous habitats, steppe zone, spruce forest belt, meadows, thickets, or open deciduous forests (Csörgő and Frink, 2003; Oprea, 2005; Sârbu et al., 2013; Zahariadi, 1966); plant communities: <i>Potentillion anserinae</i> R. Tx. 1947 (Sămărghișan and Oroian, 2011; Sârbu et al., 2013; Ularu and Parascan, 1970), <i>Molinion caeruleae</i> W. Koch 1926, <i>Calthion palustris</i> Tx. 1937, <i>Magnocaricion elatae</i> W. Koch 1926 (Csörgő and Frink, 2003), <i>Alnion incanae</i> Pawl. 1928 (Bujorean and Grigore, 1965; Maloș et al., 1967; Ularu and Parascan, 1970), <i>Salicion cinereae</i> Müller et Görs ex Passarge 1961 (Bujorean and Grigore, 1965; Oprea et al., 2015; Ularu and Parascan, 1970)	Wet, temporary inundated (Andreev, 1993; Chen and Mordak, 2000; Didukh, 2011; Golub and Saveljeva, 1991; Ivanova, 2015; Korotchenko and Orlov, 2009), often saline habitats (Artushenko, 1979; Golub, 1994; Golub and Saveljeva, 1991; Lozina-Lozinskaya, 1935; Prokudin et al., 1987); plant communities: <i>Asteretea tripolium</i> Westhoff et Beetink in Beetink 1962, <i>Molinio-Arrhenatheretea</i> R. Tx. 1937 em. Mirk. et Naumova 1986 (Golub and Saveljeva, 1991; Korotchenko and Orlov, 2009; Oprea et al., 2015), <i>Rorippo austriacae-Agropyretum repentis</i> (Timár 1947) R. Tx. 1950 (Sîrbu et al., 2019).
Flowering period	March-April	April	April-May
Fruiting period	June-July	June-July	May-July

taxa are cultivated as ornamentals, while bulbs rich in alkaloids, glycosides, saponins, steroids, and terpenoids (Du et al., 2016; Hao et al., 2013; Has et al., 2023; Qu et al., 2022) are widely used in traditional medicine for their expectorant, antitussive, and anti-inflammatory properties. They are prescribed for conditions such as tuberculosis, gout, malaria, anemia, cardiovascular disorders, and diseases of the respiratory and nervous systems (Rashid and Yazooob, 2021; Wang et al., 2021). In addition, some species display antitumor activity and have been employed in the treatment of leukemia and lung adenocarcinoma (Matsuo et al., 2013).

Habitat loss and over-collection of flowers and bulbs have raised conservation concerns for many *Fritillaria* species. As a result, numerous taxa are listed in national Red Lists, the Annexes of the EU Habitats Directive (Council of the European Communities, 1992), and the IUCN Red List (2025), which includes 22 *Fritillaria* species nominated for protection. Among these, *Fritillaria montana* is listed as Data Deficient (IUCN Red List of Threatened Species, 2025). Ecologically, *Fritillaria* species occupy habitats ranging from wet meadows and riparian woods to drier, rocky slopes and alpine zones (Tatarenko et al., 2022; Tomović et al., 2007; WFO, 2019).

In Romania, the genus is represented by three native, spring-flowering bulbous geophytes of conservation value: *Fritillaria montana* W. D. J. Koch (syn.: *F. degeniana* J. Wagner; *F. orientalis* auct. rom., non Adams; *F. tenella* auct., non M. Bieb.), *Fritillaria meleagris* L., and *Fritillaria meleagroides* Schult. & Schult. fil.

Fritillaria montana is a mesophilous species (Sârbu et al., 2013; Zahariadi, 1966), inhabiting meadows, open deciduous forests, shrublands, and rocky slopes. It has been reported from Romania since 1844, under various names (Simonkai, 1886), and was correctly referred to as *Fritillaria montana* for the first time by Zahariadi (1966). *Fritillaria meleagris* is (meso)-hygrophilous, occurring in wet meadows, shrublands, forest glades, and riparian woods (Csörgő and Frink, 2003; Oprea, 2005; Sârbu et al., 2013; Zahariadi, 1966). Documented in Romania since the early 19th century (Baumgarten, 1816), its populations have been heavily affected by over-collection and habitat disturbance (Csörgő and Frink, 2003; Pop and Sălăgeanu, 1965). These threats led to its designation as a “nature monument” and its protection under national law (Pop and Sălăgeanu, 1965; Zahariadi, 1966). *Fritillaria meleagroides*

is (halo)-hygrophilous and was recorded in Romania only recently. It occurs sporadically in seasonally flooded, slightly saline wet meadows (Oprea et al., 2015).

Both *Fritillaria meleagris* and *F. montana* are listed as Vulnerable or Rare in Romanian Red Lists (Oltean et al., 1994; Sârbu and Chifu, 2001). *Fritillaria meleagris* is considered rare and threatened across its entire range (Tatarenko et al., 2022), while *Fritillaria meleagroides* is classified as threatened throughout most of its natural habitat (Ivanova, 2015; Korotchenko and Orlov, 2009; Lozina-Lozinskaya, 1935; Petrova and Vladimirov, 2009; Yanev, 1964).

Field identification of these species is based on a limited set of morphological traits, such as leaf arrangement on the stem, perigon colour, aspect of the nectary foveolae, and capsule dimensions (Table 2). However, these features are very similar in *Fritillaria meleagris* and *Fritillaria meleagroides*, which can result in misidentification, especially outside the flowering period. In such cases, vegetative anatomical features provide a valuable complementary approach.

Recent studies have demonstrated the taxonomic value of anatomical traits for distinguishing *Fritillaria* species (Akyol et al., 2014; Kandemir et al., 2022; Kandemir et al., 2024; Koyuncu et al., 2017; Namazi et al., 2017; Novikoff and Kazemirska, 2012; Tatarenko et al., 2022; Tomović et al., 2007; Wang et al., 2009). In Romania, however, such research remains limited. Corneanu and Popescu (1981) described *Fritillaria montana* and *Fritillaria meleagris*, but their findings were not integrated into a taxonomic framework and require further elaboration. Moreover, no anatomical data are currently available for *Fritillaria meleagroides*.

To address these gaps, this research provides a comparative morpho-anatomical analysis of the three native *Fritillaria* species of Romania. The main aim is to identify structural traits with diagnostic value, particularly those linked to ecological adaptation, to improve species identification across developmental stages. The research is based on specimens collected from natural habitats, with morphological observations made in situ, and anatomical investigations carried out in the laboratory using preserved material and optical microscopy. The results provide new insights into morpho-anatomical differentiation and offer practical tools for taxonomic identification within the genus *Fritillaria* in Romania.

Table 2
Morphological features used for the identification of native *Fritillaria* species from Romania (based on Oprea et al., 2015; Sârbu et al., 2013).

<i>Fritillaria montana</i>	<i>Fritillaria meleagris</i>	<i>Fritillaria meleagroides</i>
Upper leaves opposite or whorled	All leaves alternate	All leaves alternate
External surface of the tepals dark purple – brown, to pale yellow; ±distinct spots (chessboard-like pattern)	Purple to pink (rarely white) tepals; clearly delimited spots	Tepals dark purple on the external face and green on the internal face; poorly defined spots
Nectary foveolae oblong-ovate; ~5 mm above tepal base	Linear nectary foveolae; 7–10 mm long; 8–12 mm above tepal base	Linear nectary foveolae; 12–18 mm long, 1–1.5 mm wide; 4–5 mm above tepal base
Capsule 16–30 mm long	Capsule 14–22 mm long	Capsule 15–35 mm long

2. Material and methods

2.1. Study species

This study examines the three native *Fritillaria* species of Romania: *Fritillaria montana*, *F. meleagris*, and *F. meleagroides*, which differ in ecological preferences and geographic distribution. Their main ecological, phenological, and distributional characteristics are summarized in Table 1, based on published literature.

The main diagnostic morphological traits currently used to identify the three native *Fritillaria* species of Romania, as compiled from published literature, are summarized in Table 2.

2.2. Biological material collection and analyses

Specimens were collected from natural populations located outside protected areas: (1) *Fritillaria meleagroides* (Fig. 1A–B) on April 10, 2018, from a wet meadow dominated by plant communities of the *Potentillo-Polygonetalia* R. Tx. 1947 order, North of Ștefănești, Botoșani county; (2) *Fritillaria montana* (Fig. 1C) on April 17, 2020, from Breazu Forest, North of Iași; (3) *Fritillaria meleagris* (Fig. 1D) on April 14, 2020, from a meadow Northwest of the Zamostea-Luncă forest, outside the Zamostea-Luncă Nature Reserve.

Biological material was examined in situ during anthesis and subsequently collected for laboratory analyses. Anthesis typically lasts from March to April in *Fritillaria montana*, April to May in *Fritillaria meleagroides*, and mainly in April in *Fritillaria meleagris* (Table 1). The species produce fruits by May to July (Table 1). Specimens were excavated from soil at depths of 15–20 cm (*Fritillaria meleagris*), 20–25 cm (*Fritillaria meleagroides*), and 25–30 cm (*Fritillaria montana*), using a digging tool.

Morpho-anatomical studies targeted the vegetative organs: roots, bulbs, stems, and leaves. Morphological observations were conducted in the field on 10 individuals per species, while anatomical analyses were performed in the laboratory on 5 individuals preserved in 70 % ethanol.

Field measurements included bulb size, stem length and internode number, leaf arrangement, and leaf number and size.

For anatomical investigations, transverse (cross-) and paradermal sections were prepared from the preserved material. Cross-sections were taken through the median region of roots, bulbs, above-ground stems, and leaf lamina, using manual sectioning technique (Tarnavski et al., 1981). Leaves were sampled from the middle of the above-ground stem. Epidermal structures (lamina) were examined on paradermal sections obtained by manual peeling.

Sections were processed for optical microscopy by clarification (5–7 min) with sodium hypochlorite (NaOCl), hydration with distilled water, and progressive staining with Carmine Alum (staining cellulose walls red and cytoplasm pink) followed by Iodine Green (staining lignified walls intense green and cell contents pale green) (Sârbu et al., 2014; Șerbănescu-Jitariu et al., 1983). Starch was detected using iodine in potassium iodide solution (I IK), which stains starch granules blue-violet; one drop of a diluted (30 %) I IK was applied to cross-sections that have not been previously treated with sodium hypochlorite (Sârbu et al., 2014).

Microscopic slides were examined under normal and polarized light using a DOCUVAL optical microscope and photographed with a NIKON D90 digital camera.

Microscopic measurements were performed in microns, with each value representing the mean of multiple measurements.

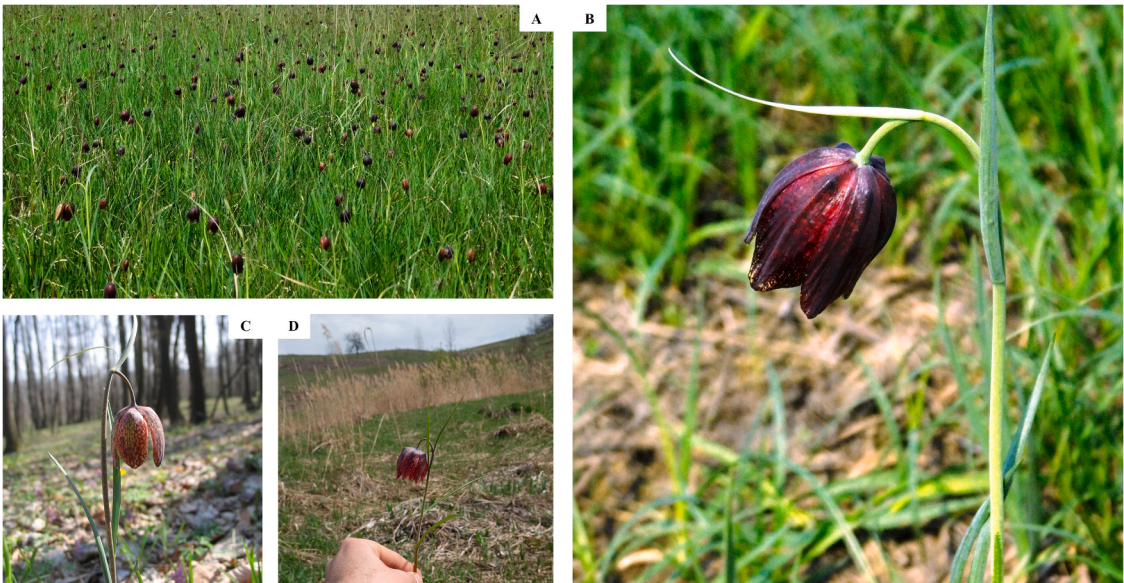


Fig. 1. Tepal coloration and pattern in the three native *Fritillaria* species from Romania. A, B) *Fritillaria meleagroides*, dark purple outer tepals with poorly defined spotting pattern. C) *Fritillaria montana*, pale-yellow outer tepals with indistinct defined spots). D) *Fritillaria meleagris*, purple to pink outer tepals with clearly delimited spots.

Table 3
Comparative morpho-anatomical traits of the analyzed *Fritillaria* species. Morphometric values represent average measurements.

Organ	Character	<i>Fritillaria montana</i>	<i>Fritillaria meleagris</i>	<i>Fritillaria meleagroides</i>
Root	Diameter (μm)	582.60	599.10	698.90
	Structure	Primary	Primary	Primary
	Rhizodermis	Single-layered	Single-layered	Single-layered
	Cortex	Compact	With air cavities	With air cavities
	Vascular cylinder (% of root diameter)	24.90	21.90	22.40
	Number of vascular bundles	6	6	6
	Central metaxylem vessel	Present	Present	Present
Bulb	Dimensions (mm)	8–12 × 11–15 (length x width)	7–8 × 10–15 (length x width)	10–12 (diameter)
	Structure (number of scales)	Two scales	Two scales	Two scales
	Epidermis	Single-layered	Single-layered	Single-layered
	Storage parenchyma	Compact	With air cavities	With air cavities
	Number of vascular bundles per scale	6–10	8–10	8–10
Above-ground stem	Length (cm)	20–40 (–80)	20–50	28–50
	Number of internodes	6–7	7–8	6–8
	Diameter (μm)	2114.60	2910.61	3200.30
	Hypodermal	121.05	145.43	156.70
	parenchyma thickness (μm)			
	Number of hypodermal cell layers	3–4 or fewer	3–4 or fewer	4–5 or more
	Sclerified parenchyma thickness (μm)	60.42	128.45	119.52
	Number of sclerified parenchyma cell layers	2–3	4–5	4–5
	Vascular cylinder diameter (μm)	1805.17	2596.05	2865.98
	Vascular cylinder (% of stem diameter)	85.38	89.20	89.53
	Number of vascular bundles	20	29	29
	Pith parenchyma particularities	Central air cavity	Air channels and tissue ruptures	Air channels and tissue ruptures
	Arrangement on stem	Upper leaves opposite or whorled	Alternate leaves	Alternate leaves
Leaf blade	Number of leaves per stem	6–7	6–7	5–7
	Dimensions (length x width, cm)	8–13 × 0.30–0.80	8–15 × 0.40–0.90	6–14 × 0.30–0.80
	Cross-sectional outline	Linear	Wide V-shaped	Semilunar
	Median rib thickness (μm)	724.73	342.78	394.50
	Rib bundle dimensions (length x width, μm)	166.20 × 173.00	155.10 × 165.20	150.15 × 142.85
	Number of vascular bundles	14	15	16
	Perifascicular sheaths	Present	Absent	Present
	Mesophyll structure	Homogeneous	Homogeneous	Homogeneous

3. Results

3.1. Root morpho-anatomical characteristics

In all three species, the roots are thin, nearly circular in cross-section, and display a primary structure (Table 3; Fig. 2). Three concentric histo-anatomical zones are present: rhizodermis, cortex, and vascular cylinder (stele).

The rhizodermis is unilayered and features absorbant hairs. The cortex is pluristratified, consisting of the exodermis, parenchymatous cortex, and endodermis. It is compact in *Fritillaria montana* (Fig. 2A), whereas in *Fritillaria meleagris* and *Fritillaria meleagroides* it contains large aeriferous cavities (Fig. 2B–C). The vascular cylinder occupies 21–25 % of the root cross-section (Table 3) and contains three xylem and three phloem bundles disposed alternately. In all three species, a central metaxylem vessel is present in the stele (Fig. 2A–C).

3.2. Bulb morpho-anatomical characteristics

The bulb varies in size and shape among the three species. In *Fritillaria meleagroides*, it is globular (10–12 mm in diameter), whereas in *Fritillaria montana* (8–12 mm length, 11–15 mm width) and *Fritillaria meleagris* (7–8 mm length, 10–25 mm width) it is broader than long. The bulb is typically composed of two fleshy scales, although in plants collected in April we observed four fleshy scales: two external scales, larger and withering remnants from the previous year, and two internal scales, smaller, firm, and white, formed during the current growing season.

Both external and internal scales are semilunar in cross-sections. The upper and lower epidermis are unilayered, composed of small cells covered by a cuticle. Between these lies a storage parenchyma fomed of living cells without chloroplasts, with thin, cellulosic walls, specialized

for starch accumulation. Each fleshy scale contains 6–8–10 collateral vascular bundles.

The storage parenchyma is compact in *Fritillaria montana* (Fig. 3A–B) but contains aeriferous cavities in *Fritillaria meleagris* and *Fritillaria meleagroides* (Fig. 3C–D).

3.3. Above-ground stem morpho-anatomical characteristics

Stem length ranges from 20–50 cm in *Fritillaria meleagris*, 20–40 (–80) cm in *Fritillaria montana*, and 28–50 cm in *Fritillaria meleagroides*. The number of internodes varies between 6 and 8, with internode lengths of 2–11 cm. *Fritillaria montana* has the thinnest stems, while *Fritillaria meleagroides* has the thickest (Table 3).

In cross-section, stems are circular in *Fritillaria montana* and *Fritillaria meleagroides*, and circular-elliptic in *Fritillaria meleagris* (Fig. 4A, D, G). All three species display a primary structure with three concentric histo-anatomical zones: epidermis, cortex, and vascular cylinder.

The epidermis is unilayered, composed of tangentially elongated cells covered by a cuticle, stomatiferous, and without trichomes. Tangential wall thickening is more pronounced in *Fritillaria meleagris* and *Fritillaria meleagroides* (Fig. 4B, E, H).

At the hypodermal level, the cortex is an assimilatory meatic parenchyma formed of 3–4 or fewer cell layers in *Fritillaria montana* and *Fritillaria meleagris*, and 4–5 or more layers in *Fritillaria meleagroides* (Table 3; Fig. 4B, E, H).

A pluristratified ring of sclerified, weakly meatic parenchyma surrounds the cortex. This ring is thin, formed of cells with uniformly thickened, partially lignified walls in *Fritillaria montana*, and about 50 % thicker and strongly lignified in *Fritillaria meleagris* and *F. meleagroides* (Table 3; Fig. 4B, E, H; Fig. 5).

The vascular cylinder is voluminous, occupying 85,38 % of the stem diameter in *Fritillaria montana*, and 89,20–89,53 % in the other two

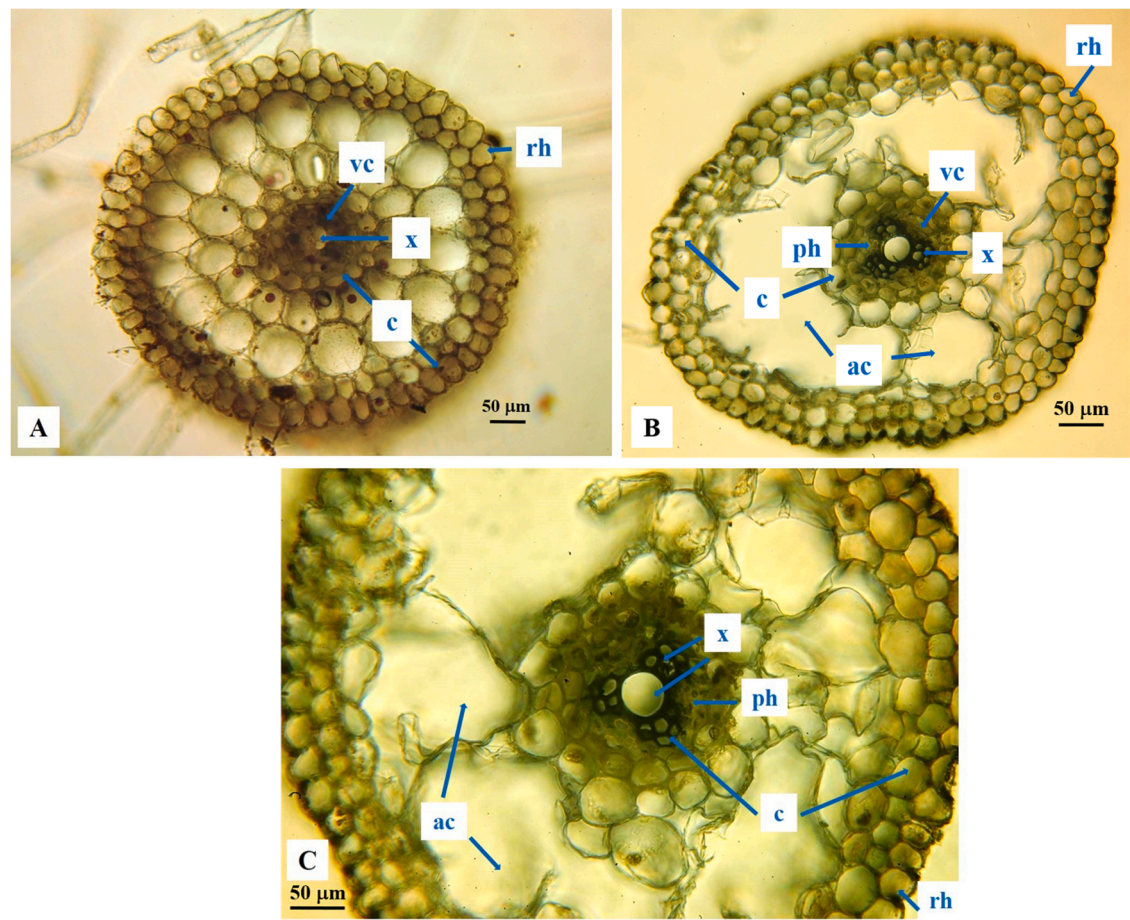


Fig. 2. Cross-sections of roots showing diagnostic anatomical features (stains: Carmine Alum, Iodine Green). **A)** compact cortex in mesophilous *Fritillaria montana*. **B)** cortex with aeriferous cavities in hygrophilous *Fritillaria meleagris*. **C)** cortex with aeriferous cavities in halo-hygrophilous *Fritillaria meleagroides*. ac: air cavity, c: cortex, ph: phloem, rh: rhizodermis, vc: vascular cylinder, x: xylem.

species (Table 3). It contains collateral vascular bundles of varying size, arranged more or less regularly in the medullary parenchyma and decreasing centrifugally. *Fritillaria meleagris* and *F. meleagroides* develop approximately 30 % more vascular bundles than *Fritillaria montana* (Table 3).

The medullary parenchyma is meatic, with aeriferous structures differing among taxa. *Fritillaria montana* has a single large central cavity, whereas *Fritillaria meleagris* and *Fritillaria meleagroides* have numerous aeriferous channels that often disorganize into irregular shaped cavities resembling ruptures (Fig. 4C, F, I). No mineral crystals were observed in any species.

3.4. Leaf morpho-anatomical characteristics

All three species have narrow, long, sessile leaves. On the above-ground stem, leaf length ranges from 8,0–15,0 cm and width from 0,4–0,9 cm, with only minor differences between species. However, the shape of the cross-section at the median area of the lamina differs consistently among taxa: linear in *Fritillaria montana*, broadly V-shaped with a prominent abaxial midrib in *Fritillaria meleagris*, and semilunar in *Fritillaria meleagroides* (Fig. 6A, C, E).

The leaf lamina is bifacial, amphistomatic, and has a homogeneous mesophyll in all three species. In paradermal sections, epidermal cells are elongated and narrow, and stomata are anomocytic. In cross-section, epidermal cells are heterodiametric in *Fritillaria montana* and *Fritillaria meleagris*, and isodiametric in *Fritillaria meleagroides* (Fig. 6B, D, F).

The mesophyll is homogeneous, meatic, and composed of rounded assimilatory cells (Fig. 6B, D, F). Vascular tissue is organized into

collateral vascular bundles of various sizes, associated with the rib structure. The number of vascular bundles shows slight variation among species (Table 3). In *Fritillaria montana* and *Fritillaria meleagroides*, the vascular bundles have prominent perivascular parenchymatous sheaths composed of large cells (Fig. 6B, F).

The three *Fritillaria* species differ in several morpho-anatomical features of their vegetative organs. The most distinctive, easily visible under optical microscopy (Table 4), were used to develop a practical identification key.

3.6. Dichotomous key for the identification of the analyzed *Fritillaria* species based on anatomical characteristics

- 1a Root cortex compact; storage parenchyma of the bulb compact; sclerified parenchyma of the above-ground stems composed of 2–3 cell layers; medullary parenchyma of the above-ground stems with a central aeriferous cavity; linear-shaped lamina in cross-section.....
F. montana
- 1b Root cortex with aeriferous cavities; storage parenchyma of the bulb with aeriferous cavities; sclerified parenchyma of the above-ground stems composed of 4–5 cell layers; medullary parenchyma of the above-ground stems with aeriferous channels and ruptures; various shapes of the lamina in cross-section.....
.....2

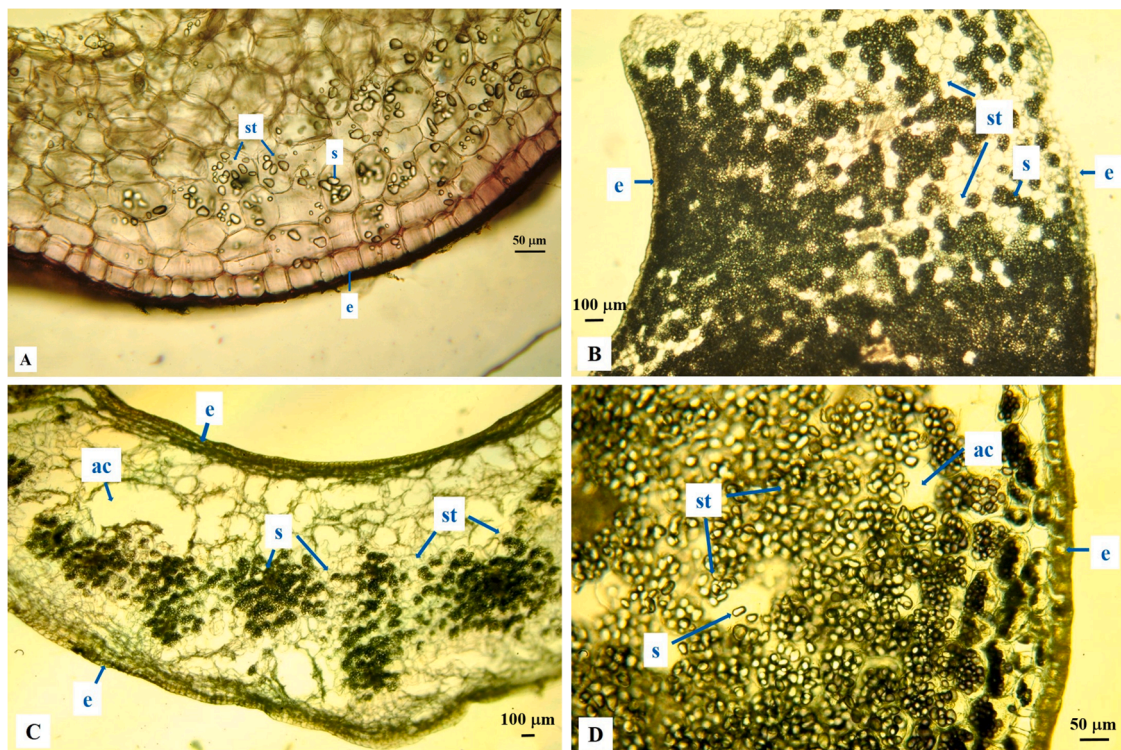


Fig. 3. Cross-sections of bulbs showing diagnostic anatomical features (stains: Carmine Alum, Iodine Green, IIK). A–B) compact storage parenchyma in the external (A) and internal (B) scales of mesophilous *Fritillaria montana*. C–D) storage parenchyma with aeriferous cavities in the external (C) and internal (D) scales of halohygrophilous *Fritillaria meleagroides*. ac: air cavity, e: epidermis, s: starch, st: storage tissue.

- 2a Broadly V-shaped lamina in cross-section*F. meleagris*
 2b Semilunar-shaped lamina in cross-section; conspicuous per fascicular sheaths in the lamina.....*F. meleagroides*

4. Discussion

The findings of this research provide new insights into the morpho-anatomical features of the vegetative body of Romania's native *Fritillaria* species. Morphological examination of the three taxa largely confirmed previously documented traits, without revealing additional diagnostic features. In contrast, anatomical analyses extended the existing structural data for *Fritillaria montana* and *Fritillaria meleagris*, provided the first detailed description of the vegetative organs of *Fritillaria meleagroides*, and identified characters enabling reliable identification outside the flowering period.

Several structural similarities were observed among the three *Fritillaria* species, including the overall histo-anatomical organization of vegetative organs, stele structure, vascular bundle type, epidermal cells with undulated walls, anomocytic stomata, and a homogeneous mesophyll in the lamina. The same features are well documented in *Fritillaria* species (Kandemir et al., 2022; Kandemir et al., 2024; Koyuncu et al., 2017; Namazi et al., 2017; Rudall et al., 2017; Sărbu, 1999; Strasburger et al., 1983; Toma and Rugină, 1998; Wang et al., 2009; Zarinkamar, 2006) and have also been reported in other Liliaceae species (Grințescu, 1985). Our observations are consistent with comparative micro-anatomical studies of *Fritillaria* taxa from China (Wang et al., 2009), Iran (Namazi et al., 2017), and the Mediterranean region (Kandemir et al., 2022), where similar traits occur alongside species-specific variations of taxonomic significance.

Structural variations in the vegetative organs are widely recognized as valuable diagnostic characters and form the basis for constructing determination keys (Francino et al., 2015; Priya and Hari, 2021;

Suwanphakdee et al., 2024). In *Fritillaria*, previous studies have shown that the anatomical features of stems, leaves, and roots are particularly informative for taxonomic identification (Akyol et al., 2014; Kandemir et al., 2024; Koyuncu et al., 2017; Namazi et al., 2017). The distinctive anatomical differences identified in our study, and their direct taxonomic value, are discussed in the following section.

4.1. Taxonomical implication

The three native *Fritillaria* species differ in several anatomical traits of the root, bulb, stem, and leaf that hold taxonomic value. These characters allow reliable distinction between taxa beyond the flowering period and complement existing morphological criteria.

The structure of the root cortex provides a consistent diagnostic feature: *Fritillaria montana* exhibits a compact parenchymatous cortex, whereas *Fritillaria meleagris* and *Fritillaria meleagroides* develop large aeriferous spaces. Similar patterns have been documented in other *Fritillaria* taxa, for instance, Namazi et al. (2017) reported large aeriferous spaces in *Fritillaria reuteri* Boiss, while Koyuncu et al. (2017) reported a compact parenchymatous cortex in *Fritillaria serpenticola* (Rix) Teksen & Aytac. These data reinforces the diagnostic value of cortex structure of the root for separating hygrophilous from mesophilous taxa.

In the bulb storage parenchyma, *Fritillaria montana* shows compact tissue, while *Fritillaria meleagris* and *Fritillaria meleagroides* have aeriferous cavities. Although comparable bulb anatomy has not been widely addressed in the literature, our findings suggest that storage parenchyma aeration may represent a useful, yet underexplored, taxonomic character in identifying *Fritillaria* species.

Stem anatomy provides multiple taxonomically informative features. The hypodermal assimilatory parenchyma and sclerified pericyclic parenchyma differ among species in both thickness and number of cell layers, traits recognized as taxonomically significant in *Fritillaria* species (Kandemir et al., 2022; Kandemir et al., 2024; Namazi et al., 2017). Variation in sclerified parenchyma have also been reported in *Fritillaria*

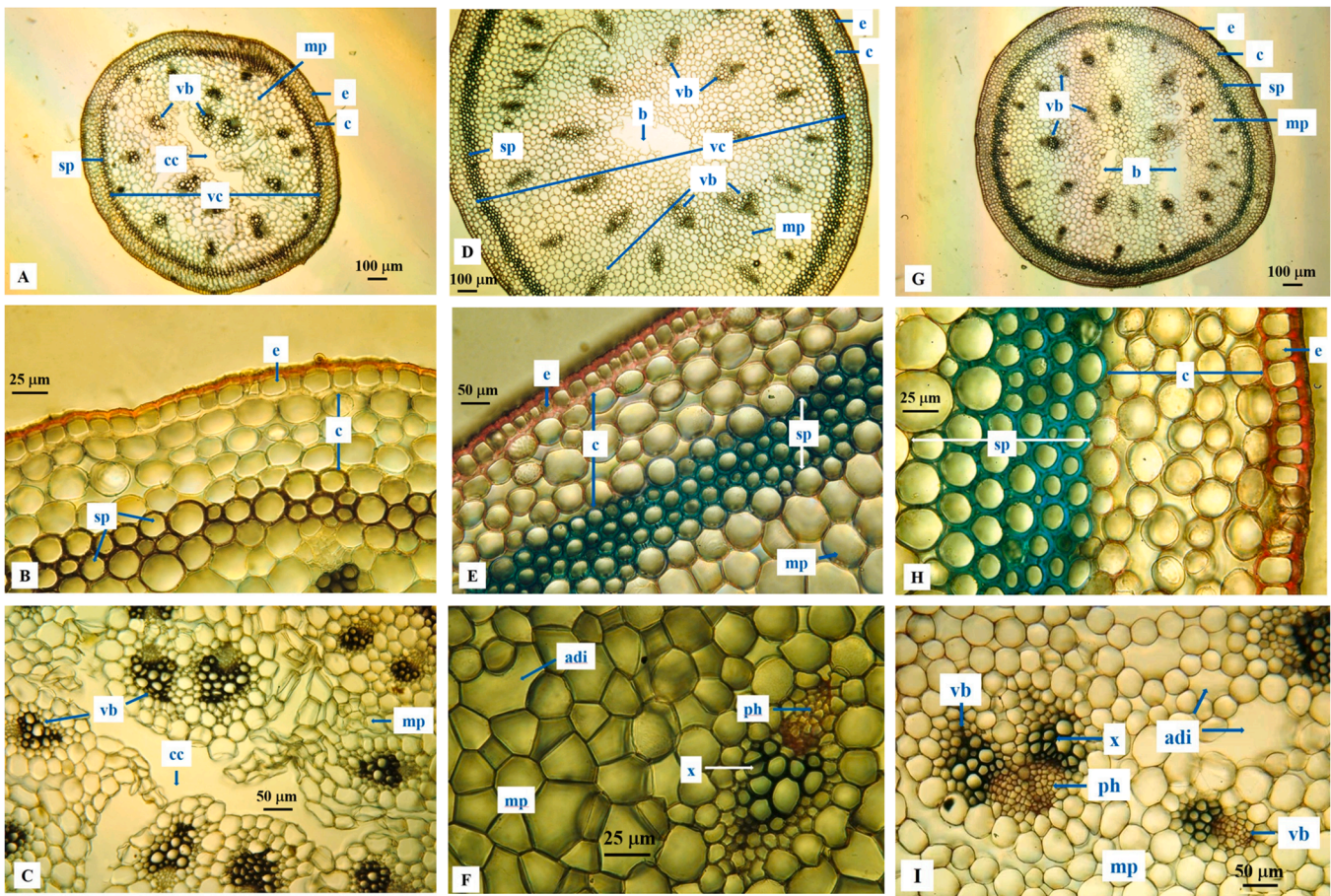


Fig. 4. Cross-sections of stems showing diagnostic anatomical features (stains: Carmine Alum, Iodine Green). **A–C** *Fritillaria montana*: circular cross-sectional outline with a central air cavity (A); 3–4 layers of cortex assimilatory parenchyma and 2–3 layers of sclerified parenchyma (B); large central air cavity in medullary parenchyma (C). **D–F** *Fritillaria meleagris*: circular-elliptic outline with ruptures in pith parenchyma (D); 3–4 layers of sclerified and lignified parenchyma (E); air channels in pith parenchyma (F). **G–I** *Fritillaria meleagroides*: circular cross-section with ruptures in pith parenchyma (G); 4–5 layers of cortex assimilatory parenchyma and 4–5 layers of sclerified and lignified parenchyma (H); pith parenchyma with air channels (I). adi: air channel, b: rupture, c: cortex, cc: central cavity, e: epidermis, mp: medullary parenchyma, ph: phloem, sp: sclerified parenchyma, vb: vascular bundle, vc: vascular cylinder, x: xylem.

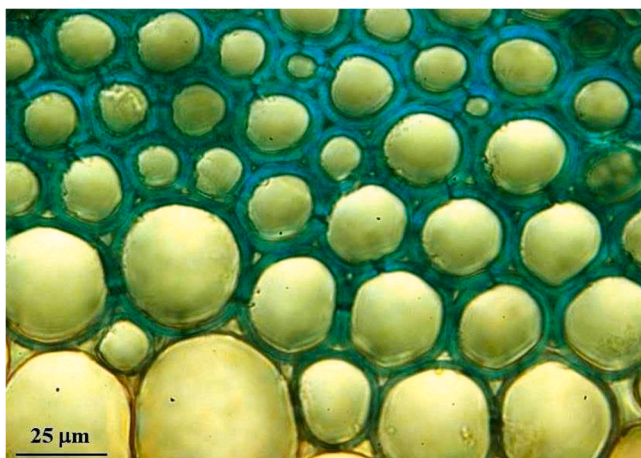


Fig. 5. *Fritillaria meleagroides*, cross-section of stem (stains: Carmine Alum, Iodine Green) showing the sclerified and strongly lignified parenchyma.

gencensis Yıld., Kılıç & Demirp. (4–11 cell layers) (Kiliç and Dermipolat, 2022), *Fritillaria persica* L. (5–6 cell layers) (Has et al., 2023), and *Fritillaria caucasica* J.F. Adam, which possesses a collenchyma ring instead (Akyol et al., 2014). Differences in sclerenchyma and assimilatory

parenchyma thickness were also noted by Corneanu and Popescu (1981) for *Fritillaria montana* and *Fritillaria meleagris* in Romania, though not previously interpreted taxonomically. The medullary parenchyma further distinguishes the species: a single large aeriferous cavity in *Fritillaria montana* versus multiple aeriferous channels and ruptures in *Fritillaria meleagris* and *Fritillaria meleagroides*. The presence of histological ruptures in the stem was first reported as a distinguishing character by Namazi et al. (2017) in studies on *Fritillaria* species from Iran.

The shape of the lamina in cross-section (linear in *Fritillaria montana*, broadly V-shaped in *Fritillaria meleagris*, semilunar in *Fritillaria meleagroides*) provides an additional, stable character. While no comparative lamina-shape data has been identified for direct reference, its constancy within species and divergence among them indicate strong potential as a taxonomic trait.

Taken together, these anatomical traits including root cortex type, bulb parenchyma aeration, stem parenchyma thickness and lignification, and lamina cross-sectional outline, are easily observable under optical microscopy and remain consistent across individuals. Their integration into a dichotomous key, as in this study, follows established approaches in *Fritillaria* taxonomy (Kandemir et al., 2024; Namazi et al., 2017).

4.2. Ecological adaptation

The anatomical variations observed among the three taxa are

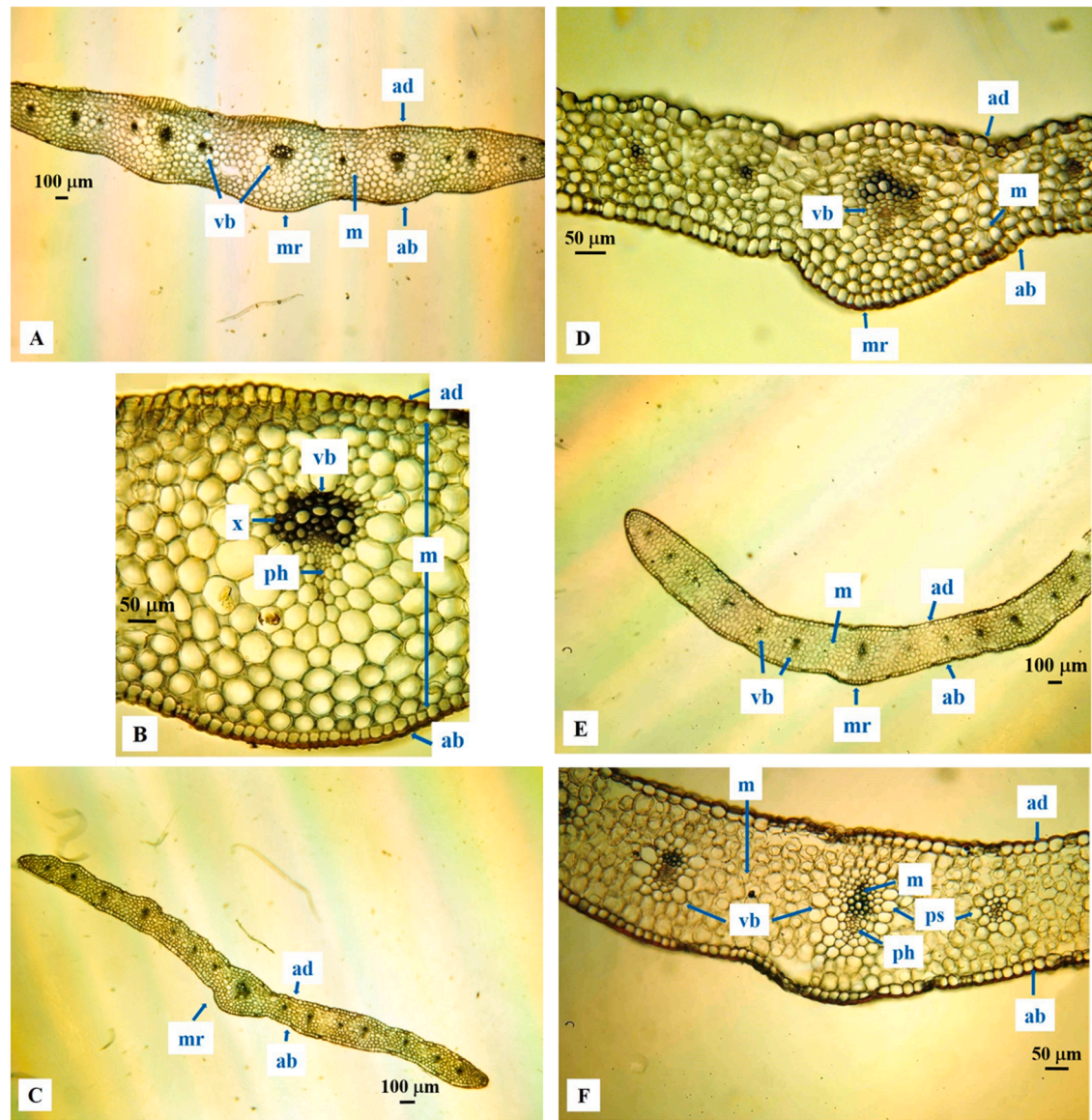


Fig. 6. Cross-sections of leaves showing diagnostic anatomical features (stains: Carmine Alum, Iodine Green). **A–B)** *Fritillaria montana*: linear cross-sectional outline (A); homogeneous meatic mesophyll with prominent perivascular parenchymatous sheaths (B); **C–D)** *Fritillaria meleagris*: broadly V-shaped cross-section (C); homogeneous meatic mesophyll (D); **E–F)** *Fritillaria meleagroides*: semilunar cross-section (E); homogeneous meatic mesophyll with prominent perivascular parenchymatous sheaths (F). ab: abaxial face, ad: adaxial face, m: mesophyll, mr: median rib, ph: phloem, ps: perifascicular assimilatory sheath, vb: vascular bundle, x: xylem.

Table 4
Anatomical features that distinguish the studied *Fritillaria* species.

Organ	Character		<i>Fritillaria montana</i>	<i>Fritillaria meleagris</i>	<i>Fritillaria meleagroides</i>
Root	Cortex	Compact	✓		
		Air cavities		✓	✓
Bulb	Storage parenchyma	Compact	✓		
		Air cavities		✓	✓
Above-ground stem	Hypodermal parenchyma	3–4 cell layers or fewer	✓	✓	
		4–5 cell layers or more			✓
	Sclerified parenchyma	2–3 cell layers	✓		
		4–5 cell layers		✓	✓
Leaf blade	Pith parenchyma	Air channels and tissue ruptures		✓	✓
		Central air cavity	✓		
	Outline in cross section	Linear	✓		
		Wide V-shaped		✓	
		Semilunar			✓
	Fascicular sheaths		✓		✓

primarily associated with adaptations to differences in water availability and related edaphic conditions. Although published studies on ecological adaptations rarely address the genus *Fritillaria* directly, many traits recorded here align with structural features documented in other species occupying similar habitats. In *Fritillaria meleagris* and *Fritillaria meleagroides*, the presence of large aeriferous cavities in the root cortex and bulb storage parenchyma represents a well-documented adaptation to periodically waterlogged soils, facilitating oxygen transport to submerged organs in hygrophilous habitats, including those subject to mild salinity (Colmer and Flowers, 2008; Voesenek and Bailey-Serres, 2015). By contrast, *Fritillaria montana* exhibits compact tissues in these organs, corresponding typically to its growth in well-aerated mesic soils, where specialized internal ventilation is unnecessary. This ecological pattern is consistent with research on dryland monocots, in which aerenchyma is generally absent under well-drained conditions but is induced when soil aeration becomes restricted (McDonald et al., 2001; McPherson, 1939; Trought and Drew, 1980).

The thicker meatic hypodermis recorded in the stem cortex of *F. meleagroides* is consistent with patterns reported for halophytes, in which hypodermal thickness increases under saline conditions and may serve as a defensive adaptation (Parida et al., 2016). Given that *F. meleagroides* occupies periodically inundated meadows with slight soil salinity, a similar functional role can be inferred.

The more strongly lignified pericyclic ring from the stem, observed in the hygrophilous *Fritillaria meleagris* and halo-hygrophilous *Fritillaria meleagroides*, may contribute to increased resistance to lodging in saturated substrates. In monocots, greater lignification of stem tissues has been shown to enhance mechanical strength and lodging resistance (Liu et al., 2019; Sun et al., 2018; Yoon et al., 2015; Zhang et al., 2016), suggesting a similar functional role is plausible here. In *Fritillaria montana*, the reduced sclerenchyma investment is likely sufficient for mechanical support in firmer, mesic soils.

Prominent perivascular parenchymatous sheaths in the lamina were recorded for *Fritillaria meleagroides* and *Fritillaria montana*. As shown in studies on various vascular plants, such tissues are considered to function as control centers for water transport, regulating the passage of water, minerals, and metabolites between xylem and mesophyll, being also implicated in modulating hydraulic flux (Barbosa et al., 2019; Sack and Holbrook, 2006; Wigoda et al., 2014). Given their occurrence in both mesophilous and halo-hygrophilous taxa, we infer that their ecological role may be context-dependent rather than directly tracking water availability, potentially reflecting different functional advantages in each habitat type.

Overall, these adaptive strategies, particularly the development of aerenchymatous formations in hygrophilous and halo-hygrophilous species, are of diagnostic value, supporting taxon identification throughout the vegetative period.

5. Conclusion

This study provides a comparative anatomical assessment of the vegetative organs in the native *Fritillaria* species from Romania, including a recently documented taxon. The research identified a set of anatomical features with taxonomic value, enabling reliable species identification throughout the vegetative period.

Diagnostic differences were observed in root, bulb, and stem parenchyma structure, mesophyll organization, and lamina cross-sectional outline. Several of these features, particularly the presence and type of aeriferous formations, also reflect ecological adaptations of species to different habitat conditions.

The distinguishing anatomical features identified were integrated into a dichotomous identification key, easily applicable using optical microscopy and practical for species identification outside their reproductive phase.

The results of this study reinforce the value of anatomical characters of vegetative organs in *Fritillaria* taxonomy and emphasize the relevance

of structural traits shaped by ecological adaptation for both systematic and ecological studies.

CRediT authorship contribution statement

Anca Sârbu: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Alina Georgiana Cişlariu:** Writing – review & editing, Validation, Methodology, Formal analysis. **Adrian Oprea:** Validation, Resources, Investigation, Conceptualization. **Culiţă Sîrbu:** Validation, Resources, Investigation, Conceptualization. **Anca-Monica Paraschiv:** Writing – original draft, Resources, Formal analysis. **Mioara Dumitraşcu:** Writing – original draft, Visualization, Investigation, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

References

- Akyol, Y., Yetişen, K., Özdemir, C., 2014. The morphological and anatomical studies on *Fritillaria caucasica* J. F. Adam (Liliaceae). SDU. J. Sci. (E-J.) 9 (1), 12–19.
- Andreev, N., 1993. Materiali i kritichni bilezhki za florata na Bulgariya. Hist. Nat. Bulg. 4, 29–38.
- Artushenko, Z.T., 1979. *Fritillaria* L. (Red.). In: Fedorov, A. (Ed.), Flora Partis Europae URSS, Flora Partis Europae URSS, 4. Leningrad: Nauka, pp. 236–237.
- Assyov, B., Petrova, A., 2006. Konspekt Na Visshata Flora Na Bulgariya, 3 rd ed. Bulgarian Biodiversity Foundation, Sofia.
- Barbosa, M.A.M., Chitwood, D.H., Azevedo, A.A., Araújo, W.L., Ribeiro, D.M., Peres, L.E. P., Martins, S.C.V., Zsögön, A., 2019. Bundle sheath extensions affect leaf structural and physiological plasticity in response to irradiance. Plant. Cell. Env. 42 (5), 1575–1589.
- Baumgarten, J.C.H.G., 1816. Enumeratio stirpium magno-transilvaniae principatus præprimis indigenarum in usum nostratum botanophilorum conscripta, inque ordinem sexuali-naturalem concinnata. Vindobonae: Libr. Camesina 1 (XXVII), 427.
- Bujorean, G., Grigore, S., 1965. *Fritillaria meleagris* L. şi ocrotirea ei. Ocr. Nat 9 (1), 61–68.
- Chen, X., Mordak, H.V., 2000. *Fritillaria* L. In: Wu, Z.Y., Raven, P.H. (Eds.), Flora of China, Science Press, Flora of China, Science Press, 24. Beijing & Missouri Botanical Garden Press, St. Louis, pp. 127–133.
- Chifu, T., Mânzu, C.C., Zamfirescu, O., 2006. Flora & Vegetația Moldovei (România). II. Vegetația. Iași: Edit. Univ. "Alexandru Ioan Cuza" Iași, p. 398.
- Colmer, T.D., Flowers, T.J., 2008. Flooding tolerance in halophytes. New. Phytol 179 (4), 964–974.
- Corneanu, G.C., Popescu, G.G., 1981. Distributional and anatomical studies on *Fritillaria* (Liliaceae) in Romania. Wildenowia 11, 307–315.
- Council of the European Communities, 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and wild fauna and flora. Off. J. Eur. Communities 7–50. L206.
- Csergő, A.M., Frink, J.P., 2003. Some phytocoenological and population structure features of *Fritillaria meleagris* L. in the upper Şard Valley (Cluj County, Romania). Contrib. Bot 38 (2), 163–172.
- Didukh, Y.P., 2011. The Ecological Scales For the Species of Ukrainian flora and Their Use in Synphytoindication. Phytosociocentre, Kyiv.
- Du, Q., Wang, D., Wang, S., 2016. The pharmaceutical research of *Bulbus Fritillariae*. Res. Rev.: J. Pharmacogn. Phytochem. 4 (1), 6–18.
- Francino, D.M.T., Coutinho, I.A.C., Dalvi, V.C., Azevedo, A.A., Conceição, A.D.E. S., Meira, R.M.S.A., 2015. Anatomical interpretations of the taxonomy of *Chamaecrista* (L.) Moench sect. *Absus* (Leguminosae-Caesalpinioideae). Plant. Syst. Evol 301, 2087–2103.
- Golub, V.B., 1994. Class Asteretea tripolium on the territory of the former USSR and Mongolia. Folia. Geobot. Phytotax 29, 15–54.
- Golub, V.B., Saveljeva, L.F., 1991. Vegetation of the lower Volga limans (basins without outflow). Folia. Geobot. Phytotax 26, 403–430.
- Grinţescu, I., 1985. Botanică. Edit. Ştiinţifică şi Enciclopedică, Bucureşti, p. 477.
- Hao, D., Gu, X., Xiao, P., Peng, Y., 2013. Phytochemical and biological research of *Fritillaria* medicinal resources. Chin. J. Nat. Med 11 (4), 0330–0344.
- Has, M., Küçük, S., Kurkuoğlu, M., Kürşat, M., 2023. Investigation on morpho-anatomical and volatile compounds of cultivated *Fritillaria persica* L. (Liliaceae). Eskişehir Technical Univ. J. Sci. Tech. C-Life. Sci. Biotech 12 (1), 1–7.

- IUCN, 2025. The IUCN Red List of threatened species. <https://www.iucnredlist.org/search?query=fritillaria&searchType=species> accessed 8 July 2025.
- Kandemir, N., Çelik, A., Ullah, F., 2022. Comparative micro-anatomical features of endemic *Fritillaria* taxa growing in the Mediterranean region (Turkey). *Flora* 290. <https://doi.org/10.1016/j.flora.2022.152049>.
- Ivanova, D., 2015. *Fritillaria meleagroides* Schult. & Schult. F. Pp. 242. In: Peev, D., et al. (Eds.), Red Data Book of the Republic of Bulgaria, Vol. 1. Plants and Fungi. BAS & MoEW, Sofia, p. 881.
- Kandemir, N., Çelik, A., Shah, N., Albasher, G., Iqbal, M., 2024. Taxonomic relevance of stem and leaf anatomy in 10 endemic species from the Mediterranean Region. *Flora* 310. <https://doi.org/10.1016/j.flora.2023.152444>.
- Kiliç, Y., Dermipolat, A., 2022. Anatomical and palynological characters of endemic *Fritillaria gencensis*. *Türk. Tarin. Ve. Doğa. Bilim. Derg.* 9 (3), 734–740.
- Korotchenko, I.A., Orlov, A.A., 2009. *Fritillaria meleagroides* Patr. ex schult. *Et schult. F.* In: Didukh, Y.P. (Ed.), *Tservona Kniga Ukraini. Roslinii svit.* 3rd ed. Globalconsalting, Kyiv, p. 912.
- Koyuncu, O., Olgun, M., Özgüşi, K., Öztürk, D., Yaylacı, Ö.K., Gökçen, Ü., Sezer, O., Erkara, I.P., 2017. Some anatomical studies on rare endemic *Fritillaria serpenticola* from Turkey and reassessment the conservation status of it. *OT. Sist. Bot. Derg.* 24 (2), 103–116.
- Liu, W., Hussain, S., Liu, T., Zou, J., Ren, M., Zhou, T., et al., 2019. Shade stress decreases stem strength of soybean through restraining lignin biosynthesis. *J. Integr. Agric* 18, 43–53.
- Lozina-Lozinskaya, A.S., 1935. *Fritillaria* L. In: Komarov, V.L. (Ed.), *Flora CCCR, Flora CCCR*, 4. Izd. Nauka, Leningrad, pp. 302–320.
- Maloş, C., Cristea, A., Maloş, A., 1967. Pădurea cu lalele peștrițe (*Fritillaria meleagris* L.) de la Botorogi. *Ocr. Nat* 11 (1), 85–89.
- Mancuso, E., Bedini, G., Peruzzi, L., 2012. Morphology, germination, and storage behaviour in seeds of Tuscan populations of *Fritillaria montana* (Liliaceae), a rare perennial geophyte in Italy. *Turk. J. Bot* 36, 161–166.
- Matsuo, Y., Shinoda, D., Nakamaru, A., Mimaki, Y., 2013. Steroidal glycosides from the bulbs of *Fritillaria meleagris* and their cytotoxic activities. *Steroids* 78, 670–682.
- McDonald, M.P., Galwey, N.W., Colmer, T.D., 2001. Waterlogging tolerance in the tribe Triticeae: the adventitious roots of *Criterson maritimum* have a relatively high porosity and a barrier to radial oxygen loss. *Plant. Cell. Env.* 24, 585–596.
- McPherson, D.C., 1939. Cortical air spaces in the roots of *Zea mays* L. *New. Phytol* 38, 190–202.
- Metin, O.K., Turktas, M., Aslay, M., Kaya, E., 2013. Evaluation of the genetic relationship between *Fritillaria* species from Turkey's flora using fluorescent-based AFLP. *Turk. J. Biol* 37, 273–279.
- Namazi, F., Sharifi-Tehrani, M., Shaleani, L., 2017. Anatomical study on *Fritillaria* species in Iran. *Bangladesh. J. Bot* 46 (1), 93–101.
- Novikoff, A.V., Kazemirskaya, M., 2012. Vascular anatomy and morphology of the flower in *Fritillaria montana* Hoppe (Liliaceae). *Mod. Phytomorphology* 1, 27–35.
- Oltean, M., Negrean, G., Popescu, A., Roman, N., Dihoru, G., Sanda, V., Mihăilescu, S., 1994. Lista roșie a plantelor superioare din România. *Stud., Doc., Ecol., Acad., Română* 1, 1–52.
- Oprea, A., 2005. Lista critică a plantelor vasculare din România. Iași: edit. Univ. "Alexandru. Ioan. Cuza 668.
- Oprea, A., Sirbu, C., Peregrym, M., 2015. *Fritillaria meleagroides* in Romania. *Acta. Horti. Bot., Bucurest* 42, 41–55.
- Parida, A.K., Veerabathini, S.K., Kumari, A., Agarwal, P.K., 2016. Physiological, anatomical and metabolic implications of salt tolerance in the halophyte *Salvadora persica* under hydroponic culture condition. *Front. Plant. Sci* 7, 351.
- Peruzzi, L., Mancuso, E., Ansaldi, M., De Angeli, E., Trombetti, G., 2008. Distribuzione, caratterizzazione e consistenza delle popolazioni toscane di *Fritillaria montana* Hoppe (Liliaceae). *Webbia* 63 (2), 309–315.
- Petrova, A., Vladimirov, V., 2009. Red list of Bulgarian vascular plants. *Phytol. Balc.* 15 (1), 63–94.
- Pop, E., Sălăgeanu, N., 1965. Monumente ale naturii din România. București: edit. Meridiane 179.
- Priya, C., Hari, N., 2021. A review on anatomical methods in plant systematics. *Plant. Arch.* 21 (1), 1417–1424.
- Prokudin, I.N., Dobrochaeva, D.N., Zaverukha, B.V., Chopik, V.I., Protopyova, V.V., Criskaia, L.I., 1987. *Opredelitel' Vyshikh Rastenii Ukrainy. Naukova Dumka, Kiev.*
- Qu, A., Wu, Q., Su, J., Li, C., Yang, L., Wang, Z., Wang, Z., Li, Z., Ruan, X., Zhao, Y., Wang, Q., 2022. A review on the composition and biosynthesis of alkaloids and on the taxonomy, domestication, and cultivation of medicinal *Fritillaria* species. *Agronomy* 12, 1844.
- Rashid, I., Yaqoob, U., 2021. Traditional uses, phytochemistry and pharmacology of genus *Fritillaria* – a review. *Bull. Natl. Res. Cent.* 45, 124.
- Rix, E.M., 1980. *Fritillaria* L. In: Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A. (Eds.), *Flora Europaea*, *Flora Europaea*, 5. Cambridge University Press, Cambridge, pp. 31–34.
- Ronsted, N., Law, S., Thornton, H., Fay, M.F., Chase, M.W., 2005. Molecular phylogenetic evidence for the monophyly of *Fritillaria* and *Lilium* (Liliaceae; Liliales) and the infrageneric classification of *Fritillaria*. *Molec., Phylogen., Evol* 35, 509–527.
- Rudall, P.J., Chen, E.D., Culler, E., 2017. Evolution and development of monocot stomata. *Am. J. Bot* 104 (8), 1122–1141.
- Sack, L., Holbrook, N.M., 2006. Leaf hydraulics. *Annu. Rev. Plant. Biol* 57, 361–381.
- Sămărghitan, M., Oroian, S., 2011. Meadows with *Fritillaria meleagris* L. at Lunca Mureșului - Aluniș, Mureș county. *Argesis. Stud., Com., Ser., Ști., Nat* 19, 31–47.
- Sărbu, A., 1999. *Biologie vegetală*. Edit. Univ. din București, București, p. 384.
- Sărbu, A., Smarandache, D., Pascale, G., 2014. Aspecte de citologie și histologie vegetală. București, edit. Ceres 263.
- Sărbu, I., Chifu, T., 2001. Lista roșie a plantelor vasculare din Moldova. *Mem. Sect., Ști., Acad., Română.* 4 24, 131–151.
- Sărbu, I., Ștefan, N., Oprea, A., 2013. Plante vasculare din România. Determinator ilustrat de teren. Victor B Victor Publishing House, București, p. 1320.
- Șerbănescu-Jitariu, G., Andrei, M., Rădulescu-Mitroiu, N., Petria, E., 1983. *Practicum de biologie vegetală*. București, Edit. Ceres.
- Simonkai, L., 1886. Erdélyi Edényes Flórájának Helyesbített Foglaltat (Enumeratio Florae Transsilvaniae vescuosae Critica). *Kiadja A Kir. Magyar Természettudományi Társulat, Budapest*, p. 678.
- Sirbu, C., Oprea, A., Peregrym, M., 2019. New data about *Fritillaria meleagroides* in Romania. *J. Plant., Dev.* 26, 123–135.
- Strasburger, F.W., Nall, F., Schenck, H., Schimper, A., 1983. *Lerbuch Der Botanik*. VEB Gustav Fischer Verlag, Jena.
- Sun, Q., Liu, X., Yang, J., Liu, W., Du, Q., Wang, H., et al., 2018. MicroRNA528 affects lodging resistance of maize by regulating lignin biosynthesis under nitrogen-luxury conditions. *Mol., Plant* 11, 806–814.
- Suwanphakdee, C., Sutthithon, P., Hodkinson, T.R., 2024. Characterization of anatomical characters of *Peperomia* (Piperaceae) from Asia for taxonomy. *Bot. J. Linn. Soc. XX*, 1–24.
- Tarnavski, I., Șerbănescu-Jitariu, G., Mitroiu-Rădulescu, N., Rădulescu, D., 1981. *Practicum de morfologie și anatomie vegetală*. București, Edit. Ceres.
- Tatarenko, I., Walker, K., Dyson, M., 2022. Biological Flora of Britain and Ireland: *Fritillaria meleagris*. *J. Ecol.* 110, 1704–1726.
- Toma, C., Rugina, R., 1998. Anatomia plantelor medicinale. *ATLAS*. Edit. Acad. Române, București.
- Tomović, G., Vukojičić, S., Niketić, M., Zlatković, B., Stevanović, V., 2007. *Fritillaria* (Liliaceae) in Serbia: distribution, habitats and some taxonomic notes. *Phytol. Balc.* 13 (3), 359–370.
- Trought, M.C.T., Drew, M.C., 1980. The developmental of waterlogging damage in young wheat plants in anaerobic solution cultures. *J. Exp. Bot* 31, 1573–1585.
- Turktas, M., Aslay, M., Kaya, E., Ertugrul, F., 2012. Molecular characterization of phylogenetic relationships in *Fritillaria* species inferred from chloroplast trnLtrnF sequences. *Turk. J. Biol* 36, 552–560.
- Ularu, P., Parascan, D., 1970. Câteva date fitocenologice asupra lalelelor peștrițe (*Fritillaria meleagris* L.) în Depresiunea Brașovului și împrejurimi. *Ocr., Nat* 14 (1), 69–72.
- Vlasova, N.V., 1987. *Fritillaria* L. In: Malysheva, L.I., Peshkova, G.A. (Eds.), *Flora Sibiri. Vol. 4. Araceae – Orchidaceae*. Novosibirsk: Nauka, Sibirskoe otделение (Siberian branch), pp. 99–101.
- Voesenek, L.A.C.J., Bailey-Serres, J., 2015. Flood adaptive traits and processes: an overview. *New. Phytol* 206, 57–73.
- Wang, Q., Zhou, S.D., Deng, X.Y., Zeng, Q., He, X.J., 2009. Comparative morphology of the leaf epidermis in *Fritillaria* (Liliaceae) from China. *Bot. J. Linn. Soc.* 160, 93–109.
- Wang, Y., Hou, H., Ren, Q., Hu, H., Yang, T., Li, X., 2021. Natural drug sources for respiratory diseases from *Fritillaria*: chemical and biological analyses. *Chin. Med* 16, 40.
- WFO, 2019. *Fritillaria* L. World Flora Online. <https://www.worldfloraonline.org/search?query=Fritillaria>. accessed 20 August 2019.
- Wigoda, N., Moshelion, M., Moran, N., 2014. Is the leaf bundle sheath a „smart flux valve” for K⁺ nutrition? *J. Plant. Physiol* 171, 715–722.
- Yanev, A., 1964. *Fritillaria* L. In: Jordanov, D. (Ed.), *Flora Na Narodna Republika Bulgaria (Flora Reipublicae Popularis Bulgaricae)*, *Flora Na Narodna Republika Bulgaria (Flora Reipublicae Popularis Bulgaricae)*, 2. Aedibus Acad. Sci. Bulgaricae, Serdicae, Bulgarian, pp. 254–265.
- Yoon, J., Choi, H., An, G., 2015. Roles of lignin biosynthesis and regulatory genes in plant development. *J. Integr., Plant. Biol* 57, 902–912.
- Zahariadi, C., 1966. *Fritillaria* L. In: Săvulescu, T., Flora, R.S. (Eds.), *Romania. Vol. 9*. București: Edit. Acad. R. S. România, pp. 287–295.
- Zarinkamar, F., 2006. Density, size and distribution of stomata in different monocotyledons. *Pak. J. Biol. Sci.* 9 (9), 1650–1659.
- Zhang, Y., Xu, W., Wang, H., Fang, Y., Dong, H., Qi, X., 2016. Progress in improving stem lodging resistance of ChinCam ese wheat cultivars. *Euphytica* 212, 275–286.