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Structural and adaptive features of the leaf in endemic species *Allium isakulii* R. M. Fritsch et F. O. Khass. and *Allium praemixtum* Vved. under natural conditions

Muxabbat Ravshanova[1]*, Guljan Duschanova[2], Sodikjon Abdinazarov[3], Akmal Yuldashev[4], Zokirjon Isomiddinov[5], Namuna Alieva[5], Kamola Ibragimova[2], Abdiraxman Saparov[6], Rajabov Doston[7], Abduraimov Muratkul[8]

1. Department of Biology, Navoiy State University, Navoiy, Uzbekistan
2. Department of Biology, Faculty of Natural Sciences, at the National Pedagogical University of Uzbekistan named after Nizami, Tashkent, Uzbekistan
3. Tashkent Botanical Garden named after Academician F.N. Rusanov at the Institute of Botany of the Academy of Sciences of the Republic of Uzbekistan, Tashkent, Uzbekistan
4. Faculty of Exact and Natural Sciences, Andijan State Pedagogical Institute, Andijan, Uzbekistan
5. Department of Biology, Faculty of Natural Sciences, Kokand State University, Kokand, Uzbekistan
6. Nukus State Pedagogical Institute named after Ajiniyaz, Nukus, Uzbekistan
7. Bukhara State Medical Institute named after Abu Ali ibn Sino, Bukhara, Uzbekistan
8. Samarkand state University of architecture and construction, Samarkand, Uzbekistan

* *Corresponding author's Email: crassula18@mail.ru*

ABSTRACT

For the first time, a comparative anatomical analysis of the leaf structure of the endemic species *Allium isakulii* and *Allium praemixtum*, distributed in the Nurata Mountain Range, has been conducted. Diagnostic and structural adaptation features characteristic of each species have been revealed. A unifacial leaf type was identified in *A. praemixtum*, while a bifacial leaf type was found in *A. isakulii*. The mesophyll of the linear leaf in *A. isakulii* was found to be of the isolateral-palisade type, whereas in *A. praemixtum*, the mesophyll of the cylindrical leaf showed a concentric anatomical structure. These identified structural-diagnostic features are useful for the taxonomic identification of *A. isakulii* and *A. praemixtum*. Additionally, various combinations of xeromorphic and mesomorphic traits were found in the leaves of both species. Based on the adaptive characteristics of the leaves, *A. isakulii* exhibits predominant xero-mesomorphic features, while *A. praemixtum* shows prevalent meso-xeromorphic traits, indicating a high degree of adaptation of these species to arid environments.

Keywords: Morphology, Anatomy, Diagnostic and adaptive traits, Leaf, *Allium isakulii*, *Allium praemixtum.*
Article type: Research Article.

INTRODUCTION

The conservation of biodiversity, the protection of plant species, and their sustainable use are among the global challenges of modern ecology. The structural and functional organization of plants is determined by a complex set of environmental parameters, including climatic and soil conditions. The Aktau Mountains of the Nurata Range, a region characterized by specific edaphoclimatic conditions, are of particular interest for studying the impact of ecological factors, as this area encompasses diverse altitudinal landscape-vegetation zones and sharply contrasting natural environments. Anatomical plant structure is one of the most accessible and recognized methods for identifying adaptive responses to various environmental conditions. The genus *Allium* L., belonging to the family Alliaceae, is a large genus comprising about 1200 species of perennial and biennial herbaceous plants with bulbs or rhizomes. The species of this genus are distributed exclusively in the Northern Hemisphere and are especially rich in endemism in regions such as North America, Asia, and the Mediterranean (Govaerts *et al.* 2018). According to molecular-genetic analyses, the genus is monophyletic, and its molecular evolution has not been

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accompanied by pronounced morphological divergence. Therefore, in addition to morphological characteristics, anatomical features of vegetative and generative organs are also used to describe species and subgenera of *Allium*. Important diagnostic traits for species identification include leaf arrangement, leaf morphology and anatomy, and the morphological and anatomical structure of the stem (Friesen 1988). Taxonomic literature on the genus *Allium* discusses at least 20 traits of the leaf blade (Seregin 2005). Generally, three main forms of leaf blades are characteristic for *Allium* species: flat without a cavity, cylindrical with a cavity, and intermediate types between flat and fistulose (rolled, semicylindrical, grooved, with a poorly defined central cavity). In a study by D. Yusupova (Yusupova 2018), the anatomical structure of the leaf of *Allium suworowii* Regel under different ecological conditions was examined, which enabled the identification of diagnostic features of this species. The adaptive traits of plants growing in the conditions of the Jizzakh region and the Tashkent Botanical Garden were determined. According to A.T. Abdullaeva (Abdullaeva 2017), during the study of *Allium verticillatum* under the introduction conditions of the Tashkent Botanical Garden, diagnostic characteristics were identified. The leaf mesophyll type was found to be isolateral-palisade; the epidermis was papillated, with a thickened and undulating outer epidermal wall. The stomata were sunken, and the vascular bundles were of the closed collateral type. In the research by O.I. Zhapova and T.P. Antsupova (Zhapova & Antsupova 2017), dedicated to the comparative anatomical characterization of the leaves and stems of *Allium bidentatum* Fisch. ex Prokh. and *Allium polyrrhizum* Turcz. ex Regel, features related to the arrangement and structure of vascular bundles were highlighted as diagnostic traits for species identification. In another study by O.I. Zhapova and T.P. Antsupova (Zhapova & Antsupova 2020), the anatomical structures of the leaf and stem in *Allium tenuissimum* L. and *Allium anisopodium* Ledeb., growing in steppe communities of Southeastern Transbaikalia, were analyzed. It was established that the cross-sectional shape of leaves and stems in these species largely depends on growing conditions. The degree of development of palisade and spongy chlorenchyma in stems and leaves is also determined by environmental factors. Species-specific traits in the anatomical structure of the stem and leaf include the number and structure of stem vascular bundles, as well as the structure of vascular bundles in the leaves. Z.R. Ramazanova, M.D. Dibirova, Z.I. Soltanmuradova, and others (Ramazanova *et al.* 2023) studied the morphological and anatomical features of the leaves of endemic *Allium* species in the conditions of Dagestan. The study involved anatomical analysis of the leaf's median formation (middle part of the leaf) and the classification of species based on traits such as leaf size: large-leaved (*A. daghestanicum, A. gunibicum,* and *A. charadze*; section Dagestanica Tscholok. Friesen) and small-leaved (*A. mirzojevii,* and *A. samurense*; section Oreiprason F. Herm.); leaf cross-sectional shape: grooved with smooth edges (*A. daghestanicum*), grooved with ribbed edges (*A. gunibicum, A. charadze*), and rounded-ribbed (*A. mirzojevii,* and *A. samurense*); and by the number and size of vascular bundles. Additionally, an evaluation of the species-specificity of anatomical features was conducted for five *Allium* species. In this context, the study of the anatomical structure of the leaves of the red-listed and endemic species *Allium isakulii* and *Allium praemixtum*, growing in the Aktau Mountains of the Nurata Range in Uzbekistan, is of scientific interest. The goal is to identify their diagnostic and adaptive features.

MATERIALS AND METHODS

The objects of this study were rare endemic bulbous plants included in the Red Book of Uzbekistan (Category I) -*Allium isakulii* subsp. nuratense (Kamelin) R.M. Fritsch & F.O. Khass. and *Allium praemixtum* Vved., perennial herbaceous species belonging to the genus *Allium* L. of the family Amaryllidaceae Juss. (Fig. 1; Khassanov & Rakhimova 2016). *Allium isakulii* subsp. nuratense (Kamelin) R.M. Fritsch & F.O. Khass. belongs to *Allium* sect. *Miniprason* R.M. Fritsch. The bulb is spherical, 1–2 cm in diameter, with blackish-brown, papery sheaths. The scape is thin, 15–35 cm tall. The leaves are linear-lanceolate, wavy along the margins, 7–20 mm wide, equal in length to the scape. The spathe is several times shorter than the umbel, shortly pointed. The umbel is loose, with 6–30 flowers, capitate or sometimes hemispherical. The pedicels are unequal, 2–10 cm long, without bracts at the base. The perianth is narrowly campanulate; the tepals are violet-pink with a dull green midvein, 20–30 mm long, acutely pointed, linear-lanceolate or lanceolate, with the outer tepals being slightly to 1.5 times wider than the inner ones, becoming firm and upright after flowering. The filaments are 2–2.5 times shorter than the perianth, fused with each other and with the perianth for 1/4–1/3 of their length, free in the upper part, the inner ones are broadly triangular, wider and 1/3 longer than the outer ones. Anthers are purple. The ovary is on a short stalk. The capsule is nearly spherical, about 6 mm in diameter. The species grows on gravelly slopes in foothills and the lower mountain belt at altitudes of 700–1500 m. Distribution: Pamir-Alai (Nuratau); Tian Shan (Mogoltau), in Tajikistan and Uzbekistan (Khassanov 2017).

A **B**

Fig. 1. General appearance of *Allium isakulii* (A) and *Allium praemixtum* (B).

Allium praemixtum Vved., or "mixed onion", belongs to *Allium* subgen. *Cepa* (Mill.) Radić, sect. *Cepa* (Mill.) Prokh. Bulbs (1–3 per plant) are attached to a rhizome, ovoid, 2.5-4 cm thick, with reddish-brown, leathery, entire sheaths. The scape is robust, 45-100 cm tall, hollow, inflated below the middle, and sheathed at the base with spreading, smooth leaf sheaths. There are 4-7 leaves, cylindrical, tapering toward the apex, fistulose, bluish-green, straight, 15-40 mm wide, and three times shorter than the scape. The spathe is approximately equal in length to the umbel and splits along one line. The umbel is dense, spherical, and many-flowered. The pedicels are equal, 3–4 times longer than the perianth, with bracts at the base. The perianth is stellate; the tepals are white with a green midvein, 4-5 mm long, equal in length, linear-oblong or oblong-lanceolate, and blunt. The filaments are 1/4 longer than the perianth, fused at the very base with each other and the perianth. The outer filaments are awl-shaped; the inner filaments are twice as wide at the base and slightly wider than the tepals, with a broad-ovate, blunt, two-toothed base, transitioning to an awl-shaped apex. The style is shorter than the capsule. The capsule is spherical-trigonous, 5 mm in diameter. The species grows in rock crevices and on stony slopes at altitudes of 800-1300 m. Distribution: Western Tian Shan, Pamir-Alai, in Tajikistan and Uzbekistan (Khassanov 2017). The material was collected at the beginning of June 2023 from natural conditions growth in the Aktau Mountain Nurata Range (Uzbekistan, Province Navoi). Aktau – the remnant mountain, part of the Tamdytau mountain system (the northern part of Tamdytau), consists of Silurian dolomi tized limestone ridges with steep slopes. Length about 20 km, height 974 m above sea level with a rather dissected relief (Shomurodov *et al.* 2018). The vegetative organs [inflated part of stem (fistular), stem and pedicels] from the middle layer in the beginning of flowering period were examined. Morphological description and phenological observations were carried out in natural habitats. To study the morphological and anatomical structure of the leaf, the leaves of *Allium isakulii* and *Allium praemixtum* were fixed in 70% ethyl alcohol. The leaf epidermis was examined using paradermal and transverse sections, while the anatomical structure of the mesophyll was studied based on transverse sections taken from the middle part of the leaf. The structure of the main tissues and cells was described according to the methods of K. Esau (Esau 1969), N.S. Kiseleva (Kiseleva 1971), and the epidermis according to N.A. Aneli (Aneli 1975) and N.K. Rakhimova, G.M. Duschanova, and A.T. Abdullaeva (Rakhimova *et al.* 2020). Hand-made preparations were stained with methylene blue and mounted in glycerin. The measurements were carried out according to the standard method in tissues and cells of the plants, with 30 replications using an MOV-1-15x eyepiece micrometer. Microphotographs were taken using a computer photomicrography system, a Canon A123 digital camera, and a BioBlue microscope model S/N – EC 2209333. The measurements were performed in thirtyfold replication, and the average values, measurement errors, and statistical significance were calculated using G.N. Zaitsev's formula in MS Excel.

RESULTS AND DISCUSSION

The leaves of *Allium isakulii* are bifacial, linear-lanceolate, wavy along the margins, measuring 20–27 cm in length and 5.5 cm in width. According to the classification by A.P. Seregin (Seregin 2005), the leaf blade is flat without a cavity (Fig. 1A, Table 1).

In paradermal sections of *Allium isakulii* leaves, the epidermal cell walls are straight, and the projection is rhomboid in type, consisting of straight- and rhomboid-walled cells (Aneli 1975). The adaxial epidermal cells are relatively large and thick-walled, measuring 26.65 ± 0.35 – 12.96 ± 0.13 µm in height. In contrast, abaxial epidermal cells are smaller and thinner-walled, measuring 23.03 ± 0.13 – 9.53 ± 0.071 µm. The number of adaxial epidermal cells per mm² was higher (204.69 ± 1.31) compared to the abaxial epidermis (175.67 ± 1.82). The leaves are amphistomatic, meaning stomata are present on both sides of the leaf blade, with rounded-oval shapes. On the adaxial surface, stomata are oval (34.14 ± 0.54 – 27.64 ± 0.261 µm), whereas on the abaxial surface they are slightly more rounded (28.21 ± 0.27 – 23.71 ± 0.34 µm). The number of stomata per mm² is significantly higher on the adaxial surface (158.21 ± 2.14) than on the abaxial side (97.28 ± 1.55), which helps reduce water loss through the upper surface of the leaf. The guard cells are of approximately equal length on both sides of the leaf. The stomatal type is anomocytic, and the stomata are sunken into the epidermis by 9.22 ± 0.22 µm (Fig. 2, Table 1). A transverse section of the flat leaf of *Allium isakulii* reveals an isolateral-palisade mesophyll type (Rakhimova *et al.* 2020). Beneath the adaxial and abaxial epidermis are palisade cells, and between them are spongy parenchyma cells, water-storing cells, laticifers (latex ducts), and vascular bundles. The total mesophyll thickness is 351.97±1.95 µm, with a small central cavity in the middle region. The outer wall of epidermal cells is heavily cutinized and covered with a thick, serrated cuticle. Between the adaxial and abaxial epidermis lie assimilating, storage, secretory, and vascular tissues. The palisade parenchyma consists of two rows of elongated cells, with a length of 82.83 ± 1.88 – 32.05 ± 0.48 µm and a width of 21.1 ± 0.31 µm. The palisade cell index was relatively high (3.95). The spongy parenchyma consists of 2–3 rows of isodiametric round cells, each with a diameter of 30.13 ± 0.41 µm. Both palisade and spongy parenchyma cells contain chloroplasts. Among them, numerous large-diameter (24.78 ± 0.31 µm) laticifers and small intercellular spaces were observed. In the central mesophyll region, 4–5 rows of large-diameter (58.43 ± 1.41 µm), oval-shaped water-storing cells are found. Due to the breakdown of cell walls, large cavities have formed within these cells. The central region of the mesophyll contains many large primary vascular bundles, while in the peripheral region, small lateral vascular bundles are arranged in two rows. The vascular bundles are closed, collateral in type, and composed of smaller protophloem (9.95 ± 0.46 µm) and metaxylem (29.78 ± 0.61 µm) elements (Fig. 2, Table 1). The leaves of *Allium praemixtum* are unifacial, cylindrical, tapering towards the apex, fistulose (hollow), bluish-gray, and straight, measuring 35–40 cm in length and 1.5–2 cm in width, and are three times shorter than the scape. According to A.P. Seregin's (Seregin 2005) classification, the leaf blade shape is characterized as cylindrical with a cavity (Fig. 3A). In the paradermal section of the *Allium praemixtum* leaf, the epidermal cell walls are straight-lined, with rhombic-type projections, composed of straight and rhomboid-walled cells (Aneli 1975). The epidermis consists of a thin-walled cuticle (6.78 ± 0.24 µm), and the epidermal cells are relatively large (26.67 ± 0.40 µm). The number of epidermal cells per mm² is 338.45 ± 6.48, which is significantly higher than in *Allium isakulii*. The leaves exhibit an amphistomatic structure. The stomata are oval-shaped, measuring 54.7 ± 0.95 µm in length and 22.51 ± 0.58 µm in width. The stomatal density is 271.06 ± 6.08 per mm², also higher than in *Allium isakulii*. This, in turn, contributes to reduced water loss from the upper leaf surface (Fig. 3, Table 1). The guard cells of the stomata have nearly identical lengths on both sides of the leaf. The stomata are of the anomocytic type and are relatively deeply embedded in the epidermal tissue, with a depth of 7.99 ± 0.13 µm. In the cross section of the cylindrical leaf of *Allium praemixtum*, a concentric anatomical mesophyll type is observed (Timonin & Ozerova 1994). Beneath the epidermal cells, there are palisade cells, and between them are spongy and water-bearing cells, as well as laticifers and vascular bundles. The thickness of the leaf mesophyll is 1299.87 ± 3.61 µm, with a large cavity formed in its central part. The outer side of the leaf is composed of a single row of large, thin-walled cells. Below the epidermis, there are two rows of large, elongated palisade parenchyma cells, with an average length of 104.7 ± 1.52 µm and width of 22.51 ± 0.58 µm. The palisade cell index is relatively high (4.65), and large intercellular spaces are present between the cells. The spongy parenchyma cells are round and isodiametric, arranged in 3–4 rows of small cells with an average diameter of 28.55 ± 0.45 µm (Fig. 3, Table 1). Both palisade and spongy parenchyma cells contain chloroplasts. Numerous relatively large laticifers (latex tubes) with an average diameter of 28.71 ± 0.68 µm are located between these cells, along with small intercellular spaces. In the central part of the leaf mesophyll, 4–5 rows of relatively large, oval-shaped water-storing cells (average diameter: 115.82 ± 2.94 µm) are located. The degradation of cell walls in this area leads to the formation of large cavities. In the peripheral region of the leaf mesophyll, small lateral vascular bundles are surrounded by water-storing parenchyma cells arranged in a ring-like manner. The vascular bundles are closed, collateral in type, and consist of relatively large elements of

protoxylem (15.02 ± 0.44 µm) and metaxylem (35.98 ± 0.70 µm; Fig. 3, Table 1). The mesophyll types described above are adapted for Calvin cycle (C_3-type) photosynthesis, which occurs in both palisade and spongy cells containing chloroplasts.

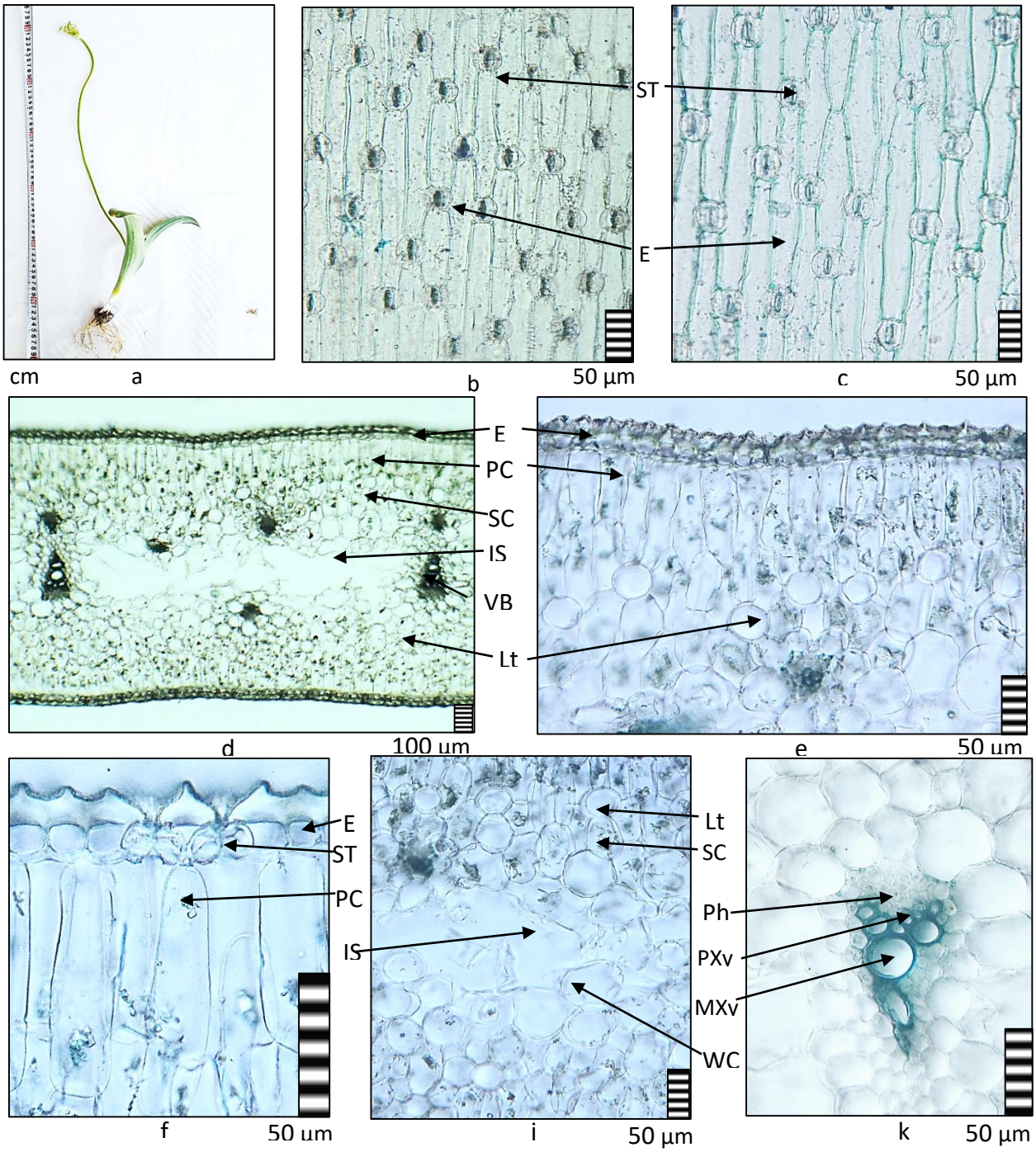

Fig. 2. Anatomical structure of the leaf epidermis and mesophyll of *Allium isakulii*: a – general view; b – adaxial epidermis; c – abaxial epidermis; d-e – detailed view of the leaf mesophyll; f – epidermis and deeply embedded stomata; j – spongy and water-storing cells; k – vascular bundle. **Legend:** ST – stoma, SC – spongy cell, PC – palisade cell, IS – intercellular space, E – epidermis, Ph – phloem, PXy – protoxylem, MXy – metaxylem, WC – water-storing cell, L – laticifer (latex duct), VB – vascular bundle.

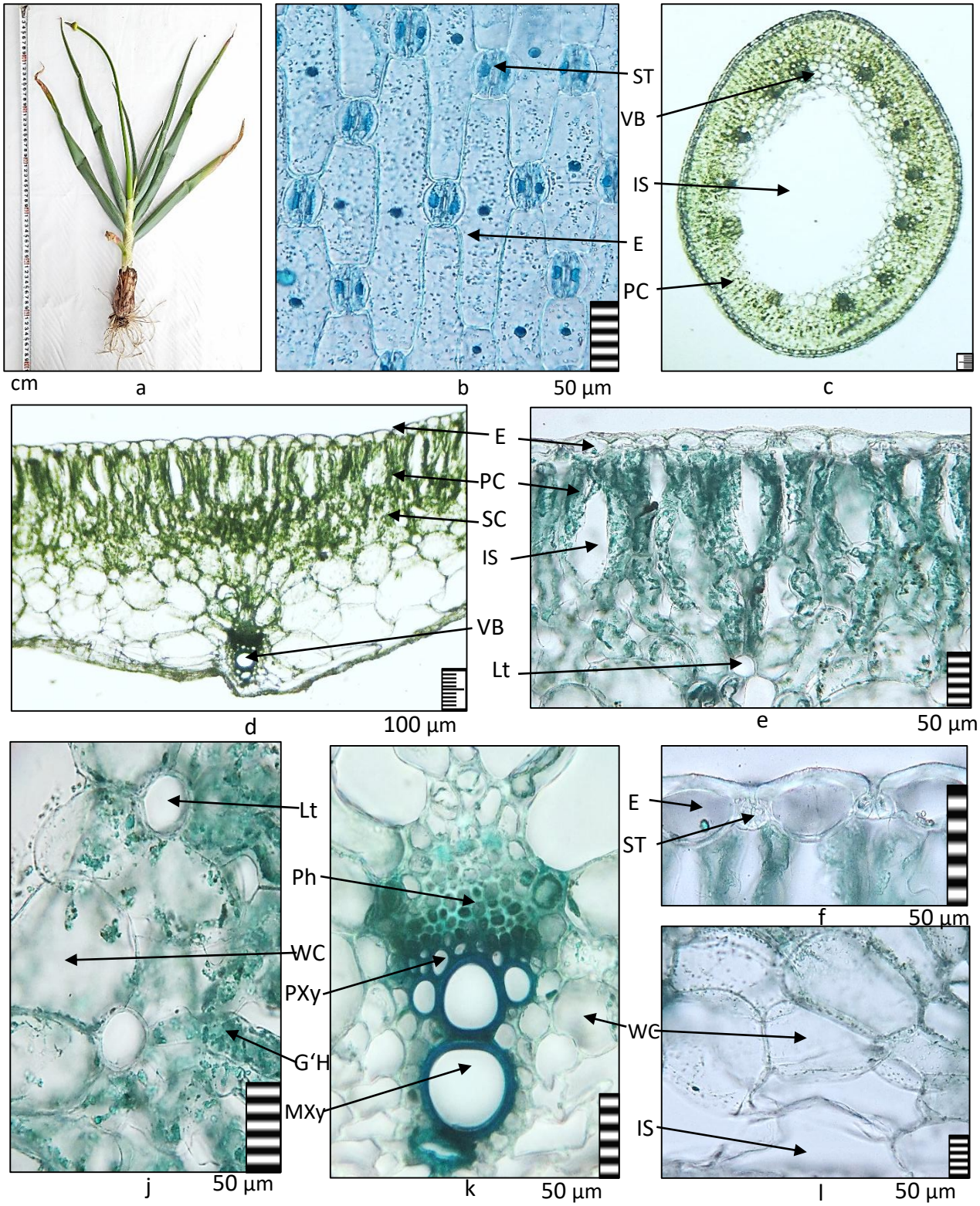

Fig. 3. Anatomical structure of the leaf epidermis and mesophyll of *Allium praemixtum*:
a – general view; b – epidermis; c – general view of the leaf mesophyll; d – detailed structure of the leaf mesophyll; e – epidermis, palisade and spongy parenchyma, laticifers; f – epidermis and deeply located stomata; j–l – laticifers and water-storing cells; k – vascular bundle. **Legend:** ST – stoma, SC – spongy mesophyll cell, PC – palisade cell, IS – intercellular spaces, E – epidermis, Ph – phloem, PXy – protoxylem, MXy – metaxylem, WC – water-storing cell, Lt – laticifer, VB – vascular bundle.

Table 1. Quantitative indicators of anatomical characteristics of leaves in some species of the genus *Allium.*

Indicators		*A. isakulii*	*A. praemixtum*
Leaf (cm):			
length		20-27	35-40
width		5.5	1.5-2
Mesophyll thickness (µm)		351.97 ± 1.95	1299.87 ± 3.61
Epidermis (µm):	adaxial side	12.96 ± 0.13	6.78 ± 0.24
Outer wall thickness	abaxial side	9.53 ± 0.071	
Cell height	adaxial side	26.65 ± 0.35	26.67 ± 0.40
	abaxial side	23.03 ± 0.13	
Number of epidermal cells per 1 mm²:	adaxial side	204.69 ± 1.31	338.45 ± 6.48
	abaxial side	175.67 ± 1.82	
Stomata (µm):	adaxial side	34.14 ± 0.54	54.7 ± 0.95
Length	abaxial side	28.21 ± 0.27	
Width	adaxial side	27.64 ± 0.261	22.51 ± 0.58
	abaxial side	23.71 ± 0.34	
Number of stomata per 1 mm²:	adaxial side	158.21 ± 2.14	271.06 ± 6.08
	abaxial side	97.28 ± 1.55	
Submerged stomata		9.22 ± 0.22	7.99 ± 0.13
Palisade parenchyma (µm):			
Height		82.83 ± 1.88	104.7 ± 1.52
Width		21.1 ± 0.31	22.51 ± 0.58
Number of layers		2	2
Palisade cell index		3.95	4.65
Spongy parenchyma (µm):			
Cell diameter		30.13 ± 0.41	28.55 ± 0.45
Number of layers		2-3	3-4
Water-bearing cell (µm):			
Cell diameter		58.43 ± 1.41	115.82 ± 2.94
Number of layers		4-5	4-5
Xylem diameter (µm):			
Diameter of protoxylem		9.95 ± 0.46	15.02 ± 0.44
Diameter of metaxylem		29.78 ± 0.61	35.98 ± 0.70
Laticifer diameter (µm)		24.78 ± 0.31	28.71 ± 0.68

Based on the statistical analysis of the quantitative anatomical characteristics of the leaves of *A. isakulii* and *A. praemixtum*, it was found that the unifacial leaf type of *A. praemixtum*, with its larger size and thicker mesophyll (35–40 cm, 1299.87 ± 3.61 µm), indicates meso-xeromorphic features. In contrast, the bifacial leaf type of *A. isakulii*, with its smaller size and thinner mesophyll (20–27 cm, 351.97 ± 1.95 µm), demonstrates xero-mesomorphy. In both species studied, the epidermal cells are straight-lined and rhomboid in shape. The small size and thick walls of epidermal cells in *A. isakulii* (23.03 ± 0.13 – 12.96 ± 0.13 µm) indicate xeromorphic characteristics, while the relatively larger size and thick cell walls of the epidermis in *A. praemixtum* (26.67 ± 0.40 – 6.78 ± 0.24 µm) reflect meso-xeromorphy. The higher number of epidermal cells and stomata per 1 mm², along with the deeply embedded stomata in *A. praemixtum* (338.45 ± 6.48 – 271.06 ± 6.08), contrast with the lower numbers and similarly deep stomatal positioning in *A. isakulii* (204.69 ± 1.31 – 158.21 ± 2.14). In both species, the large size and high index of palisade cells indicate xero-mesomorphy: *A. praemixtum* (104.7 ± 1.52 µm – index 4.65) and *A. isakulii* (31.41 ± 0.21 µm – index 4.95). In the leaf mesophyll, the thickness of the water-storing parenchyma, the large diameter and the abundance of its cells in *A. praemixtum* (115.82 ± 2.94 µm – 4–5 layers) reflect meso-xeromorphic traits, while the thinner, smaller-diameter but also numerous water-storing cells in *A. isakulii* (58.43 ± 1.41 µm – 4–5 layers) demonstrate xero-mesomorphy. In *A. isakulii*, numerous closed, collateral main vascular bundles are located in the central part of the mesophyll, while the peripheral region contains two rows of lateral vascular bundles. In *A. praemixtum*, however, the lateral vascular bundles of closed, collateral type are surrounded by water-storing parenchyma cells and are arranged in a single ring-like layer in the peripheral region of the mesophyll. The vascular bundles in *A. praemixtum* contain protoxylem and metaxylem elements of larger diameter (15.02 ± 0.44 – 35.98 ± 0.70 µm), whereas in *A. isakulii*, these elements have smaller

diameters (9.95 ± 0.46 – 29.78 ± 0.61 µm). Numerous small-diameter laticifers (latex tubes; 24.78 ± 0.31 – 28.71 ± 0.68 µm) were identified between the palisade and spongy cells in both *A. isakulii* and *A. praemixtum* leaves (Figs. 2-3, Table 1).

CONCLUSION

For the first time, the anatomical structure of the leaves of the endemic species *Allium isakulii* and *Allium praemixtum*, distributed in the Nurata Mountain System, has been studied, revealing species-specific diagnostic and structural adaptive traits. In *A. isakulii*, the epidermal cell walls are straight, with rhomboid-shaped projections and a cutinized, serrated cuticle layer (Zaitsev 1991; Barykina & Chubatova 2005). The leaves are amphistomatic, with deeply embedded anomocytic stomata located on both the adaxial and abaxial epidermis. The mesophyll exhibits an isolateral-palisade structure, and numerous laticifers are found between palisade and spongy cells. Cavities are present among the water-storing cells, and in the central part of the mesophyll, large closed collateral vascular bundles are located, while smaller bundles are found in the peripheral region (Abrorov 2019; Syman *et al.* 2024; Karakulov, *et al.* 2025). In *A. praemixtum*, the epidermal cell walls are also straight, with rhomboid-shaped projections. The leaves are amphistomatic in structure, and the mesophyll is of a concentric anatomical type (Menglikulov*et al.* 2025; Imanov *et al.* 2025; Sapaev *et al.* 2025). Numerous laticifers are located between the palisade and spongy cells. In the central region of the mesophyll, large cavities are formed due to the degradation of the walls of water-storing cells. In the peripheral part, lateral vascular bundles are arranged in a ring-like pattern. These identified structural diagnostic traits can be used in the taxonomic identification of *A. isakulii* and *A. praemixtum*. Based on their adaptive features, the leaves of *A. isakulii* exhibit predominantly xero-mesomorphic characteristics, while *A. praemixtum* shows meso-xeromorphic traits, indicating that both species are well adapted to arid environments.

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