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Leaf anatomy of valuable species of genus *Primula*

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In this research, we discovered a number of structural adaptations and informative characteristics for the leaf blades of the studied species from the genus *Primula* L. The species under study were found to have anomocytic stomatal type. The leaf blades are hypostomatic (*P. denticulata*) or with the predominant abaxial stomata (*P. macrocalyx*, *P. pallasii*). The following indicators have low variation (CV < 20 %): size of stomata, number of cells in the upper and lower epidermis, height of cells in the upper mesophyll layer, lamina thickness near the midvein and central part, phloem cross-section area, and vascular bundle area. High and very high variation level is observed for the quantitative indicators describing the leaf indument density, number of stomata and stomatal index of the upper epidermis. The data obtained can be used to evaluate the species adaptability and to develop the appropriate light and hydrothermal regime for cultivating the species in the Western Siberia sub-boreal forest environment.
Key words: *Primula denticulate; P. macrocalyx; P. pallasii;* leaf anatomy; anomocytic stomata

Introduction

The genus *Primula* L. (Primulaceae; primrose) is the largest genus in the family. It comprises 430–500 species of herbaceous plants growing predominantly in the moderate and cold regions of the Northern Hemisphere. Individual species can be found in the mountains of South America and Africa, as well as tropical Asia (Kovtonyuk, 2013; Richards, 2003). Most species are concentrated in mountain systems, which makes it possible to grow them in cold climates.

The genus *Primula* L. includes the most ornamentally valuable plants. Some species of the genus are also used as medicinal and food crops (salads). Several species of the genus *Primula* L. are used in Tibetan and folk medicine. For instance, *P. macrocalyx* Bunge and *P. veris* are used to treat respiratory, cardiovascular, and musculoskeletal diseases (arthritis, arthrosis, etc.), metabolic and endocrine disorders, as well as nervous and mental diseases (Ladynina, 1990; Lavrenov, 2004; Tolstikova, 2010). According to other sources, *P. macrocalyx* can inhibit tumor growth, accelerate wound repair, and heal blood disorders (Kurochkina, 2014).

The chemical composition and pharmacological effect of the plants of genus *Primula* L. are understudied. The raw material of various species of the genus contains triterpenoid saponins, phenolic compounds, aminoacids and organic acids, carbohydrates, carotenoids, lipophilic substances, elements of the hematopoietic microenvironment, essential oils, fatty oils, vitamin C, microelements, etc. (Latypova, 2015; Anishchenko, 2005; Okrslar, 2007). Due to their high content of ascorbic acid (2–6 %), some species are eaten as salads and seasonings (Anishchenko, 2005; Kosenkova, 2009).

A study of the shoots and roots of *P. macrocalyx* Bunge by the Central Siberian Botanical Garden (Novosibirsk) revealed bisbibenzyls riccardin C and perrottetin E acting as NOS inhibitors. This will expand the application prospects of the genus in medicine. The content of riccardin C is shown to be at its highest during the fruiting season (Kosenkova, 2009).

Extracts of individual representatives of the genus *Primula* L. provide a wide range of pharmacological effects: anticonvulsant, antimitotic, antibacterial, relaxant, sedative, antispasmodic, diuretic, etc. (Kurochkina, 2014; Okrslar, 2007; Başbülbül, 2008; Adams, 2009). Secondary metabolites (flavonoids, etc.) isolated from *P. denticulata* have a cytostatic and sensitizing effect (Tokalov, 2004).

Some species of the genus *Primula* L. found in Russia and Siberia are listed in state and regional Red Books and need protection (Red Book of the Russian Federation, 2008; Red Book of Tomsk Oblast, 2013).

The study of leaf structure is one of the reputable ways to compare plant species from various ecological and geographical groups in order to reveal their adaptive potential.
The literature data on the leaf anatomy of the species of genus *Primula* L. is scarce. Most of it focuses on revealing the diagnostic features of species that serve as medicinal raw materials (Latypova, 2012; Serebryanaya, 2010; Romanova, 2011; Aslam, 2015; Ivanova, 2017; Sinichenko, 2017) or, rarely, on the structural adaptation of plants to certain environmental conditions (Popova, 2013; Popova, 2014).
The aim of this research is to study the laminar anatomy of the three species of genus *Primula*.

Methods

The objects of anatomical research in the Siberian Botanical Garden of Tomsk State University were three species of genus *Primula* L. from two subgenera and two sections.
Subgenus *Primula*, section *Primula*.
P. macrocalyx Bunge is a species found in Eastern Europe and Asia. It grows in the south of forest areas, on forest openings and dry meadows. In mountains, it reaches the subalpine belt (Kovtonyuk, 1997). On the territory of Siberia, it is on the regional lists of protected plants including the Red Book of Tomsk Oblast (Red Book of Tomsk Oblast, 2013).
P. pallasii Lehm. is a species found in Eastern Europe and Northern Asia. It ranges on alpine and subalpine meadows, at the upper timber line, in cedar and cedar-fir woodlands, as well as on forest openings of mixed forests in northern latitudes. Socially dominant species (Kovtonyuk, 1997). On the territory of Siberia, it is listed in the Red Book of Irkutsk Oblast and Red Book of the Republic of Buryatia.
Subgenus *Primula*, section *Denticulata.*
P. denticulata Sm. ranges in the mountain regions of the Kashmir Himalayas, in the forest, subalpine, and alpine belts (Sichuan, Yunnan (China), Afghanistan, Bhutan, India, Kashmir, Nepal, Pakistan, Northern Myanmar, and Sikkim). It grows on wet meadows, grassy slopes, in scrubs, broken forests, at an altitude of 1,500–4,100 meters above sea level. The species have a wide range of tolerance to unfavorable environmental factors (Aslam, 2015).
In this research, we analyzed leaf samples of plants from the introduction nursery of Siberian Botanical Garden (city of Tomsk). *P. macrocalyx* Bunge, and *P. pallasii* Lehm. were introduced from their natural habitats in the suburbs of Tomsk (Tomsk Oblast), and *P. denticulata* Sm. from Russian and overseas botanical gardens. Most of the species under study were planted on a plot partially shaded by trees and bushes.
To study the leaf anatomy of rare and commercially valuable plants, we used a number of generally accepted methods (Belaeva et al., 2014). The stomatal index was calculated by Kästner's formula (1972).
The leaf anatomy was studied on crossing cuts using an optical microscope Carl Zeiss Axio Lab. A1 (Germany). Crossing cuts were performed in the central leaf portion using a freezing microtome MZ-2. The thickness of lamina slices was set at 60–90 μm. The leaf epidermis was peeled from the central third of a leaf. The sections were performed in quintuplicate on the leaves sampled from five sprouts; at least 25 sections were analyzed for each sample. To obtain, process, and analyze the images, we used an AxioCam ERc 5s digital camera and the Axio Vision 4.8 software package.
Statistical data processing was performed in line with standard procedures (Belaeva et al., 2014) using the Statistica 8.0 software package (StatSoft, Inc., the USA).

Results and Discussion

All the species studied are polycarpous perennial rosette short-rooted hemicryptophytes with secondary roots and a long vegetation period.
P. macrocalyx. Its leaf blade is ovate or obovate, with a blunt tip, rugose, narrowed at the base to the alate petiole almost the size of the blade; the leaf margin is crenate or denticulate, 3–15 cm long and up to 8 cm wide.
The leaf anatomy of the species was studied for the raw material evaluation (Latypova, 2012; Latypova, 2015; Serebryanaya, 2010; Romanova, 2011). Serebryanaya (2010) reports that *P. macrocalyx* has numerous simple multicellular hairs with quite a large secreting head. According to Latypova (2012), the species predominantly has headed glandular trichomes and seldom simple multicellular ones. Romanova (2011) also mentions that *P. macrocalyx* has simple two- or three-celled hairs with thin walls, widened at the base and tapered at the end, as well as glandular hairs with spherical single-celled heads. Unlike *P. veris* L., they are not filled with a grayish-brown compound. The glandular hairs of *P. macrocalyx* are mounted on a three-celled stalk.
According to our own studies, both upper and inner side of *P. macrocalyx* leaf blade is covered by a single layer of epidermis. The adaxial epidermal cells are 26.02 ± 0.9 μm high on average, with slightly curved anticlinal walls. The abaxial epidermal cells are 28.62 ± 1.23 μm high, with significantly curved thin walls (Table 1, Fig. 1). The epidermis is covered with a thin cuticle. The number of abaxial epidermal cells per 1 mm^2 is 1.7 times as high as that of adaxial cells. Stomata are anomocytic, oval or round, 31.8–34.01 μm long and 25.5–26.46 μm wide. Stomata are located mostly on the abaxial epidermis: there are 10.4 times as many of them as on the adaxial epidermis. The stomatal index is 1.43 ± 0.61 % (adaxial) and 9.15 ± 0.57% (abaxial). The epidermis has multicellular hairs, both simple and glandular, located predominantly on the edge and on the inner side of the leaf blade. The abaxial indument is almost twice as dense as the adaxial one. The leaf mesophyll on average 104.9 ± 8.3 μm thick. The mesophyll is dorsiventral, heterogeneous, differentiated into palisade and spongy parenchyma, with their thickness ratio being 1.14. Vascular bundles are tracheides forming the leaf venation on the upper and inner side (Fig. 2a). The ratio of xylem to phloem cross-section area is 0.58 ± 0.02 (Table 1).

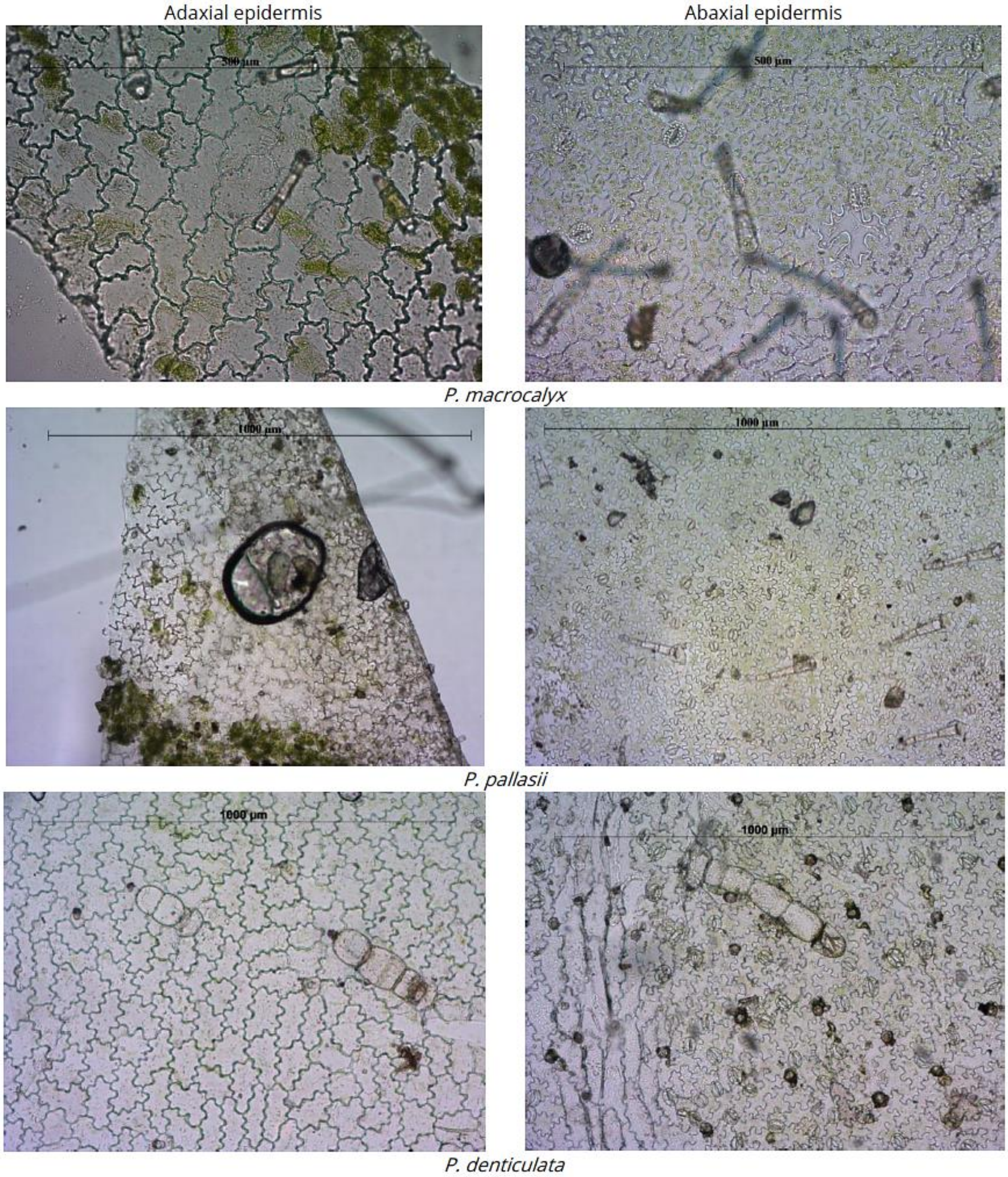

Fig. 1. Adaxial and abaxial epidermis of the studied species

The leaf blade of *P. macrocalyx* is mesomorphous, indicating the species adaptation to forest and grassland habitation: plain leaves, sapful and soft; moderately developed stomatal system, epidermis (indumentum) and conducting tissue, thin cuticle; heterogeneous mesophyll; hypostomatic leaves; greater development of translocation system elements. The common features of the leaf structure (dorsiventral mesophyll; hypostomatic leaves; anomocytic stomatal type; multicellular glandular headed trichomes; curved anticlinal walls of the epidermal cells) are in good agreement with the descriptions by other authors (Latypova, 2012; Serebryanaya, 2010; Romanova, 2011).

P. pallasii. The leaf blade is elliptic or oblong-obovate, slightly rugose, narrowed at the base to the alate petiole, twice as short as the blade; glandular indument, seldom glabrous; irregularly denticulate; 5 to 24 cm long and 2.5 to 8 cm wide.

No published data on the species anatomy has been found. The general structure is similar to *P. macrocalyx*. The adaxial epidermal cells are on average 34.41 ± 1.57 μm heigh and the abaxial ones, 26.89 ± 0.97 μm high, with curved walls. The epidermis is single-layered, covered with cuticle (Table 1, Fig. 1). The stomata are anomocytic, predominantly abaxial, on average 30.91–34.33 μm long and 25.2–29.85 μm wide. The stomatal index is 1.00 ± 0.40 % for adaxial epidermis and 11.37 ± 0.70 % for abaxial epidermis. The mesophyll is dorsiventral, on average 118.53 ± 6.36 μm thick, differentiated into palisade and spongy tissue. *P. pallasii* differs reliably ($p < 0.05$) from *P. macrocalyx* by lesser indument and lower number of adaxial stomata. The ratio of xylem to phloem cross-section area for *P. macrocalyx* is 0.58 ± 0.02 as compared to 0.78 ± 0.03 for *P. pallasii* (Table 1). Vascular bundles are collateral (Fig. 2b). Psychrophyte, mesophyte.

The leaf blades of *P. macrocalyx* and *P. pallasii* are the thinnest among the species studied (129.94–152.15 μm in the middle section) (Table 1).

Table 1. Morphometric and quantitative leaf blade structure indicators for the species of genus *Primula* L. under study

Indicators	*P. denticulata*	*P. macrocalyx*	*P. pallasii*
Number of adaxial epidermal cells per 1 mm^2, pcs.	227.84 ± 4.36 9.57	324.48 ± 7.42 11.43	305.45 ± 10.42 16.00
Number of abaxial epidermal cells per 1 mm^2, pcs.	356.48 ± 6.30 8.84	527.36 ± 9.84 9.33	510.72 ± 13.13 12.85
Number of adaxial epidermal stomata per 1 mm^2, pcs.	-	5.12 ± 2.21 215.75	3.64 ± 1.46 188.73
Number of abaxial epidermal stomata per 1 mm^2, pcs.	104.32 ± 5.07 24.30	53.12 ± 3.42 32.21	66.56 ± 4.86 36.51
Length of adaxial epidermal stomata, μm	-	34.01 ± 0.73 7.76	30.91 ± 1.06 7.64
Width of adaxial epidermal stomata, μm	-	25.52 ± 0.77 10.94	25.20 ± 0.83 7.34
Length of abaxial epidermal stomata, μm	42.92 ± 0.53 6.20	31.83 ± 0.34 5.30	34.33 ± 0.59 8.65
Width of abaxial epidermal stomata, μm	34.79 ± 0.45 6.42	26.46 ± 0.23 4.43	29.85 ± 0.46 7.63
Stomatal index, upper epidermis, %	-	1.43 ± 0.61 213.39	1.00 ± 0.40 189.68
Stomatal index, lower epidermis, %	22.43 ± 0.76 16.89	9.15 ± 0.57 31.11	11.37 ± 0.70 30.58
Lamina thickness (along the midvein), μm	1768.52 ± 18.80 5.32	1776.56 ± 5.71 1.61	1830.80 ± 6.77 1.85
Lamina thickness in the central part, μm	199.97 ± 6.27 15.68	152.15 ± 6.71 22.05	129.94 ± 4.55 17.50
Leaf mesophyll thickness, μm	107.01 ± 1.33 6.19	104.90 ± 8.30 39.55	118.53 ± 6.36 26.81
Palisade tissue thickness, μm	71.93 ± 1.81 12.59	77.81 ± 5.97 36.81	55.45 ± 1.55 14.00
Spongy tissue thickness, μm	79.14 ± 1.56 9.83	72.21 ± 7.51 49.85	45.42 ± 2.02 22.22
Palisade/spongy ratio	0.92 ± 0.03 14.55	1.14 ± 0.05 23.00	1.26 ± 0.05 19.53
Height of adaxial epidermal cells, μm	38.19 ± 1.26 16.52	26.02 ± 0.90 17.27	34.41 ± 1.57 22.76
Height of abaxial epidermal cells, μm	39.93 ± 2.09 26.22	28.62 ± 1.23 21.54	26.89 ± 0.97 18.06
Height of upper mesophyll layer cells, μm	42.90 ± 1.12 9.08	41.63 ± 2.97 15.93	32.88 ± 0.84 12.72
Width of the first mesophyll layer cells, μm	45.77 ± 3.01 22.80	29.00 ± 1.12 8.66	24.01 ± 0.70 14.62
Indument density of upper epidermis per 1 mm^2, pcs.	9.60 ± 1.60 83.33	14.08 ± 2.66 94.62	0.73 ± 0.73 469.04
Indument density of lower epidermis per 1 mm^2, pcs.	30.72 ± 3.32 54.04	29.44 ± 2.72 46.22	23.68 ± 2.79 58.90
Xylem area, μm^2	115485.74 ± 4506.56 14.60	62266.68 ± 1379.31 8.86	52095.16 ± 1512.24 14.51
Phloem area, μm^2	126787.94 ± 3619.69 10.68	108391.74 ± 3666.87 13.53	68197.07 ± 2710.46 19.87
Vascular bundle area, μm^2	232186.93 ± 2831.00 4.40	179528.95 ± 4325.51 9.64	129025.00 ± 9147.57 35.45
Xylem/phloem ratio	0.92 ± 0.04 17.27	0.58 ± 0.02 16.10	0.78 ± 0.03 17.83

Notes: arithmetic mean ± standard error of mean, coefficient of variation is given in the bottom line

P. denticulate. The leaf blades are 5–23 cm long and 2.5–10 cm wide, oblong or oblong-ovate, broad elliptic, lanceolate, with a denticulate edge, pulpous, with elongated base and blunt or rounded tip. The petiole is broad alate, weakly articulated. Adaxially, the leaf blade has a weak indument or is almost glabrous; abaxial trichomes are located along the veins and leaf edge; sometimes the leaf blade is covered with white or yellowish powdery coating. There is no organized data on the leaf anatomy. Some information is published on the structure of epidermal cells and trichomes, as well as the stomatal type (Aslam, 2015; Sinichenko, 2017).

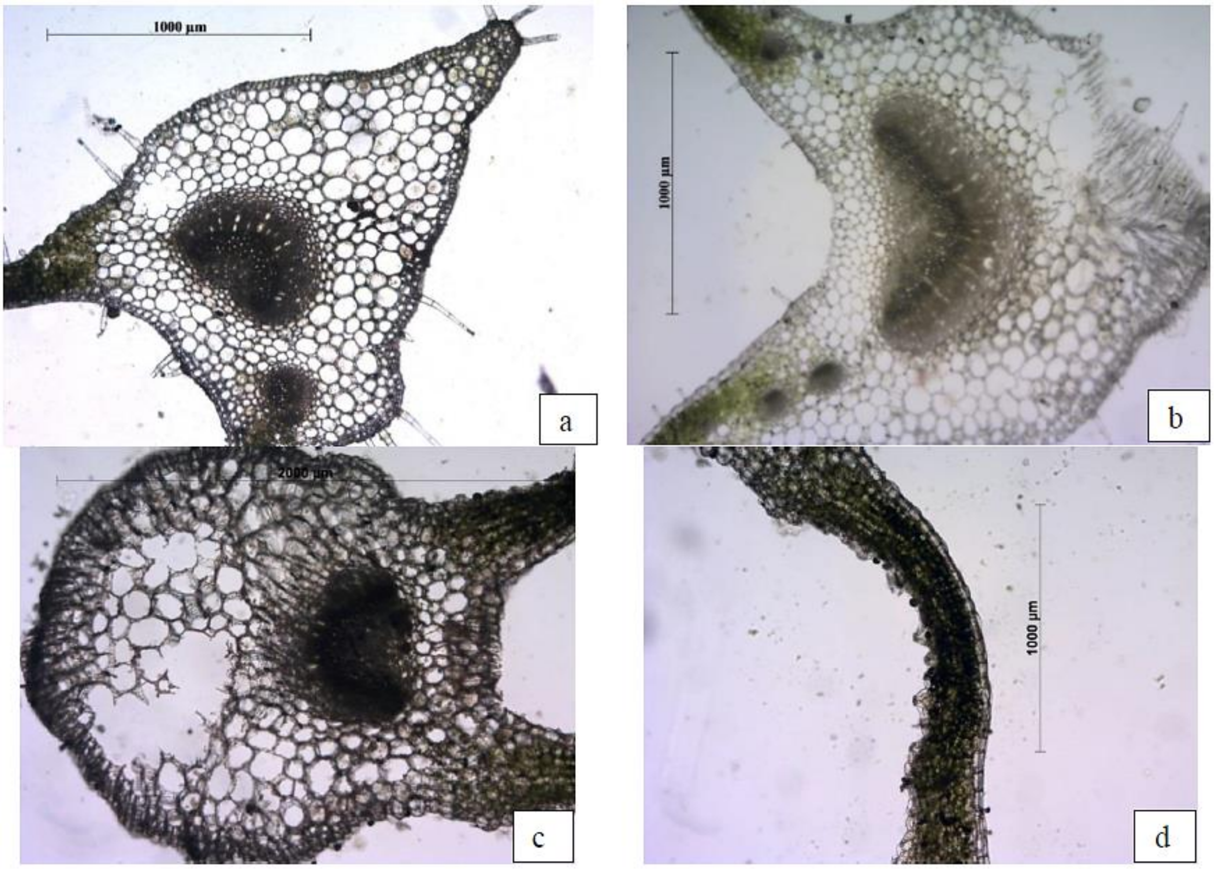

Fig. 2. Leaf blade cross section of *P. macrocalyx* (a), *P. pallasii* (b), *P. denticulata* (c, d)

Trichome structure of the species was thoroughly studied by Sinichenko, Marchyshyn, and Sira (2017), revealing the presence of small evenly located glandular hairs, consisting of short single- or two-celled stalk and a small unicellular head with dark content. Furthermore, the whole laminar surface contains large, long three- to twelve-celled hairs, with an increased density along the veins and leaf edge. Aslam, Nawchoo, and Ganai (2015) studied the correlation between the development of the stomatal apparatus in *P. denticulata* and the elevation above sea level. The size and density of stomata were regarded as the two main ecophysiological parameters. According to the research, the maximum stomata density on the leaves of *P. denticulata* was observed at the highest elevation above sea level. The number and size of trichomes with the defensive function also increased with the elevation above sea level.

Our research describes the leaf blade of *P. denticulata* as dorsiventral and hypostomatic, which is in good agreement with the published data (Sinichenko, 2017). Epidermal cells are on average 38.19–39.93 µm high, with thin and mostly curved side walls; along the veins, the cells are more elongated, with almost straight walls. The adaxial epidermis is covered with a thin cuticle without stomata (Table 1, Fig. 1). The abaxial stomata are surrounded by 5–6 epidermal cells, large (average length 42.92 ± 0.53 µm and width 34.79 ± 0.45 µm), and numerous. The stomata are anomocytic. The stoma size is comparable to the published data (Aslam, 2015). We discovered that among all the species under study, *P. denticulata* has the highest stomatal index – 22.43 ± 0.76 %, and, correspondingly, the highest density of abaxial stomata (104.32 ± 5.07). In terms of this parameter, the sample of *P. denticulata* is superior to the Himalayan species characterized by Aslam, Nawchoo, and Ganai (2015) as having the stomatal density (per 1 mm^2) in the range of 50.33–70.50. Hydatodes are present, as well as numerous specialized cells with orange contents. Abaxial epidermis is densely covered with two types of trichomes: simple and headed glandular ones. The leaf edge dents have secreting epidermis and are densely covered with multicellular long hairs. The abaxial indument 3.2 times as dense as the adaxial one. The mesophyll thickness (107.01 ± 1.33 µm on average) is comparable to that of *P. macrocalyx* and lower than that of *P. pallasii*. The central and side parallel primary veins are thick and well developed; the vascular bundle is collateral (Fig. 2c,d). The ratio of palisade to spongy parenchyma thickness as well as the ratio of xylem to phloem cross-section area is 0.92 ± 0.03 (Table 1). In the ground parenchyma and around the nodes, there are numerous ovate or rounded secretory idioblastes with dark content.

The leaf anatomy reflects the adaptation of *P. denticulata* to highlands with their cold and wet soils, low temperatures, strong winds, and high insolation. The leaves are mesomorphic: fleshy, dorsiventral (about equally developed palisade and spongy parenchyma, xylem, and phloem), with large stomata and hydatodes. At the same time, as compared to other species under study, *P. denticulata* is marked by a more developed adaxial stoma and trichome system. The anatomy of *P. denticulata* indicates that it is quite adaptive to humidity. Hydatodes contribute to the excretion of liquid spray moisture in a very humid environment. A developed system of abaxial trichomes and stomata allows the plant to adapt to the temporary insufficient water availability, especially at low temperatures.

We have evaluated the variability of the quantitative and morphometric leaf blade structure indicators for the species of genus *Primula* L. under study. The following indicators have low variation (CV < 20%): size of stomata, number of cells in the upper and lower epidermis, height of cells in the upper mesophyll layer, lamina thickness near the midvein and central part, phloem cross-section area, and vascular bundle area. According to Hodgson et al. (2010) and Ivanova (2012), the size of mesophyll cells can be defined by the genome size and life form of the plants. High and very high variation level is observed for the quantitative indicators describing the leaf indument density, number of stomata and stomatal index of the upper epidermis.

Conclusion

In this research, we discovered a number of structural adaptations and informative characteristics for the leaf blades of the studied species from the genus *Primula* L. All the species under study were found to have anomocytic stomata. The leaf blades are hypostomatic (*P. denticulata*) or with the predominant abaxial stomata (*P. macrocalyx*, *P. pallasii*). The data obtained can be used to evaluate the species adaptability and to develop the appropriate light and hydrothermal regime for cultivating the species in the Western Siberia sub-boreal forest environment.

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