ABS ACTA BIOLOGICA SIBIRICA
A journal on the biodiversity of Siberia and the adjacent lands

Acta Biologica Sibirica 11: 1703–1718 (2025)
doi: 10.5281/zenodo.18092509
http://journal.asu.ru

RESEARCH ARTICLE

Anatomical features of leaves of the Busch lily (*Lilium buschianum* G. Lodd.) in Western Siberia forest zone

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Academic editor: R. Yakovlev | Received 30 August 2025 | Accepted 20 November 2025 | Published 30 December 2025

http://zoobank.org/D0AAC93F-0C68-4074-B0EA-5DBB79823AEC

Citation: Belaeva TN, Liu S, Butenkova AN (2025) Anatomical features of leaves of the Busch lily (*Lilium buschianum* G. Lodd.) in Western Siberia forest zone. Acta Biologica Sibirica 11: 1703–1718. https://doi.org/10.5281/zenodo.18092509

Abstract

The Busch lily (*Lilium buschianum* G.Lodd.) is the least studied of the four species of lilies that grow in Siberia. In the Russian Federation, *L. buschianum* is listed in the Red Books of the Transbaikal Territory, Amur Region, Jewish Autonomous Region, and Khabarovsk Territory. The aim of this study was to investigate the anatomical features of *L. buschianum* leaf blades and compare them with those of other species in the genus growing in Siberia. The information obtained is necessary for developing effective introduction and reintroduction strategies aimed at preserving biodiversity and restoring species populations. The study revealed that the *L. buschianum* is characterized by the following anatomical features of the leaf blade: the cell walls of the epidermis are straight or wavy, dorsiventral leaves and stomata in the lower epidermis, the anomocytic stomatal apparatus, high density of cells in both the upper and lower epidermis, as well as stomata in the lower epidermis, large stomata (on average 78.3 μm long and 53.7 μm wide). The conducted study classifies *L. buschianum* as a heliophyte and mesophyte, but the plants also have a number of features that can be considered as an adaptation mechanism to arid environments. *L. buschianum* is a species with a fairly wide range of tolerance in relation to substrate moisture, which allows it to grow both in habitats with a well-balanced moisture supply and in conditions of moisture deficiency. The species is recommended for cultivation in stony gardens and open areas with good drainage.

Keywords
Leaf anatomy, *Lilium*, rare plants, Siberian species, epidermis, mesophyll, heliophyte, mesophyte

Introduction

The genus *Lilium* L. includes about 100 species distributed mainly in East and Southeast Asia (Baranova 1999). Four species of lilies growing in Siberia (Vlasova 1987) are of both scientific and practical interest. Of these, the least studied is the Busch lily (*L. buschianum* G.Lodd.), an East Asian species widespread in the forest-steppe and steppe zones of the Transbaikal Territory (Chita Region). Apart from Siberia, it is extensively distributed in the south of the Russian Far East (Primorsky Territory, Amur Region), in northeastern China, in the east of Mongolia (foothills of the Greater Khingan), and in Korea and Japan (Vlasova 1987; Songyun and Tamura 2000; Darman 2020; Baasanmunkh et al. 2022). The primary geographical distribution of the species is in China. It grows at an altitude of 600–2200 m a.s.l. in meadows, on slopes, along forest edges, and in sparse thickets of shrubs and small-leaved forests. In the Far East, it prefers dry meadows and slopes with sufficient sunlight (Vrishch 2011). Often found together with L. pumilum (Baranova 1990). O.A. Sorokopudova classifies the Busch lily as a mesophyte with moderately expressed xeromorphic features (Sorokopudova 2019).

Many taxonomists do not support the taxonomic independence of the Busch lily and classify it as a variety of the East Asian species *L. concolor* var. *partheneion* (Siebold & de Vriese) Bake (POWO 2025), or *L. concolor* var. *pulchellum* (Fischer) Regel (Songyun and Tamura 2000; Kang et al. 2022). G. H. Stephen (1986) noted the superficial similarity of *L. concolor*, including *L. concolor* var. *pulchellum*, with *L. pumilum*, but pointed out that the species differ in the different direction of the flowers in the inflorescence: in *L. concolor*, the flowers are directed upward, while in *L. pumilum*, they are directed downward. At the same time, he emphasized that the relationship of *L. concolor* with other species of the genus *Lilium* is unclear and isolated the species in a separate section, Asteridium S. G. Haw. sect. nov. According to the modern classification of the genus *Lilium*, *L. concolor* belongs to the section Sinomartagon (Pelkonen and Pirttilä 2012). A recent phylogenomic analysis has classified *L. concolor*, including *L. concolor* var. *pulchellum*, in the clade with *L. amabile*, *L. callosum* and *L. pumilum*, and revealed a high degree of conservation of the genome structure within the genus *Lilium* (Lei et al. 2021).

In this article, we accept *L. buschianum* as an independent species, adhering to the views of Russian botanists (Baranova 1990; Baykov 2005; Baykov 2012; Chepinoga et al. 2024). *L. buschianum* differs from *L. concolor* Salisb. by the presence of a bare green (rather than brownish, short, stiffly pubescent) stem; the perianth tepals are tomentose on the outside with small dark spots (Baranova 1990).

The Busch lily exhibits valuable traits, including cold resistance and high ornamental value, which makes it an ideal candidate for landscaping (Darman 2020); widely used in hybridization by breeders in many countries (Baranova 1990).

In the Russian Federation, *L. buschianum* is listed in the Red Books of the Transbaikal Territory (Polyakov 2017), Amur Region (Senchik and Malikova 2020), Jewish Autonomous Region (Rubtsova and Schlotthauer 2019), and Khabarovsk Territory (Voronov 2019). The population sizes of the species are small; in the vicinity of populated areas, the species often exhibit signs of decline due to harvesting of plants for bouquets and the economic development of territories as well as habitat disruption (fires, land cultivation, tourism, grazing). In Chita Region, *L. buschianum* is found sporadically as single individuals or small groups (Scheglova 2017).

M.V. Baranova (1990) points out that the anatomical structure of lily leaves is not only an additional diagnostic feature but also reveals information about the plant's environmental conditions. Thus, in *Lilium* of humid habitats (mesophytes), leaf tissue consists of a small number of layers of large cells (5–9) with large intercellular spaces. Palisade tissue is usually single- or double-layered and is located only on the adaxial side of the leaf. Its cells are often irregularly shaped, sometimes with outgrowths–branched cells. Stomata are located only on the abaxial side of the leaf and are few in number. The presence of cells with outgrowths in typical mesophytes of the genus *Lilium* has also been noted by some foreign researchers (Güven et al. 2014). Lilies native to arid habitats are characterized by the presence of palisade tissue on both the upper and lower surfaces of the leaf blade; its cells are rectangular, highly elongated, and the intercellular spaces are small. Stomata are present on both the upper and lower surfaces, and their number is significantly greater than in lily species native to humid habitats (Baranova 1990; Sorokopudova 2019).

M.V. Baranova (1990) notes that while leaf structure allows for a fairly accurate assessment of a species' growing conditions, the structure of the epidermis often allows for the identification of lily species. She suggests comparing species based on features such as the similarities and differences in the cell wall outlines of the upper and lower epidermis, as well as the number of stomata per unit surface area and the size of stomata and epidermal cells. She believes that many related lily species have similar epidermal tissue structures.

Yu.V. Gamaley (Gamaley 2004) also notes a certain conservatism in the structure of plant integumentary tissues and the vascular system, which allows them to be used for systematic research. At the same time, the presence of straight or slightly convoluted epidermal cell walls and reduced cell size in lily species are considered xeromorphic traits (Sorokopudova 2019), providing information about the ecological properties of plants.

Plant anatomy as a research method enables us to reveal features more constant and less affected by environmental factors than traditional morphology (Yembaturova and Korchagina 2011).

Data on the anatomy of Busch's lily available in the literature are fragmentary (Nemchenko and Novikov 1978; Sorokopudova 2019) and describe primarily the general structure of the aboveground parts of the plant. The lack of quantitative data and the absence of modern photographs of anatomical sections of vegetative organs indicate the need for further research.

The aim of this study was to investigate the anatomical features of *L. buschianum* leaf blades and compare them with those of other species in the genus growing in Siberia.

The results will allow us to assess the species range of ecological tolerance to key abiotic factors, such as light intensity and substrate moisture, at the morphological and anatomical level. The information obtained is necessary for developing effective introduction and reintroduction strategies aimed at preserving biodiversity and restoring species populations.

The results obtained are also of interest in connection with predicted climate changes in the species' natural habitats.

A comparison of the anatomical characteristics of the leaves of four Siberian lily species will expand the information on the ways in which species adapt to different growing conditions in the region, in particular in the direction of increasing drought resistance (transition from a typical dorsiventral to an isolateral mesophyll structure; an increase in the number of stomata and the thickness of the epidermis, etc.).

Materials and methods

The study was conducted in 2024–2025 in the Siberian Botanical Garden of Tomsk State University in the forest natural climatic zone. The plants were cultivated under close-to-natural conditions.

The object of the study were *L. buschianum* plants, initially sourced from their natural habitats: Amur Region, Tambov District, Bugrovoye Tract. Since 2022, it has been cultivated in the Siberian Botanical Garden.

The methodological basis for studying the leaf anatomy included generally accepted techniques (Vehov et al. 1980) and the works by K. Esau (1980a, 1980b) and A.A. Pautov (2003, 2012). The stomatal index was calculated using the formula proposed by A. Kästner (1972). The types of stomata were determined according to the classification of M.A. Baranova (1985). The material was collected during the flowering period, when the plants had fully formed leaves.

The works of N.K. Bordman (1977), T.K. Goryshina (1979), T.J. Givnish (1988), L.A. Ivanova (2014) and others were used as a methodological basis for assessing the ecological adaptations of plants to different growing conditions. The anatomical structure of the leaf directly reflects the plant's adaptive strategies to specific environments (Simioni et al. 2017; Gamaley 2004; Ivanova 2014). In addition, because leaf structure is the basis for leaf function, leaves can develop appropriate morphological structures to optimize functions with long-term exposure to the environment (Dunbar-Co et al. 2009). According to some scientists (Vasilevskaya and Butnik 1982; Ivanova 2014), the structure of the leaf mesophyll is the most ecologically flexible. For example, the type of mesophyll structure reflects the growing conditions of the species: a homogeneous type is more common in shade-loving plants, while a dorsoventral type is characteristic of light-loving mesophytes, and an isopalisade type is characteristic of xerophytes. However, to clarify the ecological properties of a species, it is necessary to take into account not only the mesophyll type, but also to conduct a comprehensive assessment of the quantitative parameters of the mesophyll, in particular the concentration of cells in the leaf (Ivanova 2014). According to the literature, xeromorphic leaf blade structure traits include the extensive development of palisade parenchyma (Butnik et al. 2009; Sorokopudova 2019), which, to some extent, according to N.A. Karnaukhova, I.Yu. Selyutina, and O.V. Dorogina (2020), compensates for the small leaf area in xerophytes. Ecological specialization of the leaf to moisture deficiency also occurs due to an increase in the number of stomata (Plennik 1989). Mesomorphic leaves have a loose structure with a developed intercellular system (Karnaukhova et al. 2020).

K.A. Sobolevskaya (1977), E.V. Tyurina (1989) considered a group of xeromesophyte plants, which acquired xeromorphic features in the process of evolution against the background of adaptation to the harsh conditions of the cryoxerophilic (cold and dry) regime of Siberia, as valuable source material for introduction.

Leaf cross sections were prepared by cutting the middle portion of the leaf by a MZ-2 freezing microtome at a thickness of 60–90 μm. For leaf anatomy, five replicates were collected from leaves of five shoots; for each sample, 30 leaf blade sections were analyzed using a light microscope (Zhukova and Minets 2020).

The number of cells and stomata per 1 mm2 of epidermis was counted after separating the epidermis from the middle portion of the leaf by simple mechanical action (Barykina et al. 2004). Images of the leaf micropreparations and microscopic measurements were taken using a Carl Zeiss Axio Lab. A1 light microscope with an AxioCam ERc 5s digital camera via the Axio Vision 4.8 program.

Morphometric parameters of leaf blades (length, width) were determined on 30 leaves from the middle part of generative shoots of 15 plants.

The measurement results were processed via Statistica 8.0. The following parameters were determined: M (Mean) – arithmetic mean; m (SE) – mean squared error, CV – coefficient of variation, MinMax – minimum and maximum values.

Anatomical characteristics of the epidermis are considered low variable at $CV < 20\%$, moderately variable at $CV = 20–40\%$, and highly variable at $CV > 40\%$ (Butnik and Timchenko 1987).

To determine the statistical significance of the differences in *L. buschianum* characteristics compared to other lily species grown in the Siberian Botanical Garden of Tomsk State University, the Student's t-test for independent samples (Zhukova and Minets 2020) was performed using Statistica 8.0. Statistically significant differences were determined at $p < 0.05$.

Results and discussion

Lilium buschianum is a herbaceous perennial plant 30–50 cm high. Bulbs oblong-ovate or ovate, compact, 2.0–3.5 cm in diameter; scales not numerous, white, dense. Stems smooth. Leaves alternate, sessile, narrowly lanceolate, linear, pointed, with a small number of hairs along margins, 5.8–10.0 cm long (average 7.2 ± 0.6 cm) and 0.4–1.0 cm wide (average 0.7 ± 0.6 cm) in the middle portion of the stem. Orange-red star-shaped flat flowers directed upwards, solitary or collected in an apical inflorescence, 4.2–5.8 cm in diameter. Perianth leaflets with small dark spots, dense, white-tomentose on the outside (Fig. 1).

Figure 1. *Lilium buschianum* in the collection plot, Siberian Botanical Garden of Tomsk State University.

The epidermis is single-layered, consists of tightly closed cells, and is covered with cuticle on either side of the leaf (Fig. 2). The epidermis cell walls are wavy, straight linear above the veins.

Lilium buschianum reliably differs from other Siberian lily species by the highest density of epidermis cells per 1 mm^2 in both the upper epidermis and the lower one

(Table 1). The upper epidermis cells are larger than those of the lower epidermis, which is typical of species of the genus *Lilium* (Baranova 1990). At the same time, *L. buschianum* is close to *L. pumilum* in the size of the upper epidermis cells and to *L. pilosiusculum* in the size of the lower epidermis cells. *L. buschianum* may have papillae along leaf margins or on the lower (abaxial) surface of the leaf in the vein area, and the epidermis may contain bubble-like cells reported earlier by E.P. Nemchenko and V.S. Novikov (Nemchenko and Novikov 1978).

The leaves of *L. buschianum* have a dorsiventral mesophyll structure with spongy and palisade parenchyma, which is most typical of species of the genus *Lilium*, according to literature data (Sorokopudova 2019). The palisade mesophyll of *L. buschianum* consists of a single layer of cells found only on the upper side of the leaf blade (Fig. 2), which distinguishes it from *L. pumilum* and makes it closer to *L. pensylvanicum* and *L. pilosiusculum*.

Lilium buschianum reliably differs from other Siberian lily species by the leaf thickness in the vein area (minimum values) and mesophyll thickness. The mesophyll of *L. buschianum* is thinner than that of *L. pensylvanicum* and *L. pumilum*, but is significantly (at $p < 0.05$) thicker than that of the scioheliophyte *L. pilosiusculum*.

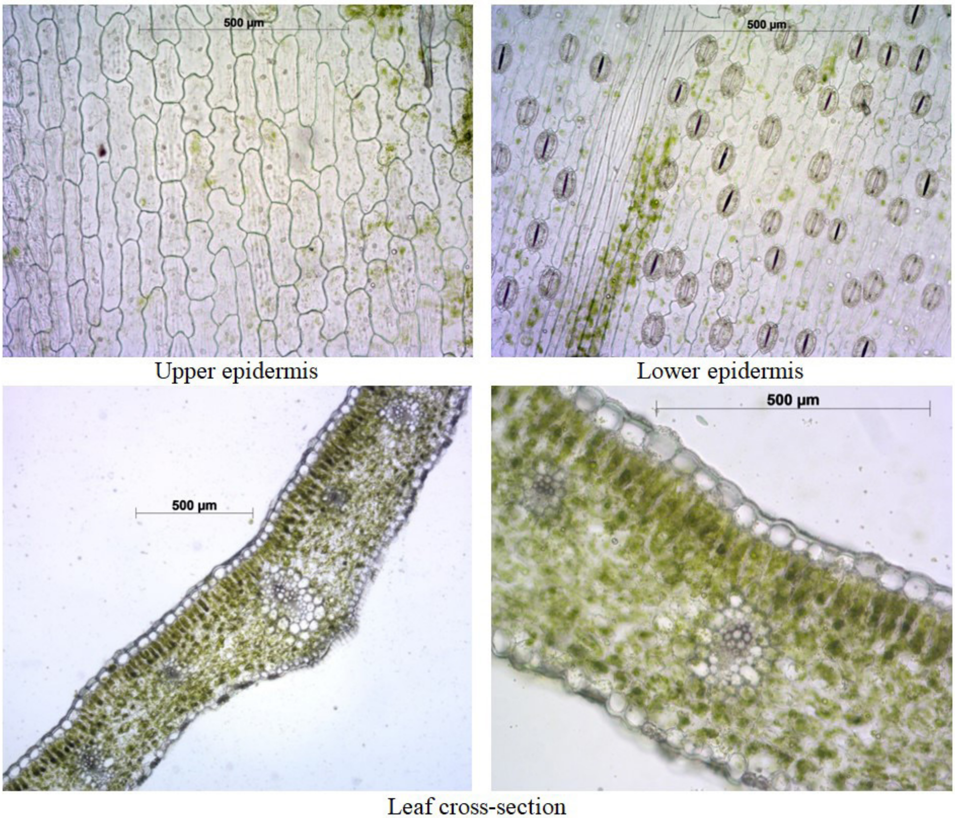

Figure 2. Leaf anatomy of *Lilium buschianum*.

Table 1. Comparative anatomical characteristics for leaves of Siberian lily species (compared to *L. buschianum*)

Characteristics	*L. buschianum*	*L. pensylvanicum*	*L. pilosiusculum*	*L. pumilum*
Number of UE cells per 1 mm^2, pcs	$115.5^{A}\pm2.9$ / 13.8	$66.4^{B}\pm2.0$ / 16.2	$55.6^{B}\pm2.7$ / 27.0	$100.8^{B}\pm3.0$ / 13.5
Number of UE stomata per 1 mm^2, pcs	–	–	–	40.8 ± 1.8 / 24.5
UE stomatal index, %	–	–	–	28.8 ± 1.3 / 17.3
Size of UE cells, μm^2	$14625.4^{A}\pm438.2$ / 16.4	$39611.1^{B}\pm1650.5$ / 22.8	$20291.2^{B}\pm1016.5$ / 27.4	$15489.5^{A}\pm852.2$ / 30.1
Number of LE cells per 1 mm^2, pcs	$118.4^{A}\pm2.9$ / 13.6	$57.6^{B}\pm3.0$ / 28.6	$77.9^{B}\pm3.0$ / 21.4	$91.7^{B}\pm3.7$ / 21.9
Number of LE stomata per 1 mm^2, pcs	$70.5^{A}\pm1.9$ / 14.4	$40.8^{B}\pm1.6$ / 20.8	$44.3^{B}\pm3.5$ / 43.2	$65.6^{A}\pm3.1$ / 25.9
LE stomatal index, %	$37.4^{A}\pm0.8$ / 12.1	$42.1^{B}\pm1.6$ / 21.3	$35.3^{A}\pm2.0$ / 30.5	$41.6^{B}\pm1.1$ / 14.5
Length of UE stomata, µm	–	–	–	85.5 ± 1.6 / 10.1
Width of UE stomata, µm	–	–	–	55.8 ± 1.4 / 14.1
Length of LE stomata, µm	$78.3^{A}\pm1.38$ / 8.8	$105.3^{B}\pm2.5$ / 12.9	$78.0^{A}\pm0.9$ / 6.4	$88.1^{B}\pm1.4$ / 8.5
Width of LE stomata, µm	$53.7^{A}\pm1.8$ / 18.4	$60.5^{B}\pm0.9$ / 7.9	$57.2^{A}\pm0.7$ / 6.6	$55.4^{A}\pm0.5$ / 4.5
Size of LE cells, μm^2	$11441.9^{A}\pm430.1$ / 20.6	$22866.7^{B}\pm1745.0$ / 41.8	$11513.3^{A}\pm792.1$ / 37.7	$14190.4^{B}\pm852.2$ / 32.9
Leaf thickness in the vein area, µm	$632.9^{A}\pm21.2$ / 18.3	$1017.6^{B}\pm21.3$ / 11.5	$989.1^{B}\pm33.6$ / 18.6	$813.3^{B}\pm14.8$ / 10.0
Leaf blade thickness, µm	$533.8^{A}\pm24.2$ / 24.8	$552.3^{A}\pm11.2$ / 11.1	$411.2^{B}\pm8.5$ / 11.4	$590.2^{B}\pm8.3$ / 7.7

Characteristics	*L. buschianum*	*L. pensylvanicum*	*L. pilosiusculum*	*L. pumilum*
UE thickness, µm	$70.4^{A}\pm6.0$ / 46.9	$49.9^{B}\pm1.2$ / 13.1	$39.4^{B}\pm1.5$ / 20.7	$43.8^{B}\pm1.5$ / 18.5
LE thickness, µm	$53.0^{A}\pm3.5$ / 35.8	$48.4^{A}\pm1.5$ / 17.0	$32.0^{B}\pm0.7$ / 12.6	$42.5^{B}\pm1.2$ / 15.0
Mesophyll thickness, µm	$383.9^{A}\pm16.8$ / 23.9	$469.3^{B}\pm9.2$ / 10.8	$332.4^{B}\pm8.8$ / 14.6	$534.8^{B}\pm7.8$ / 8.0
Thickness of palisade mesophyll, µm	$164.5^{A}\pm12.9$ / 43.1	$130.2^{B}\pm4.5$ / 18.8	$112.0^{B}\pm2.5$ / 12.1	$188.2^{A}\pm5.7$ / 16.5
Thickness of spongy mesophyll, µm	$212.6^{A}\pm11.1$ / 28.5	$351.3^{B}\pm6.8$ / 10.5	$220.9^{A}\pm7.8$ / 19.4	$333.0^{B}\pm12.8$ / 21.1
Palisade/spongy mesophyll ratio	$0.8^{A}\pm0.1$ / 50.7	$0.4^{B}\pm0.0$ / 19.0	$0.6^{B}\pm0.0$ / 26.4	$0.7^{A}\pm0.1$ / 108.3
Length of cells of the upper mesophyll layer, µm	$72.2^{A}\pm3.2$ / 24.4	$90.3^{B}\pm2.3$ / 13.8	$70.9^{A}\pm2.0$ / 15.5	$89.4^{B}\pm2.7$ / 16.7
Width of cells of the upper mesophyll layer, µm	$28.0^{A}\pm1.2$ / 24.1	$40.4^{B}\pm1.4$ / 18.7	$34.3^{B}\pm1.0$ / 16.4	$25.5^{A}\pm0.9$ / 19.3

Note: * – anatomical features of leaves of three lilies Siberian species (*L. pensylvanicum*, *L. pilosiusculum*, *L. pumilum*) were previously studied in detail by the authors of the article (Belaeva at al. 2024). In this study data on previously studied species are provided for ease of comparison. Statistically significant differences are reported only for *L. buschianum* and do not take into account differences between the three previously studied species: A – means that there are no statistically significant differences in the compared pair of values, B – means that the data have statistically significant differences from A at $p < 0.05$. Abbreviations: UE – upper epidermis, LE – lower epidermis, "–" – means that it is impossible to obtain data due to the absence of stomata in the upper epidermis. Data are presented as follows: above the line – arithmetic mean ± error of the mean, below the line – the coefficient of variation.

The leaves are of the hypostomate type, which is confirmed by literature data (Nemchenko and Novikov 1978; Sorokopudova 2019). The stomatal apparatus is anomocytic. The stomata located in the lower epidermis are rather large, 78.3 µm long and 53.7 µm wide. The number of stomata per 1 mm² on the lower epidermis in *L. buschianum* reliably exceeds that in *L. pensylvanicum* and *L. pilosiusculum* studied under the introduction conditions in Tomsk, and is close to *L. pumilum* (Table 1). E.P. Nemchenko and V.S. Novikov (Nemchenko and Novikov 1978), who studied the leaf anatomy of 15 lily species during introduction in the Botanical Garden of Moscow State University, revealed a similar pattern: the Busch lily exhibited the highest density of stomata in the lower epidermis compared to other taxa.

Overall, published data on the anatomical structure of the leaf blades of *L. buschianum* plants cultivated in Moscow and Novosibirsk are consistent with our results. Quantitative differences can be explained by variability of the species, associated with different agroclimatic cultivation conditions and the different origins of the introduced specimens. Unfortunately, quantitative characteristics of the anatomical traits of the *L. buschianum* leaf blade available in the literature are sparse, preventing a more detailed analysis.

In general, the four studied Siberian species of the genus *Lilium*, including the previously studied *L. pensylvanicum*, *L. pilosiusculum* and *L. pumilum* (Belaeva at al. 2024), are characterized by the single-layer epidermis with cuticle, anomocytic stomatal apparatus, and close values of the stomatal index of the lower epidermis (from 35.3% to 42.1%), large stomata.

Lilium buschianum is close to *L. pumilum* in the size of the upper epidermis cells, the number of the lower epidermis stomata per 1 mm^2, the stomata width, the palisade mesophyll thickness, the palisade/spongy parenchyma ratio, and the width of the upper mesophyll layer cells. The species is also close to *L. pensylvanicum* in the leaf blade thickness and the lower epidermis thickness. At the same time, the size of stomata, the size of lower epidermis cells, stomatal index values, the spongy mesophyll thickness, and the length of the upper mesophyll layer cells bring *L. buschianum* closer to *L. pilosiusculum*.

Low variability is typical of the quantitative anatomical characteristics of the *L. buschianum* leaf blade, such as the size and the number per 1 mm^2 of the upper and lower epidermis cells, the size and the number per 1 mm^2 of the upper and lower epidermis stomata, and the stomatal index.

The leaf thickness in the vein area and the lower epidermis thickness exhibit medium variability. The thickness of the leaf blade, upper epidermis, mesophyll, palisade and spongy mesophyll, the size of cells of the upper mesophyll layer, and the palisade/spongy parenchyma ratio show high variability (CV 23,9%–50.7%). Therefore, these are not suitable as diagnostic features of the *L. buschianum* leaf blade.

Lilium buschianum specimens from Novosibirsk (Sorokopudova 2019) exhibited thinner leaves with a thickness of 315 μm compared to our data. At the same time, the leaf thickness in Moscow specimens (394–470.2 μm) (Nemchenko and Novikov 1978) is close to that in the specimens reported in this study (533.8 μm). Tomsk specimens have an intermediate stomatal number of 70.5 pcs per 1 mm^2 (between Moscow (98 pcs per 1 mm^2) and Novosibirsk (58.8 pcs per 1 mm^2)).

The most important abiotic factors determining the distribution of the species are illumination and soil moisture. The conducted study attributes *L. buschianum* to heliophytes (high density of epidermis cells leading to increased density of epidermis and stomata in the lower epidermis, which increases their total surface area and enhances absorption of carbon dioxide by mesophyll; developed palisade mesophyll; wavy or straight walls of the upper epidermis) and mesophytes (dorsiventral leaf, stomata located in the lower side of the leaf plate; developed spongy mesophyll). On the other hand, the following features should be considered as an adaptation mechanism to arid environments: narrow leaves with minimal mesophyll thickness among Siberian species, reduced leaf area and, consequently, lower transpiration losses, high density of epidermis cells and stomata in the lower epidermis, small epidermis cells, thick upper epidermis. Xerophytic and heliophytic traits also include certain morphological features of the species: pubescence of the buds, the presence of fairly narrow, few leaves, and compact semi-tunicate bulbs with a small number of scales (Baranova 1999; Sorokopudova 2019). Lily species with this bulb structure are confined to open habitats and grow in forest edges, mountain meadows, and steppes.

The anatomical data obtained during the study are consistent with the information on the phytocoenotic confinement of *L. buschianum* published in the literature (Vlasova 1987; Baranova 1990; Songyun and Tamura 2000; Darman 2020; Baasanmunkh et al. 2022; Vrishch 2011). In natural populations, *L. buschianum* is characterized by a wide range of moisture tolerance, growing in both well-watered and poorly watered conditions, preferring well-lit habitats.

As shown by our previous studies (Belaeva et al. 2024), two Siberian species (*L. pensylvanicum* and *L. pilosiusculum*) are classified as mesophytes. Of these, *L. pilosiusculum* is the only representative of the group of ancient mesophytic species of the genus *Lilium* in Siberia, growing in diffused light (scioheliophyte). According to M.V. Baranova (1999), the development of mesomorphic forest species of lilies was associated with the formation of deciduous broadleaf forests of Tertiary origin. The remaining Siberian species of lilies are classified as heliophytes. According to a number of researchers (Baranova 1990; Sorokopudova 2019), the most xeromorphic species of the genus is *L. pumilum*, native to Siberia. According to published data (Korolyuk 2006), the ecological optima for *L. pilosiusculum* and *L. pensylvanicum* across a soil moisture gradient for southern Siberia are 61.5 and 55.5, respectively, compared to 54 for *L. pumilum*. Unfortunately, there are no published data on the ecological optima for *L. buschianum*.

A comparison of leaf sizes of four Siberian species introduced into the Siberian Botanical Garden of Tomsk State University showed that the largest leaf blades were found in *L. pilosiusculum* and *L. pensylvanicum*, while the smallest and narrowest were found in the xerophyte *L. pumilum* (Table 2). By the length of leaf blades, *L. buschianum* is most similar to L. pumilum, but has wider leaves. The length of *L. buschianum* leaves is 1.9–2 times smaller, and the width of leaves is 2.1–2.7 times smaller than those of *L. pilosiusculum* and *L. pensylvanicum*, however, the number of stomata per unit area in *L. buschianum* leaf blades is 1.6–1.7 times greater than that of *L. pilosiusculum* and *L. pensylvanicum*.

This study found that *L. buschianum*, which often grows in natural biocenoses next to alongside *L. pumilum*, exhibits the substantial greate similarity to this species in a range of anatomical characteristics, however, it differs from it in its dorsoventral leaves, and is classified as a mesophyte with some xeromorphic features. Common morphological and biological features of *L. buschianum* and *L. pumilum* include the presence of equal-sided, slightly slanted semi-tunicate bulbs with few scales, fairly narrow leaves, above-ground and rapid seed germination, and a short virginal period (2–3 years) (Baranova 1999). Both species, according to M.V. Baranova (1999), grow in similar ecological conditions: drier habitats (steppes, foothills, steppe meadows, intermontane dry basins) compared to most other species of the genus. These two species likely evolved in parallel, adapting to the cryoxerophilic (cold and arid) conditions of Eastern Siberia.

Table 2. Morphometric parameters of leaf blades of *L. buschianum* compared to three species of Siberian lilies upon introduction to the Siberian Botanical Garden of Tomsk State University

Species	Leaf length, cm	Leaf width, cm
L. buschianum	$7.2^{A}\pm0.4$	$0.7^{A}\pm0.06$
L. pensylvanicum	$14.5^{B}\pm0.2$	$1.5^{B}\pm0.08$
L. pilosiusculum	$13.9^{B}\pm0.2$	$1.9^{B}\pm0.09$
L. pumilum	$8.4^{B}\pm0.2$	$0.2^{B}\pm0.01$

Note: Statistically significant differences are reported only for *L. buschianum* and do not take into account differences between the three previously studied species: A – means that there are no statistically significant differences in the compared pair of values, B – means that the data have statistically significant differences from A at $p < 0.05$. Data are presented as follows: arithmetic mean ± error of the mean.

Conclusion

The study revealed that the *L. buschianum* is characterized by the following anatomical features of the leaf blade: the cell walls of the epidermis are straight or wavy, dorsiventral leaves and stomata in the lower epidermis, the anomocytic stomatal apparatus, high density of cells in both the upper and lower epidermis, as well as stomata in the lower epidermis, large stomata (on average 78.3 µm long and 53.7 µm wide).

Reliable differences between *L. buschianum* and the other three studied Siberian species of the genus *Lilium* were established based on quantitative traits such as the number of cells per unit area in the upper and lower epidermis, leaf vein thickness, and mesophyll thickness. Of these, the first two traits exhibit low levels of variation.

The species is most close to *L. pumilum* by complex of the quantitative anatomical characteristics, but it differs significantly by the presence of dorsiventral (rather than isolateral) leaves.

Lilium buschianum is classified as a species with a fairly wide range of tolerance in relation to substrate moisture, which allows it to grow both in habitats with well-balanced supply of moisture and in conditions of moisture deficiency.

The species is recommended for cultivation in stony gardens and open areas with good drainage.

Acknowledgements

The study was performed within the framework of a state assignment of the Ministry of Science and Higher Education of the Russian Federation (project No. FSWM-2024-0006).

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