RESEARCH ARTICLE

Micromorphological traits of the leaf surface in species of the genus *Sansevieria* Thunb. s.str. (Asparagaceae)

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Abstract

This study investigated the leaf surface micromorphology of 12 species of the genus *Sansevieria* using light microscopy and scanning electron microscopy. The research focused on identifying micromorphological traits associated with plant stress tolerance, including epidermal cell shape, cuticle thickness, stomatal distribution and density, and cuticular characteristics with epicuticular wax deposits. In most of the studied *Sansevieria* species, the leaves are amphistomatic, whereas hypostomatic leaves are observed in *S. cylindrica, S. canaliculata*, and *S. suffruticosa*. In all studied taxa, the epidermis consists of a single layer of cells and lacks trichomes.

The examined *Sansevieria* species are characterized by a well-developed cuticular layer and the presence of wax deposits that perform protective and water-conserving functions. The thickness of the cuticle and its ornamentation vary both among species and between leaf surfaces within the same species. The abaxial leaf surface generally exhibits a more developed cuticle than the adaxial surface, a feature particularly pronounced in *S. cylindrica, S. canaliculata, S. kirkii, S. roxburghiana, S. gracilis, S. suffruticosa*, and *S. intermedia*. All investigated species possess anomocytic stomata. Stomatal density on the abaxial leaf surface ranged from 9 to 27 mm^2 among the studied species. These interspecific variations reflect distinct strategies for optimizing water balance under arid conditions.

At the level of leaf micromorphology, amphistomaty, the spatial organization of epidermal cells, the presence of a cuticular layer with epicuticular wax deposits of various configurations, differences in stomatal sunkenness and density, and the occurrence of underdeveloped stomata can be considered markers of stress tolerance in this genus. The identified micromorphological markers provide insight into the adaptive xeromorphic traits of *Sansevieria* and have potential applications in applied research, including biotechnological projects and phytoremediation, including green infrastructure development.

Keywords: *Sansevieria*, light microscopy, scanning electron microscopy, cuticle, epidermis, stomatal apparatus, micromorphology, phytoremediation

Introduction

Representatives of the genus *Sansevieria* s.str. have been actively studied in recent years with a view to their use in phytoremediation (Boraphech & Thiravetyan, 2015; Tariq et al., 2017), phytochemistry and phytopharmacology (Tkachenko et al., 2017; Maryniuk et al., 2018; Thu et al., 2020), biotechnology, and ornamental horticulture. To date, the general morphology of representatives of the genus (Koller & Rost, 1988a), their general anatomy (Koller & Rost, 1988b; Klimko et al., 2018) and the structure of water-storing tissue in leaves (Koller & Rost, 1988b), as well as the structure of the epidermis of individual species (Shkrum et al., 2012; Klimko et al., 2018). The vast majority of works are devoted to the cultivation of S. *trifasciata* Prain varieties (Babu & Srinivasa Prabhu, 2023).

However, despite the large number of publications devoted to various aspects of the biology of this genus, modern anatomical and morphological studies of the genus *Sansevieria* remain insufficient, especially in the context of searching for functional traits that could be used in plant introduction for the purpose of *ex situ* biodiversity conservation, phytoremediation (thanks to ability of these plants to withstand abiotic stresses and absorb heavy metals), pharmacognosy, and biotechnological developments as donors of stable traits for *in vitro* cultivation or the search for biologically active substances.

The genus *Sansevieria* s.str. comprises ca. 100 species and infraspecific taxa, most of which have been described over the last three decades (Newton, 2020; Burkart et al., 2023). According to recent molecular phylogenetic studies, the genus *Sansevieria* Petagna was nested within the genus *Dracaena* Vand. ex L. (Takawira Nyenya et al., 2018; van Kleinwee et al., 2022), which belongs to the family Asparagaceae, subfamily Nolinoideae, order Asparagales (Kim et al., 2010; Chen et al., 2013; Lu & Morden, 2014; The Angiosperm Phylogeny Group et al., 2016). Within this work, we use the term *Sansevieria* to refer to the monophyletic group within *Dracaena* – the *Sansevieria* clade (van Kleinwee et al., 2022).

Sansevieria species occupy a wide range of ecological niches. This is a group of xerophytic, perennial succulent plants, distributed mainly in tropical and subtropical Africa, Madagascar, the Arabian Peninsula, and the Indian subcontinent. Most representatives of the genus are adapted to conditions of limited water supply. Typical habitats of *Sansevieria* species include termite mounds, river floodplains, and rocky outcrops. Some species form clumps at the base of tree trunks (Takawira & Nordal, 2002). Members of the *Sansevieria* genus are found in various tropical biomes within so-called 'hotspots' that serve as priority areas for biodiversity conservation (Burkart et al., 2025).

Leaf micromorphology is one of the key indicators of plant adaptation to environmental conditions. During evolution, certain structural features have developed that correlate well with indicators of plant water status, drought resistance, the ability to regulate gas exchange, and the ability to withstand stress factors.

Data on the micromorphological features of the leaf were used to differentiate species of the genus *Phaedranassa* Herb. (Amaryllidaceae, Asparagales) along an altitude gradient (Zhila & Marinyuk, 2017), to assess the 'adaptation syndrome' when transferring juvenile plants of *Guarianthe bowringiana* (O'Brien) Dressler & W.E.Higgins (Orchidaceae) from *in vitro* culture to greenhouse conditions (Buyun et al., 2021). The taxonomic significance of the micromorphological features of the vegetative organs of *Dracaena* s.l. (Klimko et al., 2018), as well as other genera of the Asparagaceae family, including *Aspidistra* Ker Gawl. (Vislobokov et al., 2021) and *Chlorophytum* Ker Gawl. (Nalawade & Gurav, 2017) has been proved earlier.

Therefore, our work aimed to conduct a comparative study of the micromorphological features of the leaf blade of *Sansevieria* model species as a marker of adaptive traits for use in biodiversity conservation and eco-biotechnology.

Material and methods

The study materials were collected in the greenhouse of the Department of Tropical and Subtropical Plants at the M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine. The objects of the study were plants of 12 *Sansevieria*

species: S. *aethiopica* Thunb., S. *canaliculata* Thunb., S. *cylindrica* Bojer ex Hook., S. *gracilis* N.E.Br., S. *grandis* Hook.f., S. *intermedia* N.E.Br., S. *kirkii* Baker, S. *parva* N.E.Br., S. *roxburghiana* Schult. & Schult.f., S. *suffruticosa* N.E.Br., S. *trifasciata* Thunb., S. *metallica* Gérôme & Labroy.

Mature leaves of the middle formation were used for the study. The samples were taken from the central part of the leaf blade.

When studying the leaf blade surface with light microscopy (LM), the Palacci replica technique was used, in which the collodion solution was replaced with a transparent varnish (Furst, 1979; Karupu, 1984). The scraping method described by Cutler et al. (2007) was also applied with minor modifications for sample preparation.

For scanning electron microscopy (SEM) examination, the samples were immersed in 100 % tert-butanol for 1 h at –10 °C. Metal containers with frozen samples were placed on a table cooled to –60 °C in the working volume of a vacuum universal post (VUP-5M). During vacuuming of the working volume, the samples were dried by sublimation of frozen tert-butanol. The dried leaf samples were coated with carbon in VUP-5M and platinum using a JFC-1600 Auto Fine Coater (JEOL, Japan). The micromorphology of the leaf surfaces of the studied *Sansevieria* species was visualized using a JSM-6700F scanning electron microscope (JEOL, Japan) at an acceleration voltage of 15 kV in high vacuum mode.

The epidermal surface of the leaves of the study species was described using terminology commonly accepted in plant cytology (Fahn, 2002; Dickison, 2000). The density of stomata and their linear dimensions were determined using ImageJ software. The types of stomata were determined according to Baranova's (1985) classification. Epicuticular wax deposits were evaluated by applying the Barthlott et al. (1998) technique.

For biometric studies of epidermal cells and the stomatal apparatus, a Primo Star B 48-0071 (Carl Zeiss) light microscope equipped with a Canon PowerShot A640 digital camera was used. Measurements were performed using licensed AxioVision Rel. 4.7 (Carl Zeiss) software.

The stomatal index (S_I) was determined using the Willmer (1983) formula:

$S_I = S/(E+S) \times 100\,\%$, where

S_I – stomatal index;

S – number of stomata per unit of leaf surface area;

E – number of ordinary epidermal cells, including secondary cells, per unit of area.

Statistical processing of the data was performed using standard methods with Excel 2010 software.

Results

Epidermis and ordinary epidermal cells

The epidermis of all studied taxa is represented by a single layer of cells without trichomes. The ordinary epidermal cells on the adaxial and abaxial surfaces are oriented along the long axis of the leaf and are arranged in more or less regular rows (Figs. 1 & 2). The cells are polygonal (4–7 angles), varying in elongation, with anticlinal walls ranging from straight to slightly curved. In most species, the anticlinal walls are thickened, except in S. *parva*, S. *trifasciata*, and S. *metallica* (Fig. 2 A–D, H, I).

The dimensions of epidermal cells vary significantly between species: length varies from 105.06 ± 16.19 µm (S. *grandis*, adaxial surface) to 53.99 ± 7.52 µm (S. *intermedia*, abaxial surface); width – from 41.53 ± 3.31 µm (S. *aethiopica*) to 13.81 ± 1.13 µm (S. *suffruticosa*); height – from 38.99 ± 4.65 µm (S. *grandis*) to 20.44 ± 3.10 µm (S. *gracilis*) (Table 1).

The data obtained on the density of the ordinary epidermal cells demonstrate significant interspecific variability among the studied *Sansevieria* species. In general, most species exhibit higher cell density on the abaxial surface, which is probably due to the functional specialization of the lower epidermis, particularly its more intensive participation in transpiration and protection of the leaf from overheating. The density of ordinary epidermal cells per unit area (1 mm²) in the studied species varies more than twofold (Table 1).

The highest epidermal cell density values were observed in S. *gracilis* (996 cells/mm² on the adaxial surface and 1145 cells/mm² on the abaxial surface) and S. *suffruticosa* (1017 cells/mm² on the abaxial surface). Such high values may indicate adaptation of these
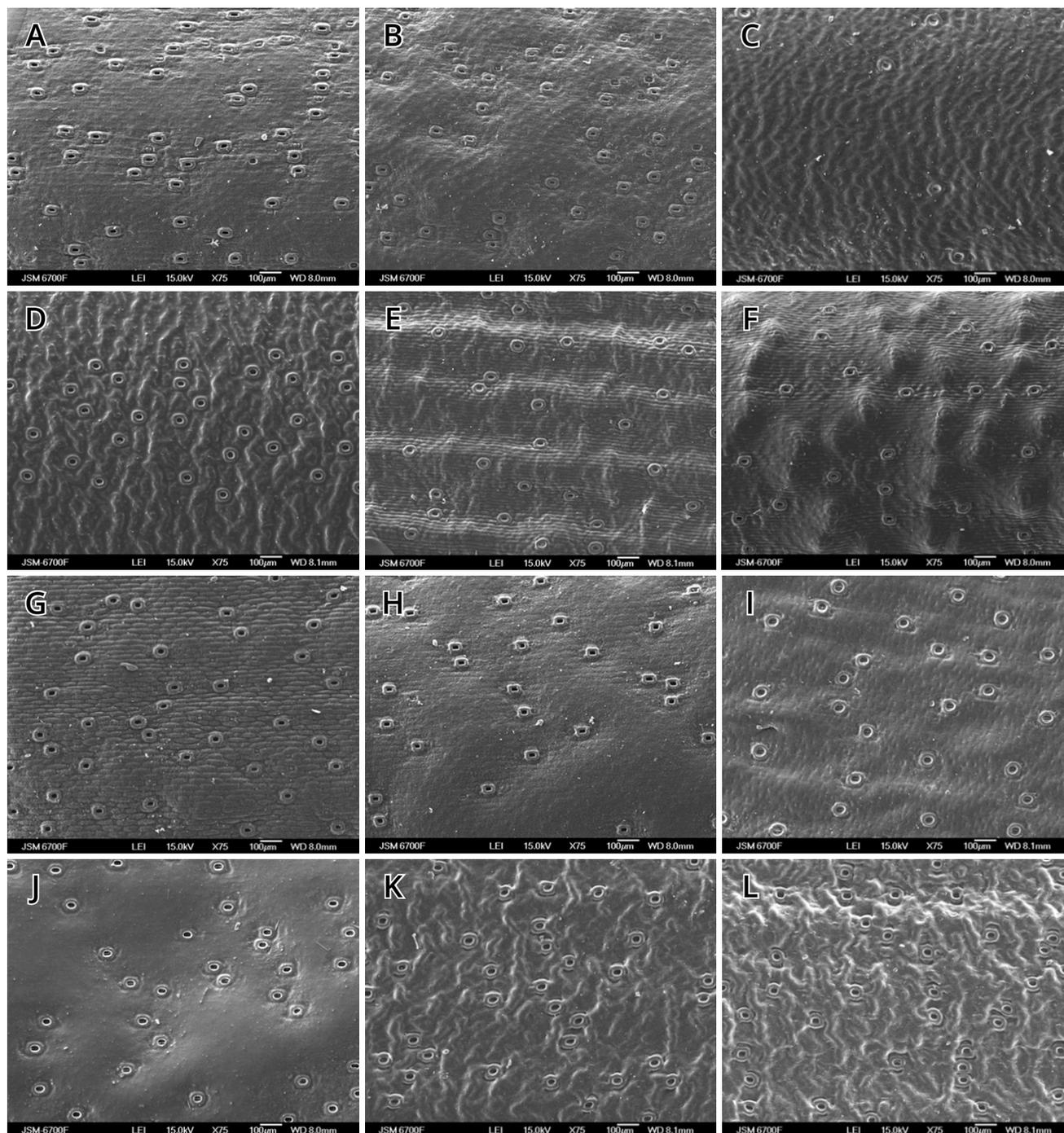
Figure 1. SEM micrographs of *Sansevieria* leaf surfaces: *S. aethiopica* (**A** – adaxial surface, **B** – abaxial surface); *S. canaliculata* (**C** – abaxial surface); *S. cylindrica* (**D** – abaxial surface); *S. gracilis* (**E** – adaxial surface, **F** – abaxial surface); *S. grandis* (**G** – adaxial surface, **H** – abaxial surface); *S. intermedia* (**I** – adaxial surface, **J** – abaxial surface); *S. kirkii* (**K** – adaxial surface, **L** – abaxial surface).

species to conditions of increased insolation and aridity, consistent with their natural ecology.

In contrast, S. *roxburghiana* and S. *trifasciata* show moderate density values, which may be related to a wider ecological amplitude and less dependence on xeromorphic conditions (Table 1).

The lowest stomatal density values were observed in S. *aethiopica* and S. *grandis*, which also correlate with the relatively larger size of their epidermal cells: the larger the cell area, the fewer stomata per unit area.

In most species, the abaxial surface contains more epidermal cells than the
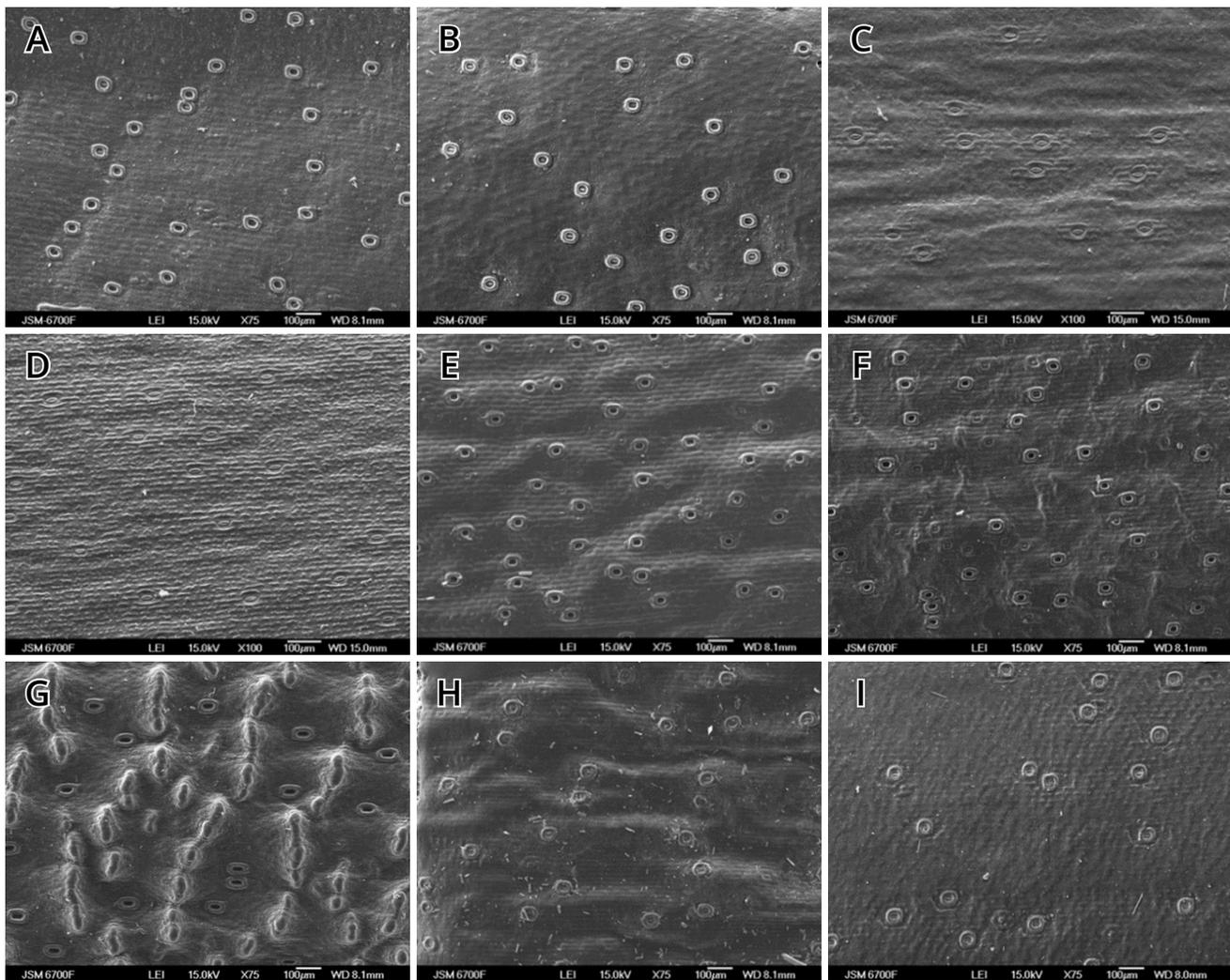
Figure 2. SEM micrographs of *Sansevieria* leaf surface: *S. metallica* (**A** – adaxial surface, **B** – abaxial surface); *S. parva* (**C** – adaxial surface, **D** – abaxial surface); *S. roxburghiana* (**E** – adaxial surface, **F** – abaxial surface); *S. suffruticosa* (**G** – abaxial surface); *S. trifasciata* (**H** – adaxial surface, **I** – abaxial surface).

adaxial surface. This is a typical feature of many succulent plants and species with stiff leaves, in which the lower epidermis plays a more significant mechanical and regulatory role: it provides better transpiration control, greater leaf mechanical strength, and better thermoregulation. This directly applies to the studied *Sansevieria* species, which are succulent xerophytes. Among the species we studied, only two (S. *grandis* and S. *trifasciata*) had a higher density of ordinary epidermal cells on the adaxial surface. Thus, the analysis clearly illustrates differences among *Sansevieria* species in epidermal cell density and suggests the existence of species-specific adaptive strategies related to their anatomical and ecological peculiarities.

Cuticle and wax deposits

The studied *Sansevieria* species are characterized by a well-developed cuticular cover and the presence of wax deposits that perform a protective and water-saving function. The distinctiveness of the cuticular cover and the details of its external structure vary both between species and between the surfaces of leaves of the same species. The abaxial surface of the leaf blade usually has a denser cuticular cover compared to the adaxial surface. This is particularly evident in S. *canaliculata*, S. *cylindrica*, S. *gracilis*, S. *intermedia*, S. *kirkii*, S. *roxburghiana*, and S. *suffruticosa* (Fig. 1 B, C, F, J, L; Fig. 2 F, G).

Differences are also observed in the density of the cuticular covering at the boundary of the ordinary epidermal cells. Areas of the surface located above the

Table 1. Morphometric characteristics of the leaf epidermis in the *Sansevieria* genus.

Species	Cuticle thickness (µm)		Ordinary epidermal cells sizes (µm)						Ordinary epidermal cells density (pcs./mm²)	
	Adaxial surface	Abaxial surface	Adaxial surface			Abaxial surface			Adaxial surface	Abaxial surface
			Length (µm)	Width (µm)	Height (µm)	Length (µm)	Width (µm)	Height (µm)		
S. aethiopica	5.13 ± 0.65	6.19 ± 0.54	88.89 ± 13.41	41.53 ± 3.31	33.63 ± 3.29	85.31 ± 14.66	33.47 ± 3.77	35.05 ± 3.83	393 ± 18.38	478 ± 82.02
S. cylindrica	—	7.89 ± 0.95	—	—	—	63.93 ± 11.12	18.42 ± 2.02	31.26 ± 4.11	—	888 ± 90.87
S. canaliculata	—	7.63 ± 0.84	—	—	—	60.72 ± 11.05	19.38 ± 2.70	33.52 ± 4.28	—	743 ± 45.40
S. grandis	5.24 ± 0.45	5.26 ± 0.56	105.06 ± 16.19	30.34 ± 3.50	38.99 ± 4.65	102.1 ± 21.20	32.91 ± 7.7	31.07 ± 4.34	405 ± 22.76	373 ± 9.98
S. parva	3.39 ± 0.50	3.82 ± 0.69	92.90 ± 20.63	28.90 ± 3.89	32.63 ± 4.06	96.30 ± 14.07	25.30 ± 3.04	22.82 ± 3.48	441 ± 16.26	468 ± 8.49
S. kirkii	7.93 ± 0.69	8.51 ± 0.81	90.93 ± 12.80	22.66 ± 2.31	30.75 ± 3.28	85.85 ± 12.68	21.92 ± 2.72	25.69 ± 2.57	483 ± 25.4	595 ± 30.26
S. roxburghiana	6.31 ± 0.35	8.22 ± 0.63	67.37 ± 9.47	26.39 ± 2.73	33.72 ± 3.08	61.99 ± 11.19	18.47 ± 2.06	30.73 ± 2.94	650 ± 23.15	913 ± 32.47
S. gracilis	7.52 ± 1.31	7.51 ± 0.75	65.90 ± 8.11	19.19 ± 2.18	20.44 ± 3.10	59.38 ± 7.95	17.51 ± 2.25	24.15 ± 3.32	996 ± 124.86	1145 ± 48.81
S. suffruticosa	—	11.43 ± 1.71	—	—	—	57.35 ± 8.84	16.26 ± 2.15	37.40 ± 5.76	—	1017 ± 63.80
S. trifasciata	4.71 ± 0.56	5.87 ± 0.56	74.21 ± 7.79	24.14 ± 2.13	24.83 ± 2.76	71.12 ± 9.28	24.11 ± 2.62	24.22 ± 2.37	706 ± 41.42	648 ± 33.58
S. intermedia	9.23 ± 0.95	9.92 ± 1.20	61.55 ± 11.25	22.01 ± 2.25	36.84 ± 3.41	53.99 ± 7.52	19.35 ± 2.08	37.21 ± 3.35	692 ± 28.15	816 ± 53.29
S. metallica	4.66 ± 0.72	5.60 ± 0.54	99.82 ± 16.73	22.69 ± 2.80	23.34 ± 2.41	101.9 ± 23.07	20.29 ± 3.40	20.20 ± 1.61	528 ± 53.82	671 ± 63.60

anticlinal walls are less covered with wax than the tangential walls of the cells. In *S. cylindrica*, *S. gracilis*, *S. kirkii*, *S. roxburghiana*, and *S. suffruticosa*, there are cuticular ridges oriented perpendicular to the longitudinal rows of epidermal cells (Fig. 1 C, E, F, K, L; Fig. 2 F, G). In *S. gracilis*, the cuticular grooves on the adaxial surface are slightly less pronounced (Fig. 1 E), while in *S. roxburghiana*, cuticular ridges on the adaxial surface are absent (Fig. 2 E).

The thickness of the cuticle also varies between species and leaf surfaces. On the adaxial side, it ranged from 3.39±0.50 µm (*S. parva*) to 9.23±0.95 µm (*S. intermedia*), and on the abaxial side from 3.82±0.69 µm (*S. parva*) to 11.43±1.71 µm (*S. suffruticosa*) (Table 1).

Wax deposits on both leaf sides are represented by a crust (Fig. 3 A–C), a continuous layer of granular (lumpy) wax (Fig. 3 D), or a continuous layer (Fig. 3 E). Crystalloid wax occurs in the form of irregular crystals (Fig. 3 F–H), occasionally assembled into rosettes (Fig. 3 A) or in the form of smooth plates of various shapes and sizes (Fig. 3 I). Wax crystals can be oriented perpendicular or at various angles to the surface of the leaf blade. The crust is mainly localized on the cells' surface near stomata, while wax plates are located around stomata. The depressions formed by the immersion of the stomata are also covered with wax deposits, which is an important component of the xeromorphic structure (Fig. 3).

Table 2. Morphometric characteristics of the leaf stomata in the *Sansevieria* genus.

Species	Stomata sizes (µm)				Stomata density (pcs./mm²)		Stomatal index (%)	
	Adaxial surface		Abaxial surface		Adaxial surface	Abaxial surface	Adaxial surface	Abaxial surface
	Length (µm)	Width (µm)	Length (µm)	Width (µm)				
S. aethiopica	26.65 ± 2.90	14.62 ± 1.63	20.88 ± 1.88	13.14 ± 1.47	19 ± 3.08	22 ± 4.94	4.61	4.40
S. cylindrica	−	−	25.38 ± 1.71	14.14 ± 1.15	−	25 ± 2.09	−	2.73
S. canaliculata	−	−	33.27 ± 2.23	15.17 ± 1.14	−	9 ± 1.62	−	1.19
S. grandis	29.59 ± 2.49	14.49 ± 1.29	29.54 ± 3.76	16.34 ± 3.34	12 ± 2.41	12 ± 2.39	2.87	3.11
S. parva	34.76 ± 2.31	15.54 ± 2.04	38.52 ± 2.29	13.19 ± 1.74	14 ± 0.82	15 ± 0.96	3.07	3.10
S. kirkii	36.08 ± 2.66	15.70 ± 1.31	31.72 ± 1.88	16.19 ± 1.48	11 ± 1.89	12 ± 1.87	2.22	1.97
S. roxburghiana	22.83 ± 1.88	12.44 ± 0.97	22.59 ± 1.56	12.96 ± 1.00	16 ± 2.08	18 ± 2.88	2.32	1.93
S. gracilis	26.60 ± 1.88	12.83 ± 1.05	25.12 ± 2.09	11.99 ± 1.05	13 ± 2.68	13 ± 2.63	1.28	1.12
S. suffruticosa	−	−	28.34 ± 2.04	14.74 ± 1.67	−	27 ± 4.02	−	2.58
S. trifasciata	28.28 ± 1.83	19.12 ± 1.97	33.18 ± 2.06	15.92 ± 1.41	12 ± 1.8	12 ± 1.77	1.68	1.67
S. intermedia	31.31 ± 2.81	18.35 ± 1.34	37.55 ± 2.14	18.47 ± 1.50	14 ± 1.74	17 ± 2.45	1.98	2.04
S. metallica	35.71 ± 2.47	14.57 ± 1.17	36.99 ± 2.41	15.70 ± 1.40	14 ± 2.06	14 ± 1.41	2.59	2.05

Stomatal apparatus

In most of the studied *Sansevieria* species, the leaves are amphistomatic, while hypostomatic leaves are observed in *S. cylindrica*, *S. canaliculata*, and *S. suffruticosa*. The stomatal apparatus is of the anomocytic type: the guard cells of the stomata are surrounded by subsidiary cells that do not differ from the rest of the epidermal cells and have a uniform structure. The aperture is oriented along the long axis of the ordinary epidermal cells. Stomata are unevenly distributed on the surface of the leaf blade. They occur solitary, in groups of two or three, or can be organized in rows. Exclusively solitar stomata are found in *S. parva*, while in most other species, both solitar stomata and groups of two or three stomata are observed. The most significant number of stomatal groups is recorded in *S. kirkii* on both surfaces of the leaf.

In *S. cylindrica*, the stomata are located on the surface of the leaf blade between the cuticular ridges – stripes, forming more or less regular groups and rows.

Regarding the location of stomata relative to the level of the ordinary epidermal cells, the most deeply immersed stomata are observed in *S. aethiopica*, *S. cylindrica*, *S. suffruticosa*, *S. grandis*, and *S. roxburghiana*. Stomata of medium immersion characterize *S. gracilis*, *S. kirkii*, *S. metallica*, *S. intermedia*, and *S. canaliculata*. In contrast, in *S. parva* and *S. trifasciata*, the stomata are located almost at the same level as the ordinary epidermal cells (Fig. 4).

The guard cells of the stomata in most species, except for *S. parva*, are surrounded
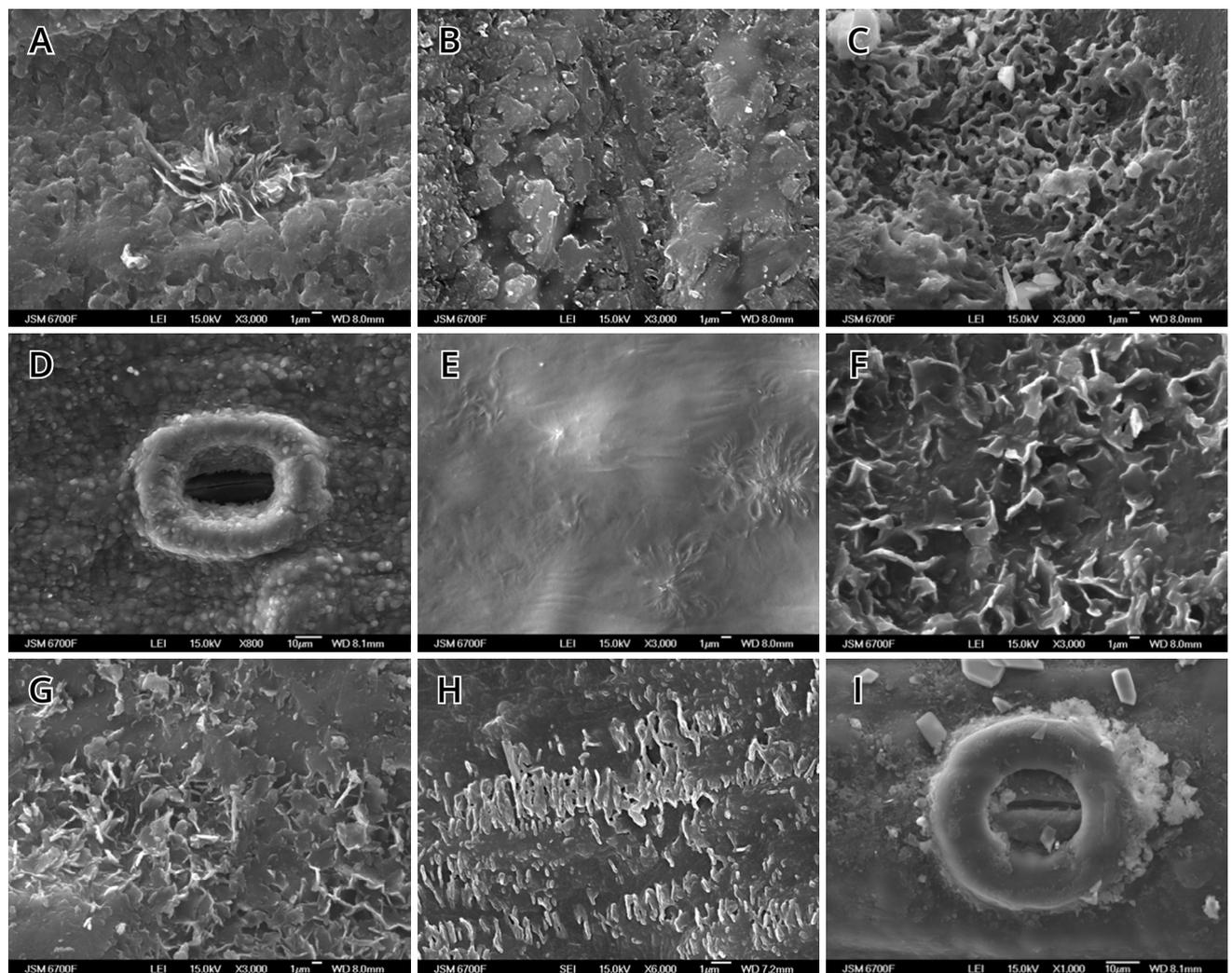
Figure 3. SEM micrographs of different types of epicuticular wax on the leaf surface of *Sansevieria* species: *S. aethiopica* (**A** – adaxial surface); *S. metallica* (**B** – adaxial surface); *S. cylindrica* (**C** – abaxial surface); *S. suffruticosa* (**D** – abaxial surface); *S. parva* (**E** – adaxial surface); *S. grandis* (**F** – adaxial surface); *S. aethiopica* (**G** – adaxial surface); *S. intermedia* (**H** – abaxial surface); *S. trifasciata* (**I** – adaxial surface).

by a distinct cuticular ridge of rounded or rectangular shape (Fig. 4), a characteristic mainly found in xerophytic plants. The cuticle of these ridges is significantly thickened and raised above the general surface of the epidermis. In S. *parva*, the cuticular ring is absent. All species also have large sub-stomatal cavities (Fig. 4).

The data obtained indicate that the density of stomata on the adaxial and abaxial sides of the leaf in all studied species is low, ranging from 9 to 27 per 1 mm². The highest number of stomata per unit area is found in S. *cylindrica*, S. *suffruticosa*, and S. *aethiopica*, which have cylindrical (functionally abaxial) or vertically oriented leaves. The highest density of stomata compared to other species was found in S. *suffruticosa* (27±4.02 per 1 mm²), and the

lowest in S. *canaliculata* (9±1.62 per 1 mm²) (Table 2).

In the studied species with amphistomatic leaf blades, there is no clear predominance of stomata on the adaxial or abaxial surface. Both sides of the leaf have almost the same stomatal density. This is probably due to the specific position of the leaf blade, which is vertical in most species. As a result, approximately the same amount of solar radiation falls on the upper and lower surfaces of the leaf, which leads to a relatively uniform distribution of stomata on both sides to optimize gas exchange and minimize water loss.

The length of the stomata varies from 38.52±2.29 µm (S. *parva*, adaxial surface) to 20.88±1.88 µm (S. *aethiopica*, abaxial surface). The width of the stomata varies from
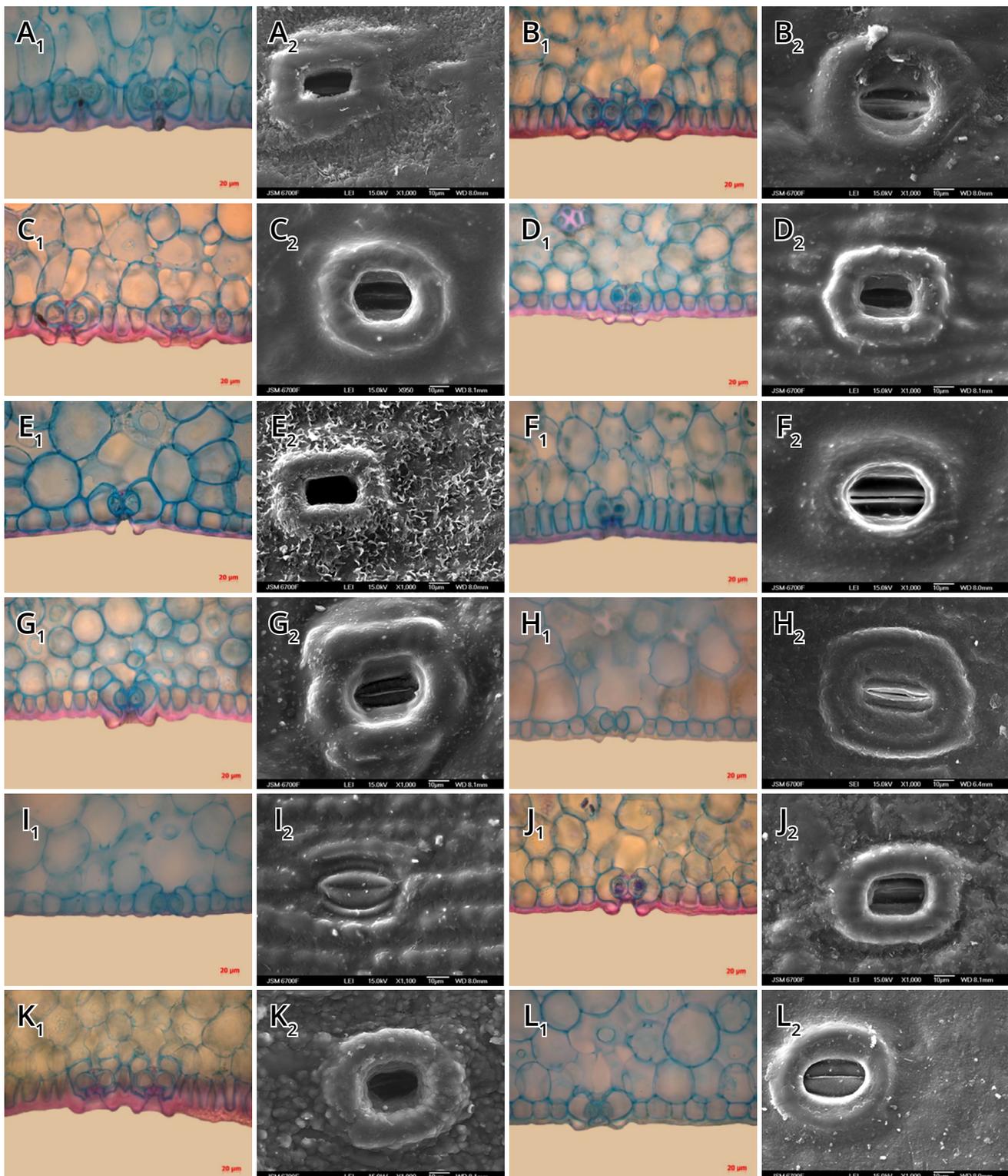
Figure 4. Microstructure of *Sansevieria* stomata on a leaf cross-sections (**1**) and their SEM micrographs (**2**): *S. aethiopica* (**A**); *S. canaliculata* (**B**); *S. cylindrica* (**C**); *S. gracilis* (**D**); *S. grandis* (**E**); *S. intermedia* (**F**); *S. kirkii* (**G**); *S. metallica* (**H**); *S. parva* (**I**); *S. roxburghiana* (**J**); *S. suffruticosa* (**K**); *S. trifasciata* (**L**).

19.12±1.97 µm (S. *trifasciata*, adaxial surface) to 11.99±1.05 µm (S. *gracilis*, abaxial surface) (Table 2).

There were also cases in which stomata formed clusters, contacting each other, mainly laterally (Fig. 4 A₁, B₁, K₁).

Our research has revealed that some of the stomata on the leaf surface of the studied *Sansevieria* species remain underdeveloped (Fig. 1 A, B, G; Fig. 2 E, F, H, I). We observed underdevelopment of stomata in all species studied, except S. *suffruticosa*, S. *cylindrica*, and S. *canaliculata*. In S. *roxburghiana* and S. *trifasciata*, more than half of the stomata remain underdeveloped; however, no apparent connection with the location on the surface (adaxial or abaxial) was observed. These results are entirely consistent with the data from the experimental work of Kagan & Sachs (1991), which states that in S. *trifasciata* up to half of the potential stomata remain 'immature'. Kagan & Sachs (1991) remains the most cited on the phenomenon of 'immature' stomata in *Sansevieria* and examines the mechanism of development and spatial distribution of mature/immature stomata.

Stomatal index

The stomatal index varies from 4.4 (S. *aethiopica*) to 1.12 (S. *gracilis*). Low values correspond to pronounced xeromorphic traits and a higher epidermal cell density.

Discussion

The data obtained indicate that representatives of the *Sansevieria* genus exhibit a wide range of anatomical and micromorphological adaptations to minimize water loss and optimize gas exchange in arid environments. The most informative features are obviously the thickness of the cuticle, the type of wax deposits, the density of stomata and the degree of their immersion, the stomatal index, and the ratio of the sizes and density of epidermal cells.

Certain data on the *Sansevieria* genus we found in this study contradict the reports of other authors. In particular, Shewale et al. (2022) and Jasna et al. (2025) reported the presence of unicellular trichomes in S. *cylindrica*, but trichomes were not observed during our research.

Considering that most *Sansevieria* species grow in environments with periodic droughts but without intense ultraviolet radiation, i.e., often under the cover of sparse forest (Takawira & Nordal, 2002; Burkart et al., 2025), the absence of trichomes is a justifiable and evolutionarily argued trait.

Unlike other succulent plants, in which trichomes act as structures that reduce evaporation or scatter excess light, *Sansevieria* species implement a different xeromorphic strategy: thickening of the cuticle and development of epicuticular wax (Klimko et al., 2018; Maděra et al., 2020), pronounced depression of stomata (Klimko et al., 2018), and the presence of thick-walled epidermal cells (Maděra et al., 2020). Such a set of characteristics compensates for the functional significance of trichomes, since other morphological mechanisms ensure water retention capacity.

Data on the density and size of ordinary epidermal cells in the studied *Sansevieria* species reflect a compromise between epidermal cell size and density that is universal for plants: as cell size decreases, their number per unit area increases, consistent with the results (John et al., 2017). This pattern is due to structural limitations of the tissue and is well described for leaf epidermis. The increased cell density on the abaxial surface, observed in most of the species studied, corresponds to the general anatomical trends characteristic of xerophytic plants (Fahn, 2002; Ogburn & Edwards, 2010), and can be considered an adaptive feature associated with reduced transpiration losses and enhanced mechanical stability of the leaf.

The presence of cuticular ridges and variability in cuticle thickness reflects interspecific differences in adaptation strategies. Higher values of cuticle density and thickness on the abaxial surface may provide additional protection against water loss and mechanical damage. In contrast, a less dense cuticular covering on the adaxial surface may promote optimal gas exchange through stomata.

The species S. *aethiopica*, S. *cylindrica*, and S. *suffruticosa* are characterized by a complex of pronounced xeromorphic features: thickened cuticle, deeply recessed stomata, high density of wax deposits, and low stomatal index. This is consistent with their ecology, as

these species grow in regions with minimal rainfall on dry rocky slopes and in seasonally dry tropical biomes with prolonged drought (POWO, 2025). In contrast, S. *canaliculata* exhibits a different adaptive model: low stomatal density, but larger stomata and shallower stomatal depth. This combination may be related to the optimization of the ratio of transpiration to nighttime CO_2 uptake in plants with CAM metabolism (Martin et al., 2019).

In species with vertically oriented or cylindrical leaf blades (i.e., S. *intermedia*, S. *metallica*, S. *grandis*), there is no significant predominance of stomata on any of the surfaces. However, most angiosperms are characterized by a predominance of stomata on the abaxial surface of amphistomatic leaves (Fahn, 2002). Most probably, in the above-mentioned *Sansevieria* species, the violation of this pattern is explained by the uniform illumination of both sides of the leaf. These species also tend to increase epidermal cell size while simultaneously reducing cell density, suggesting species-specific strategies to minimize evaporation.

Amphistomatousness is characteristic of *Sansevieria* species with bifacial leaves (i.e., S. *aethiopica*, S. *trifasciata*) and, in some species, can be interpreted as an adaptive trait to intense illumination. It is combined with changes in the number and size of ordinary epidermal cells, which ensure a more uniform distribution of light flux and stable gas exchange.

Leaf stomata are not only an essential regulatory element that ensures a balance between photosynthesis and transpiration, but also a key structure that influences atmospheric carbon and water cycles (Hetherington & Woodward, 2003). Stomatal density and size are important traits that show significant variability among plant species in response to environmental factors such as temperature, light intensity, water content, soil nutrient levels, and atmospheric CO_2 concentration (Dow et al., 2014; Durand et al., 2020).

The anomocytic stomata we found in all studied *Sansevieria* species, according to Rudal et al. (2017), probably represent the original (plesiomorphic) state in monocots, although many reversions have occurred during their evolution. However, Babu & Srinivasa Prabhu (2024), in their comprehensive investigation of S. *trifasciata*, refer to the tetracytic type of stomata in this species.

The presence of 'immature' stomata is interpreted as a developmental reserve that allows individual cells to be potentially activated or completed depending on the environment, especially in young leaves (Han et al., 2021). Underdeveloped stomata do not seem to be a random defect, but the result of specific regulation of epidermal development. In many plants, including S. *trifasciata*, some stomata fail to develop at an early stage. This has several biological reasons and can be considered an adaptive phenomenon.

In this context, the presence of underdeveloped stomata may indicate the genus's adaptive capabilities. For *Sansevieria*, which naturally exists in conditions of periodic drought, high-intensity lighting, and limited water availability, such a system of stomatal development offers several advantages: water conservation, tissue stability during fluctuations in moisture, maintenance of CAM photosynthesis, and the ability to respond quickly and flexibly to changes in growing conditions. In other words, underdeveloped stomata are not only a result of development but also a structural feature that contributes to *Sansevieria* high ecological resilience and its ability to survive in arid environments or conditions of introduction (Kagan & Sachs, 1991).

The stomatal index proved to be an informative diagnostic parameter that enables comparison of adaptive gas exchange models across closely related taxa.

Plants of S. *gracilis* and S. *roxburghiana*, which grow in less extreme conditions, are characterized by less pronounced xeromorphic features – an increase in the size of epidermal cells, which corresponds to their ecological niche. Mesomorphic traits are also found in S. *parva* – its stomata are located almost at the same level as the epidermal cells, and there is no cuticular roller around the stomata. This indicates adaptation to conditions with a less pronounced moisture deficit.

The functional relationship between leaf surface microstructures and the maintenance of water balance was also demonstrated in a study by Jura-Morawiec & Marcinkiewicz (2020) on *Dracaena draco* (L.) L. The authors showed that micromorphological features

of the leaf surface affect wettability, water absorption, and the ability to store water temporarily. These properties are directly related to the micromorphology of the cuticle and wax layer and reflect adaptations to arid conditions.

Conclusions

Hence, analysis of the micromorphological features of the epidermis of the studied *Sansevieria* species revealed a complex of xeromorphic traits consistent with their ecological survival strategies in arid conditions. At the level of leaf micromorphology, amphistomatousness, spatial organization of epidermal cells, the cuticular cover with epicuticular wax deposits of various configurations, varying degrees of stomatal immersion, and variation in their density, as well as the presence of underdeveloped stomata.

The interspecific differences identified indicate distinct ways of optimizing water balance, which are shaped by similar but not identical growing conditions. In general, this study can be considered a model, and its results can be extrapolated to other members of Asparagaceae and Asparagales.

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Мікроморфологічні особливості поверхні листка видів роду *Sansevieria* Thunb. s.str. (Asparagaceae)

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У дослідженні за допомогою світлової мікроскопії та сканувальної електронної мікроскопії вивчено мікроморфологію поверхні листків 12 видів роду *Sansevieria*. Основну увагу зосереджено на виявленні мікроморфологічних ознак, пов'язаних зі стійкістю рослин до стресових умов, зокрема форми клітин епідерми, товщини кутикули, розподілу та щільності продихів, а також особливостей кутикулярного покриву з епікутикулярними восковими відкладеннями. У більшості досліджених видів *Sansevieria* листки є амфістоматичними, тоді як гіпостоматичні листки виявлено у *S. cylindrica, S. canaliculata* та *S. suffruticosa*. У всіх досліджених таксонів епідерма представлена одним шаром клітин і позбавлена трихом.

Рослини досліджених видів *Sansevieria* характеризуються добре розвиненим кутикулярним шаром і наявністю воскових відкладень, що виконують захисну та водозберігаючу функції. Ступінь розвитку кутикули та її структура варіює як між видами, так і між поверхнями листка в межах одного виду. Абаксіальна поверхня листкової пластинки зазвичай має більш розвинений кутикулярний покрив порівняно з адаксіальною, що особливо чітко проявляється у *S. cylindrica, S. canaliculata, S. kirkii, S. roxburghiana, S. gracilis, S. suffruticosa* та *S. intermedia*. Усі досліджені види мають аномоцитні продихи. Щільність продихів на абаксіальній поверхні листка коливалася в межах 9–27 мм² залежно від виду. Виявлені міжвидові відмінності відображають різні стратегії оптимізації водного балансу за аридних умов.

На рівні мікроморфології листка амфістоматичність, просторова організація клітин епідерми, наявність кутикулярного покриву з епікутикулярними восковими відкладеннями різної конфігурації, різний ступінь занурення та щільності продихів, а також наявність недорозвинених продихів можуть розглядатися як маркери стійкості рослин цього роду до стресових факторів. Виявлені мікроморфологічні маркери поглиблюють уявлення про адаптивні ксероморфні ознаки *Sansevieria* та мають потенційне прикладне значення для біотехнологічних розробок і фіторемедіації, зокрема для розбудови зеленої інфраструктури.

Ключові слова: *Sansevieria*, світлова мікроскопія, сканувальна електронна мікроскопія, кутикула, епідерма, продиховий апарат, мікроморфологія, фіторемедіація