

STRUCTURAL DIVERSITY AND ANATOMICAL ADAPTATIONS OF LEAVES IN BRASSICACEAE SPECIES

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Abstract. This study presents a comparative anatomical description of leaf structure in several species of the family Brassicaceae Burnett, including *Alyssum dasycarpum*, *A. turkestanicum*, *A. szovitsianum*, *Diptychocarpus strictus*, *Goldbachia laevigata*, *Hymenolobus procumbens*, *Isatis minima*, and *I. violascens*. Microscopic analysis revealed distinct interspecific variations in trichome type, stomatal distribution, and mesophyll organization. Most studied species possess amphistomatic leaves with isolateral-palisade mesophyll and sclerenchymatized vascular bundles, reflecting xeromorphic and heliophilous adaptations. Differences were observed in palisade thickness, degree of pubescence, and epidermal cell morphology. These anatomical characteristics provide valuable diagnostic features for taxonomy and ecological adaptation studies within the Brassicaceae family.

Keywords: brassicaceae; leaf anatomy; isolateral-palisade mesophyll; amphistomatic leaves; xeromorphic adaptation; *Alyssum*; *Isatis*; *Hymenolobus procumbens*; *Diptychocarpus strictus*; *Goldbachia laevigata*; epidermal structure; trichomes; stomatal types; vascular bundles.

Introduction

The Brassicaceae Burnett (Cruciferae) family includes numerous species adapted to diverse environmental conditions, particularly arid and semi-arid regions. According to C.R. Metcalfe and L. Chalk (1957), the leaves of Brassicaceae species are predominantly dorsiventral but may also be isolateral-palisade. The trichomes are structurally diverse, and stomata are typically anisocytic on both sides of the leaf. Idioblasts containing myrosin, which exhibit red or purple coloration upon coagulation, serve as a diagnostic feature for the family. E.I. Volkova (1960) investigated the anatomy of ten ephemeral Brassicaceae species from Kopetdagh and the Moscow region, noting an increase in mesomorphy under introduction conditions. Later, N. Rao and I. Inamdar (1983) examined leaf morphology and venation in 35 Brassicaceae species, describing them as simple, alternate, and predominantly craspedodromous. G.F. Begbaeva (1995) characterized the mesophyll structure of *Isatis* species, emphasizing their anatomical and nutritional value (Karimov et al., 1965). However, detailed information on the anatomical structure of desert Brassicaceae species remains limited. Therefore, this study aims to provide a comparative anatomical analysis of selected Brassicaceae species to identify diagnostic and adaptive features related to their ecological conditions.

Aim of the research: The study aims to investigate the anatomical features of leaves in selected Brassicaceae species and to reveal diagnostic and adaptive structural traits related to their ecological distribution, particularly in arid and semi-arid habitats.

Object of the research: The objects of this study are the leaves of eight Brassicaceae species—*Alyssum dasycarpum*, *A. turkestanicum*, *A. szovitsianum*, *Diptychocarpus strictus*, *Goldbachia laevigata*, *Hymenolobus procumbens*, *Isatis minima*, and *Isatis violascens*—analyzed through comparative anatomical methods.

2. Materials and Methods

The study examined leaves of *Alyssum dasycarpum*, *A. turkestanicum*, *A. szovitsianum*, *Diptychocarpus strictus*, *Goldbachia laevigata*, *Hymenolobus procumbens*, *Isatis minima*, and *I. violascens*.

Fresh leaf samples were collected from natural populations and fixed in a 70% ethanol solution. Temporary microscopic slides were prepared using standard paraffin embedding and microtome sectioning techniques. Paradermal and transverse sections were stained with safranin and fast green to visualize cell walls and tissues. Observations were made under a light microscope. Morphological features—including epidermal structure, trichome type, stomatal distribution, mesophyll organization, and vascular bundle arrangement—were analyzed and compared among species.

3. Results and Discussion

3.1. *Alyssum dasycarpum*. Leaves are simple, broad-lanceolate (6–8 mm × 4–6 mm), entire, and pubescent with 5–8-rayed stellate hairs. The epidermis is single-layered; cells have slightly sinuous walls with thickened outer layers. The leaf is amphistomatic, with oval, hemiparacytic, anisocytic, and rarely anomocytic stomata. The mesophyll is isolateral-palisade and loose; palisade tissue is single-layered on both sides, while the spongy parenchyma has three layers. Vascular bundles (25–30) are sclerenchymatized.

3.2. *Alyssum turkestanicum* Leaves are simple, oblong (9–11 mm × 2–3 mm), densely pubescent with 16-rayed stellate hairs. The epidermis is single-layered, with wavy cell walls and slightly thickened outer walls. Leaves are amphistomatic; stomata are elongated, anisocytic, and tetracytic. The mesophyll is isolateral-palisade with 2–3 layers of palisade cells on the adaxial side and one layer on the abaxial side. The spongy tissue has 4–6 layers. The vascular bundles (19–21) are sclerenchymatized.

3.3. *Alyssum szovitsianum* Leaves are oblong-pointed (7–9 mm × 4–6 mm), pubescent with 8–16-rayed stellate hairs. The epidermis is single-layered, with amphistomatic surfaces. Stomata are anomocytic and hemiparacytic. The mesophyll is isolateral-palisade, with 2–3 layers of palisade cells on the adaxial side, 1–2 layers on the abaxial side, and 3–4 layers of spongy tissue in between. The central bundle is weakly sclerenchymatized.

3.4. *Diptychocarpus strictus* Leaves are simple, oblong-linear with sharp serrations, covered with simple and glandular hairs. The epidermis is single-layered with wavy (adaxial) and sinuous (abaxial) walls. The leaf is mainly dorsiventral with three layers of palisade cells and 5–6 layers of spongy tissue. Vascular bundles (20–22) are strongly sclerenchymatized.

3.5. *Goldbachia laevigata* Leaves are heart-shaped at the base, petiolate (8–10 mm × 1.5–2 mm), and sparsely serrated. They are covered with simple unicellular hairs. The leaf is amphistomatic with small anomocytic and hemiparacytic stomata. The mesophyll is isolateral-palisade with 2–3 layers of palisade cells on both sides and 6–7 layers of spongy parenchyma. Vascular bundles are sclerenchymatized, surrounded by a parenchymatous sheath.

3.6. *Hymenolobus procumbens* Leaves show pronounced heterophylly: basal leaves are lyrate lobed, while upper leaves are entire and sessile. Epidermal cells have wavy walls, and stomata are anisocytic and hemiparacytic. The mesophyll is isolateral-palisade (277.9 µm thick) with 3 palisade layers adaxially, 2 abaxially, and 6 spongy layers between. Vascular bundles are sclerified, indicating xeromorphic adaptation.

3.7. *Isatis minima* Leaves are simple, with finely serrated margins. The epidermis is single-layered, amphistomatic, and consists of wavy-walled cells. Stomata are anomocytic and anisocytic. The mesophyll is isolateral-palisade, with 2–3 palisade layers adaxially and 1 abaxially, and 6–7 loose spongy layers. All vascular bundles are sclerenchymatized.

3.8. *Isatis violascens* Leaves are broad at the base, tapering toward the apex, and bear thin filamentous and hook-shaped trichomes. Anthocyanin pigmentation occurs in abaxial epidermal cells. The leaf is amphistomatic, with numerous anomocytic and anisocytic stomata. The mesophyll is dorsiventral with 2 palisade and 7–8 spongy layers. Vascular bundles (24–26) are heavily sclerified.

All studied Brassicaceae species share several diagnostic features: amphistomatic leaves, non-sunken stomata, stellate or simple trichomes, and single-layered epidermis with thickened outer walls. Most species exhibit isolateral-palisade mesophyll, reflecting xeromorphic and heliophilous adaptations to arid conditions. The genus *Alyssum* demonstrates notable interspecific variation: *A. dasycarpum* has broad-lanceolate leaves with moderate pubescence, *A. turkestanicum* displays elongated leaves and a high palisade ratio (63%), and *A. szovitsianum* has thicker mesophyll with fewer sclerenchymatized bundles.

Species such as *Hymenolobus procumbens* and *Isatis minima* show transitional features between mesomorphic and xeromorphic types, suggesting adaptive flexibility. The presence of anthocyanin in *I. violascens* may enhance protection against high solar radiation. Overall, the anatomical diversity observed among these species indicates evolutionary responses to habitat conditions, confirming that leaf structural traits in Brassicaceae are valuable diagnostic and ecological indicators.

Family Brassicaceae Burnett In the comprehensive work by C.R. Metcalfe and L. Chalk (1957), it is noted that the leaves of species in the Brassicaceae family are predominantly dorsiventral but can also be isolateral-palisade. The trichomes are highly diverse. The stomata are anisocytic on both sides of the leaf. Idioblasts containing myrosin are present in all organs, which turns red or purple upon coagulation, making it a useful diagnostic feature. E.I. Volkova (1960) studied the structure of 10 ephemeral species, including Brassicaceae species, in the conditions of Kopetdagh and the Moscow region. She noted the diversity of leaf types and an increase in mesomorphy under introduction conditions in the Moscow region.

N. Rao and I. Inamdar (1983) described the morphology and venation of the leaves of 35 Brassicaceae species, including species of the genus *Alyssum*. The leaves are simple and alternate, but the shape of the blade is highly variable. The venation is primarily craspedodromous. G.F. Begbaeva (1995) described the type of mesophyll in the leaves of two *Isatis* species. *Isatis* species are valuable for their nutritional content, containing all essential amino acids and significant amounts of carbohydrates (Karimov et al., 1965). Thus, information about the leaf structure of desert species in the Brassicaceae family is scarce.

Alyssum dasycarpum: The leaf is simple, broad-lanceolate, entire, and smoothly transitions into a petiole. The leaf blade is 6–8 mm long and 4–6 mm wide, evenly pubescent on both sides with 5–8-rayed stellate hairs. The epidermis is single-layered, with 4–5-sided cells with slightly sinuous walls in paradermal sections. Their outer walls are slightly thickened. On the abaxial side, the epidermal cells are smaller and lower than on the adaxial side in cross-section. The leaf is amphistomatic. The stomata are superficial, oval, hemiparacytic, anisocytic, and rarely anomocytic. The mesophyll is isolateral-palisade and loose. The palisade tissue is single-layered on both sides, and the spongy tissue is three-layered. The vascular bundles are sclerenchymatized, with 25–30 bundles in cross-section.

Alyssum turkestanicum: The leaf is simple, oblong, and almost sessile. The blade is 9–11 mm long and 2–3 mm wide, entire, and densely pubescent with 16-rayed stellate hairs, denser on the adaxial side. The epidermis is single-layered. In paradermal sections, the cells are 4–5-sided with slightly sinuous walls on the adaxial side and wavy walls on the abaxial side. The outer walls are slightly thickened. On the adaxial side, the epidermal cells are larger and taller than on the

abaxial side. The leaves are amphistomatic. The stomata are elongated-oval, anisocytic, and tetracytic. The mesophyll is isolateral-palisade, with 2-3 rows of palisade cells on the adaxial side and one row on the abaxial side. The palisade tissue occupies most of the mesophyll volume, with the height of the palisade cells being twice their width. The spongy tissue is 4-6 layers thick. The vascular bundles are numerous, with 19-21 in cross-section, and are sclerenchymatized.

Alyssum szovitsianum: The leaf is simple, oblong-pointed, with a blade 7-9 mm long and 4-6 mm wide, entire, and pubescent on both sides with 8-16-rayed stellate hairs (mainly 8-rayed on the upper side and 16-rayed on the lower side). The epidermis is single-layered. The leaves are amphistomatic. In paradermal sections, the walls of the adaxial epidermis are slightly wavy, while the abaxial walls are sinuous. The stomata are anomocytic and hemiparacytic, larger but fewer in number on the adaxial side of the leaf. The mesophyll is isolateral-palisade, with 2-3 rows of palisade cells on the adaxial side and 1-2 rows on the abaxial side. Between them are 3-4 rows of loose spongy cells. The intercellular spaces are large throughout the mesophyll. The vascular bundles are small, the lateral bundles are not sclerenchymatized, and the central bundle has a few sclerenchyma cells on the abaxial side and is surrounded by parenchyma.

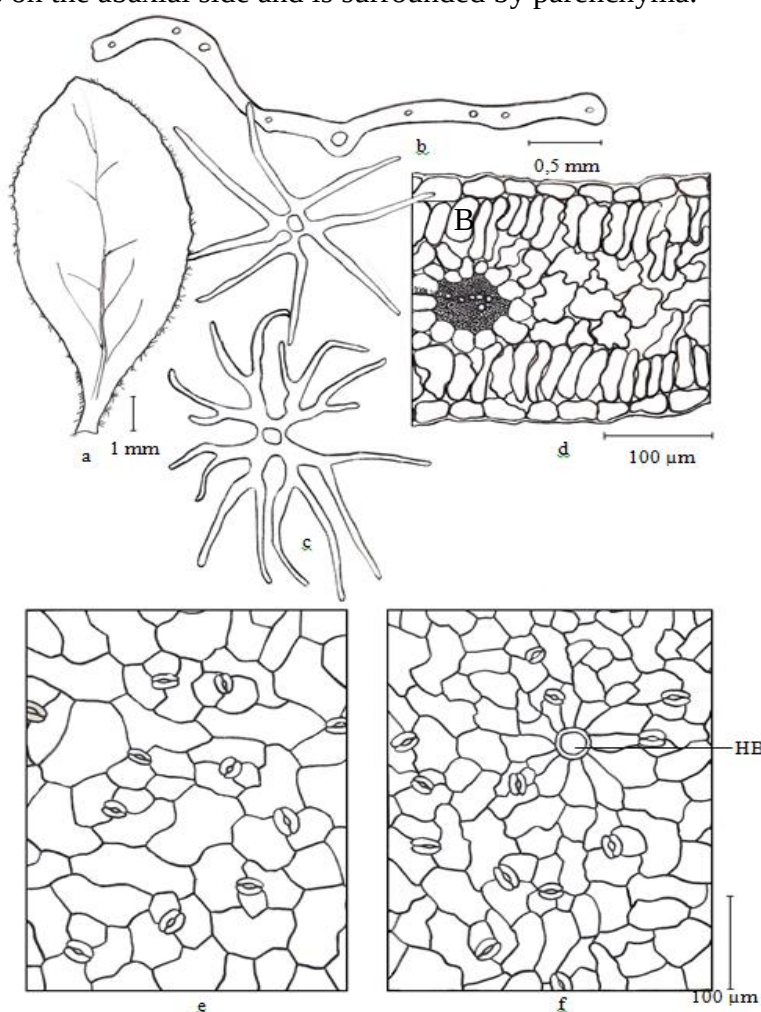


Fig. 1. Structure of the leaf of *Alyssum dasycarpum*:

- a – external appearance;**
- b – cross-section diagram;**
- c – dendroid trichomes;**
- d – detail of the mesophyll;**
- e – adaxial epidermis;**
- f – abaxial.**

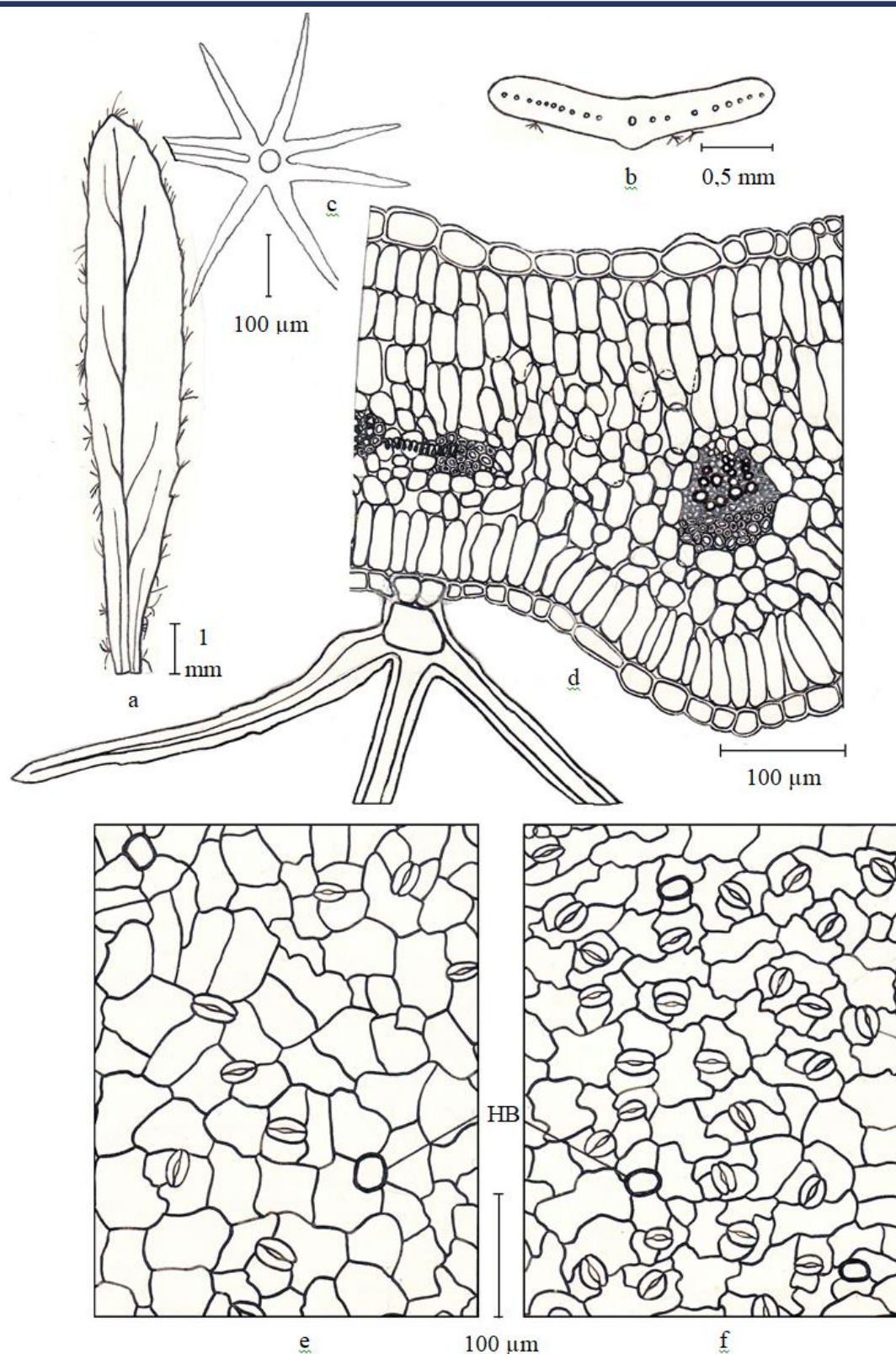


Fig. 2. Structure of the *Alyssum turkestanicum* leaf:

- a* – external appearance;
- b* – cross-section diagram;
- c* – trichomes;
- d* – detail of the mesophyll;
- e* – adaxial epidermis;
- f* – abaxial.

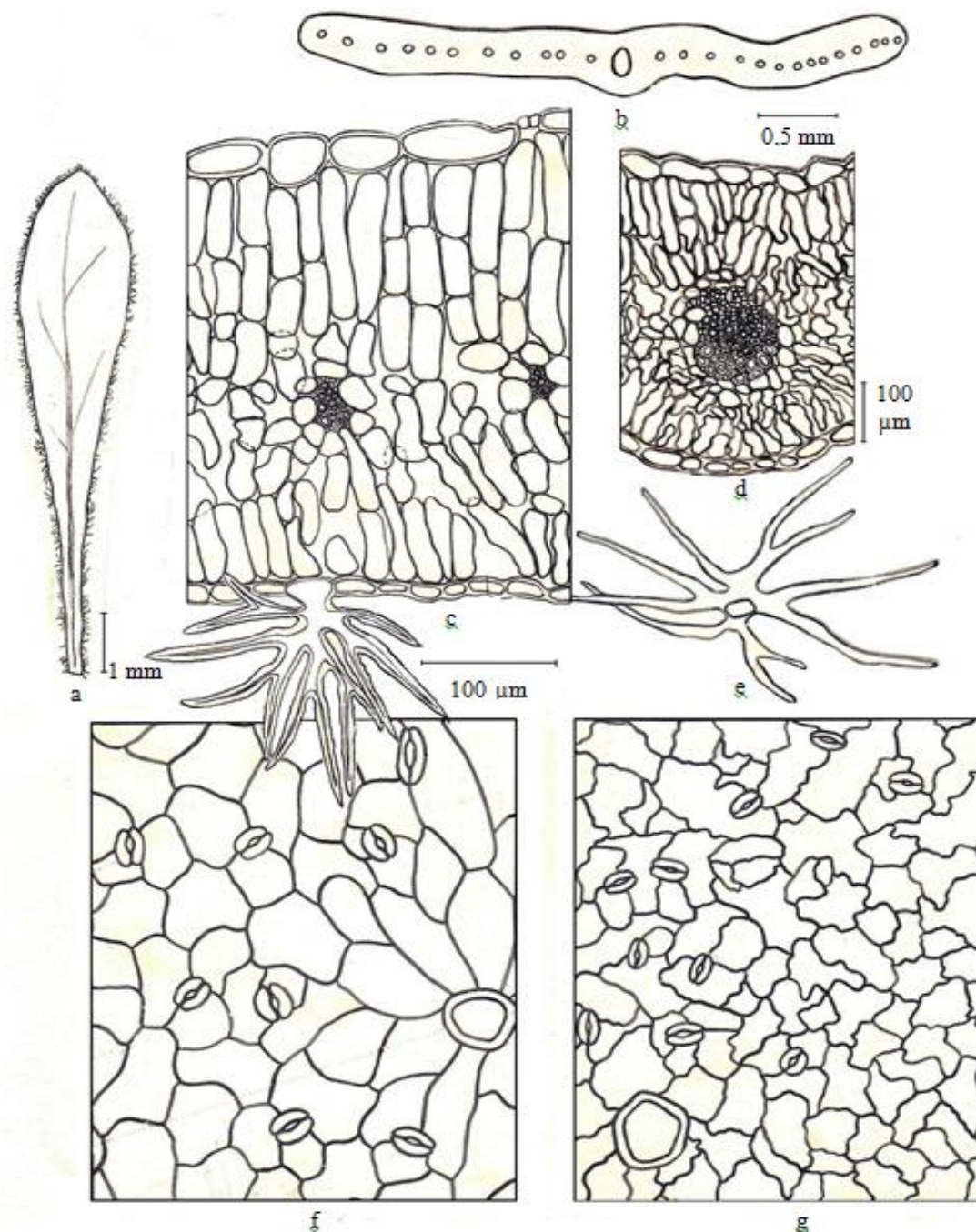


Fig. 3. Structure of the leaf of *Alyssum szovitsianum*:

- a – external appearance;**
- b – cross-section diagram;**
- c – detail of the mesophyll;**
- d – main vein;**
- e – dendroid trichome;**
- f – adaxial epidermis;**
- g – abaxial.**

The leaves of *Alyssum szovitsianum*, *A. turkestanicum*, and *A. dasycarpum* share the following common traits: they are covered with stellate hairs, amphistomatic (having stomata on both sides), the stomata are non-immersed, and the adaxial epidermal cells are larger than the abaxial ones. The mesophyll is of the isolateral-palisade type. However, the leaves of species in the *Alyssum* genus differ in the following diagnostic features:

Alyssum szovitsianum is characterized by a lanceolate leaf shape and thick mesophyll.

Alyssum turkestanicum has an elongated leaf shape, a thinner leaf, and more pronounced palisade tissue (palisade ratio – 63%).

A. dasycarpum has a broad-lanceolate leaf shape.

In the ontogeny of plants, xeromorphic and heliomorphic structures of assimilating organs intensify: from dorsiventral cotyledons to isolateral-palisade leaves.

Diptychocarpus strictus: The leaf is simple, oblong-linear, with sharp serrations, and covered with simple and glandular hairs on a 4-celled stalk. The epidermis is single-layered. The surface cells are flattened, with wavy cell walls on the adaxial side and sinuous on the abaxial side. The stomata are numerous, especially on the abaxial side, anomocytic, hemiparacytic, anisocytic, and non-immersed.

The mesophyll is dorsiventral, with three rows of wide palisade cells on the adaxial side and loose spongy cells on the abaxial side. The spongy tissue consists of 5-6 layers. The vascular bundles (main and 20-22 lateral) are sclerenchymatized.

Goldbachia laevigata: The leaf is laminar, heart-shaped at the base, petiolate, sparsely serrated along the edges, 8-10 mm long, 1.5-2 mm wide, tapering at the tip. It is covered with simple unicellular hairs on a two-celled base. The epidermal cells in paradermal sections are flattened and slightly wavy; in cross-sections, they are swollen with a thickened outer wall. The leaf is amphistomatic. The stomata are small, numerous, anomocytic and hemiparacytic, and non-immersed. The mesophyll is isolateral-palisade, with 2-(3) rows of palisade cells on both sides and 6-7 rows of spongy cells in the center. The median vascular bundle is larger than the lateral ones and is surrounded by a sclerenchymatous sheath.

Hymenolobus procumbens: The leaves exhibit homoblastic heterophylly. The basal leaves are alternate, numbering 3-5, up to 1.5 cm long and 0.8 cm wide, lyrate-pinnate-lobed with 5-8 lobes. The lower stem leaves are 1.5-1.8 cm long and 0.5 cm wide, dissected with 4-5 lobes. The middle leaves are 1.2-1.5 cm long and 0.4-0.5 cm wide, less dissected, oblong, with an elongated, slightly pointed apex and a drawn-out base, short-petiolate or sessile. The upper leaves are 0.5-1 cm long and 0.1-0.3 cm wide, entire, and sessile. In cross-sections of the middle leaves, the epidermis is single-layered, and the outer walls are thickened (4.7 µm).

Table 1

Mesophyll characteristics of leaves of Asteraceae species									
Kind	Thickness, µm		Coefficient frontage, %	Palisade cells adaxial, µm			Palisade cells abaxial, µm		
	mesophyll	palisade layer		height	width	palisade index	height	width	palisade index
<i>Alyssum dasycarpum</i>	267,4±21,6	93,9±8,2	35,1	38,6± 3,2	18,5±1,6	2,1	–	–	–
<i>Alyssum szovitsianum</i>	311,5±23,5	156,2±12,3	56,5	40,6± 4,0	12,6±1,1	3,2	–	–	–
<i>Alyssum turkestanicum</i>	158,6±12,1	100,8±9,3	63,6	26,9± 2,1	12,1±0,9	2,2	–	–	–
<i>Hymenolobus procumbens</i>	277,9±26,3	124,0±11,2	44,6	39,0± 3,8	19,0±1,8	2,0	–	–	–
<i>Goldbachia laevigata</i>	399,7±32,5	ад. 174,0±17,0	74,7	55,0±	25,0±2,3	2,2	48,5±4,4	23,4±2,1	2,0
		аб. 124,8±11,2		5,3					
<i>Lachnoloma lechmanii</i>	291,9±28,8	ад. 117,5±10,3	73,6	64,5±	21,9±2,0	2,9	57,3±5,1	18,5±1,7	3,1
		аб. 97,5±9,0		6,3					
<i>Stigozella africana</i>	286,5±27,3	ад. 133,5±13,0	61,4	68,1±	22,5±2,1	3,0	43,9±4,2	22,8±2,2	1,9
		аб. 42,4±4,2		6,3					

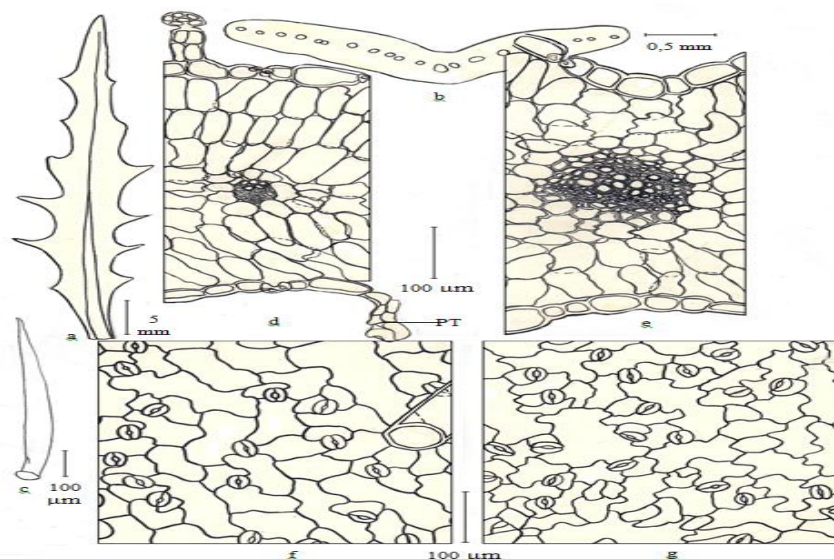


Fig. 4. Structure of the leaf of *Diptychocarpus strictus*:

- a – external appearance;**
- b – cross-section diagram;**
- c – trichome;**
- d – detail of the mesophyll;**
- e – main vein; f– adaxial epidermis; g – abaxial.**

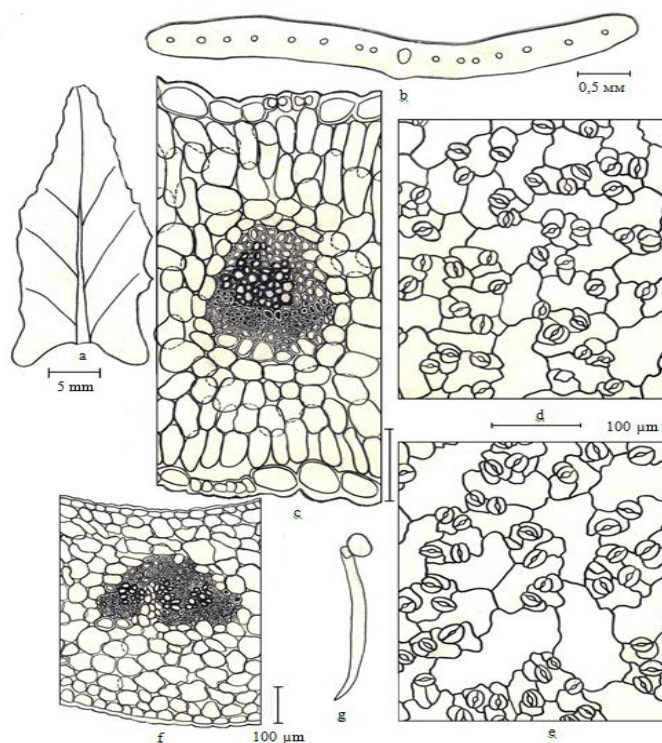


Fig. 5. Structure of the *Goldbachia laevigata* leaf:

- a – external appearance;**
- b – cross-section diagram;**
- c – detail of the mesophyll;**
- d – adaxial epidermis;**
- e – abaxial;**
- f– main vein;**
- g – trichomes.**

On the paradermal section, the epidermal cells are elongated, with wavy walls on both sides of the leaf. The stomata are anisocytic and hemiparacytic, less frequently anomocytic, non-sunken, and randomly oriented. The mesophyll is isolateral-palisade, with a thickness of 277.9 μm . On the adaxial side, there are 3 layers of palisade cells, and on the abaxial side – 2 layers with large intercellular spaces and 6 layers of spongy cells in between. The palisade coefficient is 45%, and the palisade index of the cells is 2. The median vascular bundle has 10-15 vessels, with 10-12 small lateral bundles. All bundles are sclerified due to the thickening of the walls of the phloem parenchyma (Table 1; Fig. 3). In the ontogeny of *H. procumbens*, there is a change in the adaptation of assimilating organs towards an increase in heliophilous and xeromorphic traits, expressed in the transition from dorsiventral mesophyll in cotyledons to isolateral-palisade mesophyll in leaves. However, the structure of vegetative organs also has mesomorphic features: wavy epidermal cells, large intercellular spaces in the leaf mesophyll, and numerous small non-sunken stomata.

Isatis minima. The leaf is simple, with finely serrated edges and a prominent vein on the abaxial side. The epidermis is single-layered. The epidermal cells are flattened, their walls are wavy, higher on the adaxial side, wavy and larger on the abaxial side. The leaf is amphistomatic. The stomata are numerous, small, anomocytic, rarely hemiparacytic and anisocytic, and non-sunken. The mesophyll is isolateral-palisade, with 2-(3) rows of palisade cells on the adaxial side and 1 row on the abaxial side. The spongy tissue is 6-7-layered, loose, with large intercellular spaces. The median vascular bundle protrudes from both the adaxial and, even more so, the abaxial sides. There are 10 lateral vascular bundles on the transverse section. All bundles are sclerified (Fig. 4).

Conclusion

The comparative anatomical analysis of eight Brassicaceae species—*Alyssum dasycarpum*, *A. turkestanicum*, *A. szovitsianum*, *Diptychocarpus strictus*, *Goldbachia laevigata*, *Hymenolobus procumbens*, *Isatis minima*, and *I. violascens*—demonstrates that leaf structural traits within this family serve as reliable indicators of ecological adaptation and taxonomic differentiation. Despite species-specific diversity, all studied taxa share a set of diagnostic features characteristic of Brassicaceae: amphistomatic leaves, non-sunken stomata, a single-layered epidermis with slightly thickened outer walls, and the presence of simple or stellate trichomes. These attributes collectively reflect adaptation to environments with high solar radiation and fluctuating moisture availability.

Most species exhibit isolateral-palisade mesophyll, a xeromorphic and heliophilous trait that enhances photosynthetic efficiency under arid and semi-arid conditions. Variations in palisade thickness, trichome density, and degree of vascular bundle sclerenchymatization further reveal evolutionary adjustments to microhabitat conditions. The genus *Alyssum* demonstrates pronounced interspecific differentiation, particularly in leaf shape, palisade ratio, and degree of pubescence, confirming its high ecological plasticity. Species such as *Hymenolobus procumbens* and *Isatis minima* display transitional features between mesomorphic and xeromorphic types, indicating flexible responses to moisture availability typical of desert and foothill ecosystems. The presence of anthocyanin pigmentation in *I. violascens* suggests an additional photoprotective mechanism against excessive irradiance.

Overall, the structural diversity of leaves across the examined species reflects complex evolutionary responses to arid habitats and supports the ecological significance of anatomical traits in Brassicaceae. These findings not only refine diagnostic criteria for species identification but also contribute to understanding adaptive strategies in desert and semi-desert floras, where anatomical modifications play a key role in survival under environmental stress.

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