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ADAPTIVE SHOOT STRUCTURES OF SELECTED SPECIES OF THE BORAGINACEAE AND HELIOTROPIACEAE IN THE FLORA OF ARMENIA

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Abstract
Using several Boraginaceae and Heliotropiaceae species from Armenia as examples, this study identifies ecologically important anatomical traits within these taxa. Based on both abiotic factors and structural data obtained from shoot analysis, the examined species were classified into three habitat types. The mesophyte group comprises *Myosotis alpestris*, *Heliotropium europaeum*, *H. supinum*, *Buglossoides tenuiflorum*, and *Anchusa arvensis* subsp. *orientalis*. The mesoxerophyte group includes *Nonea polychroma*, *N. pulla*, and *Tournefortia sibirica*. The xerophyte group encompasses *Onosma sericea*, *O. gracilis*, and *Alkanna orientalis*. Mesophytes possess dorsiventral leaves and poorly developed mechanical tissues. Mesoxerophytes exhibit isopalisade leaves, podium-type trichomes, and druse crystals within the pith and xylem. Xerophytes display distinctly xeromorphic characteristics, such as the presence of several trichome types, well-developed mechanical tissues, and a multilayered palisade mesophyll. This study refines previous ecological classifications, identifies key adaptive features, and demonstrates the diagnostic value of anatomical traits as indicators of environmental specialization. The results confirm that ecologically significant characteristics of different organs often complement one another, jointly determining the degree of species adaptation to their habitats and their specific traits.

Keywords: Adaptive structures; Anatomy; Armenia; Boraginaceae; Heliotropiaceae; leaf; stem

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ساختارهای تطبیقی ساقه در گونه‌های منتخب از تیره‌های *Boraginaceae* و *Heliotropiaceae* در فلور ارمنستان

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چکیده: با استفاده از نمونه‌هایی از برخی گونه‌های تیره‌های Boraginaceae و Heliotropiaceae در ارمنستان، ویژگی‌های تشریحی با اهمیت بوم‌شناختی برای این گروه ازآرایه ها شناسایی شد. مطالعه حاضر، با تکیه بر عوامل غیرزنده و داده‌های ساختاری به‌دست‌آمده از تحلیل صفات تشریحی ساقه‌ها، گونه‌ها را

در سه نوع زیستگاه طبقه‌بندی می‌کند. گروه مزوفیت شامل *Myosotis alpestris*، *Heliotropium europaeum*، *H. supinum*، *Buglossoides tenuiflorum* و *Anchusa arvensis* subsp. *orientalis* است. گروه مزوگزروفیت شامل *Nonea polychroma*، *N. pulla* و *Tournefortia sibirica* می‌شود. در نهایت، گروه گزروفیت شامل *Onosma sericea*، *O. gracilis* و *Alkanna orientalis* می‌باشد. مزوفیت‌ها دارای برگ‌های پشتی–شکمی (dorsiventral) و بافت مکانیکی کم بودند، در حالی که در مزوگزروفیت‌ها برگ‌های با پارانشیم نردبانی در هر دوسطح، کرک‌های روی برجستگی‌های اپیدرم و بلورهای اکسالات کلسیم در مغز و چوب دیده می‌شوند. گزروفیت‌ها ویژگی‌های بارز خشکی‌زی از جمله انواع مختلف کرک، بافت‌های مکانیکی توسعه‌یافته و لایه‌های چندگانه پارانشیم نردبانی را نشان دادند. این پژوهش طبقه‌بندی‌های بوم‌شناختی پیشین را اصلاح می‌کند، ویژگی‌های کلیدی سازگاری را مشخص می‌سازد و بر اهمیت صفات تشریحی به‌عنوان شاخص‌های قابل‌اعتماد بوم‌شناختی تأکید می‌نماید. ثابت شده است که ویژگی‌های بوم‌شناختی مهم اندام‌های مختلف اغلب مکمل یکدیگر هستند و به طورمؤثری میزان سازگاری گونه‌ها با محیط را اصلاح و ویژگی‌های فردی آن‌ها را تضمین می‌نمایند.

INTRODUCTION

Armenia, a small country in the southern Caucasus, is characterized by remarkable environmental diversity. Among its flora, the family Boraginaceae is one of the leading groups. The highest diversity of this family is concentrated in the Ancient Mediterranean region, which encompasses the modern Mediterranean and Irano-Turanian floristic regions, to which Armenia belongs.

Armenia's diverse natural conditions determine the ecological variability of its flora, which is particularly relevant for taxonomic studies. K. G. Tamanyan (2011) conducted a systematic review of the Boraginaceae family in Armenia, analyzing 25 genera and 83 species. She also proposed ecological classifications for these taxa based on their habitat characteristics.

Working with herbarium specimens of borage, the authors of the present study integrated recent data on the molecular taxonomy of this group. According to modern classifications, two families of this complex are represented in the flora of Armenia: Boraginaceae sensu stricto and Heliotropiaceae (Takhtajan 2009; APG IV, 2016). These families occupy ecologically distinct habitats (Avetisyan 1980; Popova 1980; Tamanyan 2011). A distinctive feature of these taxa is the great diversity of morphological and anatomical traits associated with their ecology. In several cases, these data appeared inconsistent with the ecological classifications proposed by Tamanyan (2011). Therefore, the present study aims to provide a more comprehensive understanding of this group by analyzing both macro- and micromorphological features in relation to environmental factors.

To date, substantial information has been accumulated in this field of botany, contributing to a deeper understanding of both abiotic and biotic features of arid habitats. In the context of ongoing climate change, it is important to clarify: 1) the anatomical and morphological characteristics of taxa from different habitat types, and 2) their ecological classification. The present study refines the composition of ecological groups and identifies key adaptive features that characterize these taxa.

The theoretical foundation for analyzing the obtained data is based on numerous studies in plant ecological anatomy and morphology as summarized by V. K. Vasilevskaya (1954). Vasilevskaya asserts that a comprehensive examination of plant adaptability requires particular attention to the leaf and stem, which serve as the primary carriers of adaptive traits within taxa. Various arid habitats are highly characteristic of Armenia’s natural environment (Bush 1936; Takhtajan 1937; Magakyan 1941; Grossheim 1948; Faivush & Aleksanyan 2016). Although true deserts are absent, small areas are occupied by xerophytic formations. Brief descriptions of such communities are provided in «The Flora of Yerevan» (Takhtajan & Fedorov 1972). Cold deserts, typical of Central Asia, Kazakhstan, and Mongolia, are also not represented in Armenia. The structural adaptations of desert types have been studied, using Central Asian deserts as a model system (Vasilevskaya 1940). These habitats are characterized by persistently dry conditions and dominance of semi-shrubs with reduced leaves. The process of tissue degradation in these environments appears so intense that semi-shrubs resemble perennial herbs. Their anatomical structure is characterized by the absence of sclerified tissues, a high proportion of thin-walled parenchyma cells rich in storage compounds (such as oils, mucilage, sugars), and the presence of typical xeromorphic traits, including small cell size, columnar palisade parenchyma, reduced spongy mesophyll, thickened epidermal cell walls (mainly pectic in nature), dense venation, and narrow xylem vessels.

The climatic conditions of hot (or Mediterranean-type) deserts typical of Armenia have given rise to a distinct form of xeromorphism due to precipitation. The first half of the growing season is characterized by high rates of assimilation and transpiration. These deserts are notable for the abundance of ephemerals and ephemeroids. Depending on edaphic conditions, they are classified into sandy, rocky, and clayey deserts.

Sandy deserts are the richest in life forms and species diversity. Many plants exhibit woody life forms and reduced leaves, although not as strongly as in the Central Asian deserts. Leaves, shoots, and petioles of many species are modified into spines. Woody stems are largely composed of mechanical tissues with narrow lumens, typical of sclerophytes. However, some species exhibit features that appear contradictory to their environment. Ephemerals and ephemeroids, for example, employ phonological strategies that allow them to complete their life cycles during the most favorable periods of the growing season. The anatomical structure of desert plants has been studied by numerous authors (Gamaley & Shiirevdambo 1988; Butnik & al. 2009), whose findings align with the present understanding of plant structural adaptations to arid conditions.

MATERIALS AND METHODS

Eleven species from the families Boraginaceae and Heliotropiaceae were analyzed using herbarium specimens collected in previous years (Table 1). Specimens were selected to reflect the taxonomic and ecological characteristics of the taxa.

Table 1. Herbarium specimens of the examined species from the families Heliotropiaceae and Boraginaceae collected in Armenia.

Taxa	Locality
Heliotropiaceae	
Heliotropium europaeum	Armenian SSR, Kapan Region, vicinity of the village Aragadzor. 20.08.1972. N. Khandjian, K. Tamanyan, 104401 (ERE).
H. supinum L	Armenian SSR, Artashat Region, Geganlu state farm. 06.07.1954. A. Barsegyan. 91276 (ERE)
Tournefortia sibirica L.	Armenia, Meghri Region, between Meghri and Aldara in the valley of the Araqs River, on dry, stony slopes. 08.05.1996. E. Gabrielian, 144263 (ERE).
	Armenia, region of Meghri, vicinity of the village of Aldara in the direction of Meghri. Araks River valley, stony slopes, 400 m a.s.l.08.05.1996. E. Gabrielian, 144561 (ERE)
Boraginaceae	
Anchusa arvensis subsp. *orientalis* (L.) Nordh.	Armenia, Ararat Region, vicinity of the town of Ararat near the dam of the gold processing plant. 05.05.1999. K. Tamanyan, 202191 (ERE)
	Armenia, Ararat province, between Yeraskhavan and Tigranashen, 1020 m a.s.l. 13.05.2006. E. Vitek et al., 201453 (ERE)
	Armenia, Aragats province, besides the road to Melikgjugh, 2080 m a.s.l. 04.06.2006. E. Vitek et al., 201455 (ERE)
Onosma sericea Willd.	Armenian SSR. Ashtarak Region, Vicinity of Dzorap village, Mt. Aragats. 02.05.1989. K. Tamanyan, 202021 (ERE)
	Armenia, Aragatsotn province, track between water reservoir and village Kakavadzor, 1880 m a.s.l. 23.06.2007. E. Vitek et al., 173027 (ERE)
	Armenia, Vayots Dzor province, NW above Yeghegis, 1570-1650 m a.s.l. 31.05.2009. E. Vitek et al., 173029 (ERE)
Onosma gracilis Trautv.	Armenia, Yeghegnadzor Region, slopes of the gorge at the exit from Yeghegnadzor towards Vayk. 1300–1400 m a.s.l. 27.06.1999. G. Fayvush, K. Tamanyan, & G. Melkonyan, 202020 (ERE)
	Armenia, Province Vayotsdzor, road Vajk, Voprotan pass, E. Vajk, gorge of Darb river. 15.06.2008. E. Vitek et al., 173014 (ERE)
	Armenia, Ararat province, NNE of Zangakatun, mount slope of Gortun, 2165 m a.s.l. 14.06.2009. E. Vitek et al., 173012 (ERE)

Table 1. continued

Taxa	**Locality**
Nonea polychroma Selvi et Bigazzi	Armenia, Ararat Region, vicinity of Eraskh. 23.04.2002. K. Tamanyan et al., 201862 (ERE)
	Armenia, Ararat Region, Gorovan Sands – protected area. 13.03.2014. E. Gabrielian, O. Fragman, 201868 (ERE)
	Armenia, Ararat province, Ararat district, Erah range, ESE of Kaghcrashen, road to Vedi, 1114 m a.s.l. 11.06.2004. E. Vitek, 186596 (ERE)
Nonea pulla (L.) DC	Armenian SSR. Vardenis District, vicinity of Gyuney village, Sevan Ridge gorge. 28.06.1984. K. Tamanyan, 202014 (ERE)
	Armenia, Gegharkunik Province, eastern side of Lake Sevan, c. middle of the northern side of the peninsula west of Artanish (Mt. Adatapa), 40º 21' 49" N, 45º 18' 37" E; 1930 m a.s.l., 05.05.2005. G. Fayvush, K. Tamanyan, M. Oganesyan, H. Ter-Voskanyan, S. Standinger, M. Standinger, E. Vitek, 201879 (ERE)
	Armenia, Vokhchaberd near Jrvezh, in semi-desert. 23.05.1959. A. Takhtajyan, E. Gabrielian, Y. Mulkidjanyan, 91243 (ERE)
Buglossoides tenuiflora (L.f,) Johnst.	Armenia, Tavush province, area WNW of Berd, beside road H-37 above Parakavar. 820 m a.s.l., 40º 58´48´´N 45º21´25″E. 05.31.2006. M. Oganesyan, H. Ter-Voskanyan, E. Vitek, 201976 (ERE)
	Armenia, Gegharkunik province, 8km SSE of village Lchashen, “Polposht”. 2180 m a.s.l. 14.06.2002. G. Fayvush et al., 186456(ERE)
	Armenia, Syunik province, below the small village Ayriget, 1880 m a.s.l. 13.06.2007. E. Vitek et al., 201597(ERE)
Alkanna orientalis (L.) Boiss.	Armenia. Ararat Province, N of road Garni–Lanjazad / Azat reservoir. 1100-1110 m a.s.l., 40º 58′ 48″ N 45º21′25″ E. 07.02.2015. G. Fajvush, M. Oganesyan, J. Koopman, H. Wiectaw, E. Vitek, 201974 (ERE)
	Armenia, Kapan District, western vicinity of the village Chkaten, eastern slopes of the spurs of Mount Khustup. 02.05.1976. V. Manakyan, 113682 (ERE)
	Armenia, Meghri District, between Shvanidzor and Gyumarants, juniper sparse woodland. 11.06.1978. G. Oganezova, 121616 (ERE)
Myosotis alpestris F. W. Schmidt	Armenia. Flora Sevanensis. Elenovka, m. Arcanoz, 6500'-8000'. 17.06.1928. A. Schelkovnikov et E. Kara-Murza, 579 (ERE)
	Armenia, Syunik province road to Kurdkulakh, c. 1km from the main road, 1285 m a.s.l. 02.05.2005. E. Vitek, 168454 (ERE)
	Armenia, Lori province, mt. Lalvar E of village Sverdlov, 2470 m a.s.l. 30.06.2003. E. Vitek et al., 168452 (ERE)

In the descriptions provided below, the studied species were ecologically grouped according to the classification of Tamanyan (2011). Shoot analysis was conducted primarily using the classical method of comparative anatomy.

At least three samples of each species were examined. Herbarium specimens were preliminarily prepared to facilitate anatomical investigations. Specimens were rehydrated over 5-8 days in a tripartite solution consisting of water, glycerol, and ethanol in equal proportions (1:1:1). The sections were prepared using a safety razor blade. Leaf and stem sections were treated with a chlorine-based agent DOS-GEL (GRASS, Germany), for 0.5–1 minute to straighten and partially decolorize cell walls, thereby improving the clarity of microscopic observations. Additionally, certain sections were prepared using a rotary microtome (Leica Histocore Nanocut R, Germany). For this purpose, herbarium specimens were fixed in a formalin-aceto-alcohol (FAA) solution (Barykina & al. 2004), dehydrated through a graded ethanol series, and cleared in xylene (Gerlach 1984). Specimens were subsequently embedded in paraffin using a modular tissue embedding center (Myr EC 500, Spain). Microscopic observations were conducted with an Olympus microscope (Germany). Photographic documentation was obtained using a C-B18+ microscope (China). When necessary, sections were stained with methylene blue.

RESULTS

Mesophytes

Myosotis alpinus

Stem. In cross-section is unevenly ribbed (Fig. 1A). Epidermal cells exhibit significant thickening of the periclinal walls, possess a thin cuticle, and simple unicellular trichomes. Beneath the epidermis in the major ribs, groups of lamellar collenchyma are developed. These groups are absent in other parts of the stem. In these other parts, the epidermis is supported by 1–2 layers of chlorenchyma. Below the chlorenchyma lies the cortical parenchyma, composed of 2–3 layers of tangentially elongated, thin-walled cells. In some areas, slightly tangentially elongated cells of the endodermis can be distinguished. The primary phloem consists of 2–3 layers of cells with thickened walls. It sometimes forms arcs above the phloem and elsewhere appears as a continuous layer. The phloem is 2–3 layers thick, composed of small cells with indistinct elements. The cambium is not differentiated. The xylem comprises 4–5 layers of cells with pronounced cell wall thickening, and vessels are arranged in radial rows. The pith consists of large, thin-walled cells.

Leaf. Amphistomatic, with dorsiventral structure. Both epidermal layers bear simple unicellular long trichomes. (Fig. 1B). The upper epidermis is composed of nearly isodiametric cells with slightly thickened outer cell walls and a thin cuticle. Beneath it lie two layers of palisade tissue: the first layer is nearly devoid of intercellular spaces, whereas the second layer has noticeable intercellular spaces. The spongy mesophyll consists of approximately 3–4 layers of tangentially elongated cells with well-developed intercellular spaces. Vascular bundles, including the central vein, are surrounded by a chlorenchymatous sheath. The lower epidermis consists of small, tangentially elongated cells with thickened outer walls and a thin cuticle.

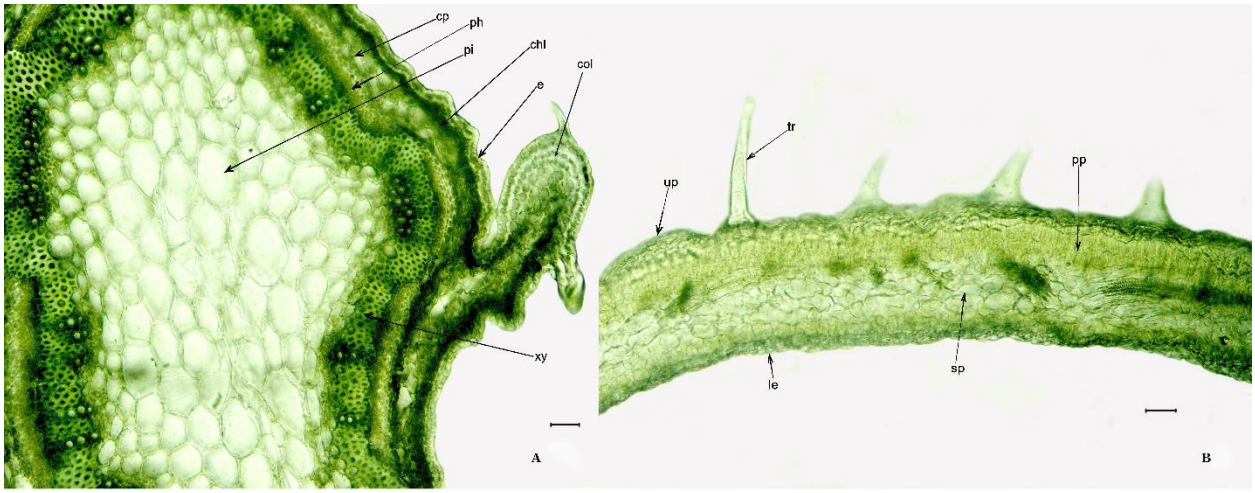

Fig. 1. *Myosotis alpinus*. A, cross-section of the stem. B, cross-section of the leaf. **tr**=trichome, **up**=upper epidermis, **le**=lower epidermis, **pp**=palisade parenchyma, **sp**=spoongy parenchyma, **e**=epidermis, **col**=collenchyma, **chl**=chlorenchyma, **cp**=cortical parenchyma, **ph**=phloem, **xy**=xylem, **pi**=pith. Scale bars: A=50 µm, B=50 µm.

Heliotropium supinum

Stem. Simple trichomes and trichomes with multicellular bases (pedestals) (Fig. 2B, 2C) are distributed across the entire stem surface. Epidermal cells have thickened outer cell walls with a papillose central protrusion (Fig. 2A). The cuticle is thin. Beneath the epidermis lies a layer of chlorenchyma, followed by 1–2 layers of lamellar collenchyma composed of tangentially elongated cells. The cortical parenchyma is radially compressed. The primary phloem is represented by discrete groups of several cells or solitary cells with evenly thickened walls. are developed intercellular spaces. Lower epidermal cells small, slightly tangentially elongated, with mildly Phloem cells are also radially compressed and difficult to distinguish. Xylem vessels are arranged in radial rows and evenly distributed. Medullary rays are 1–2 cells wide. Pith cells are large and thin-walled.

Leaf. Amphistomatic, with a dorsiventral structure. Epidermal cells are morphologically similar to those of the stem epidermis and are oriented tangentially. Trichomes are simple, unicellular, long, and appressed to the epidermis. Beneath the epidermis lies a single layer of palisade tissue with few intercellular spaces. The spongy mesophyll consists of 3–4 layers; most cells are slightly tangentially elongated and have well-thickened walls. Trichomes are simple.

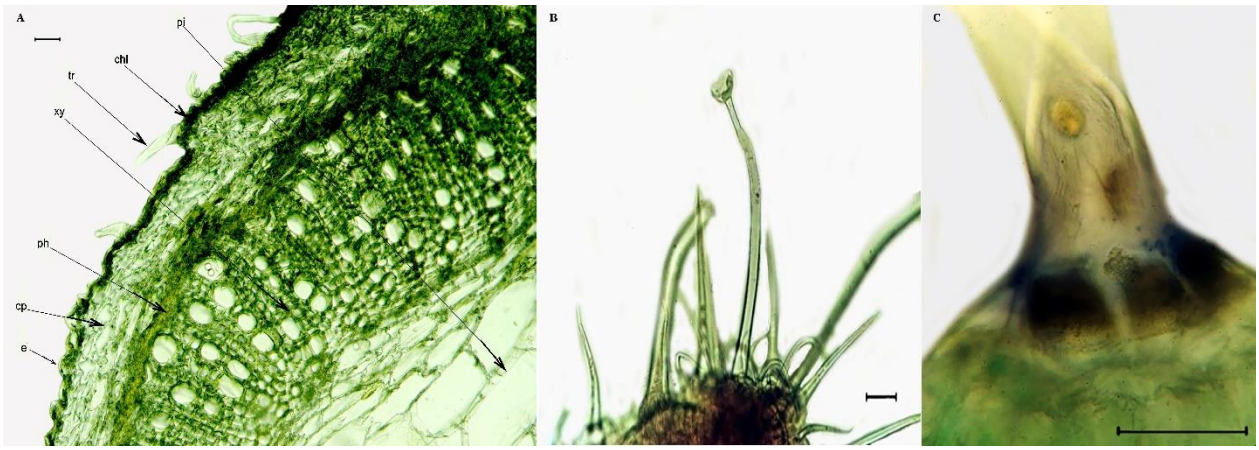

Fig. 2. *Heliotropium supinum*. A, cross-section of the stem. B, trichome types; C, podium trichome. **tr**=trichome. Scale bars: A=50 µm, B=50 µm, C=250 µm.

Mesoxerophytes

Heliotropium europaeum

Stem. The epidermis is composed of small, tangentially elongated cells with slightly thickened outer cell walls (Fig. 3A). The cuticle is thin. Epidermal trichomes are located on small podiums composed of several basal cells and a pointed apical cell. Beneath the epidermis, two layers of chlorenchyma cells, similar in shape to the epidermal cells, are present. These are followed by two layers of larger lamellar collenchyma cells. The cortical parenchyma comprises 2–3 layers of thin-walled cells. The primary phloem is discontinuous, represented by small groups of 2–3 cells with thickened walls. The phloem consists of 4–5 layers of cells. Cambium is not distinguishable. The xylem is represented by conducting vessels evenly arranged in radial rows. The radial rays are uniseriate, and the mechanical tissue cells are numerous. The pith consists of large, isodiametric cells. On the longitudinal section, druse crystals are observed in both xylem and pith cells.

Leaf. Amphistomatic and dorsiventral. The upper epidermis is composed of small, tangentially elongated, thin-walled cells with a thin cuticle. The leaf surface is densely covered with creeping simple trichomes (Fig. 3B). Beneath the upper epidermis, a layer of tall palisade tissue develops, with practically no intercellular spaces. The spongy tissue consists of approximately two layers of tangentially oriented cells. The lower epidermis bears numerous flask-shaped trichomes containing crystals.

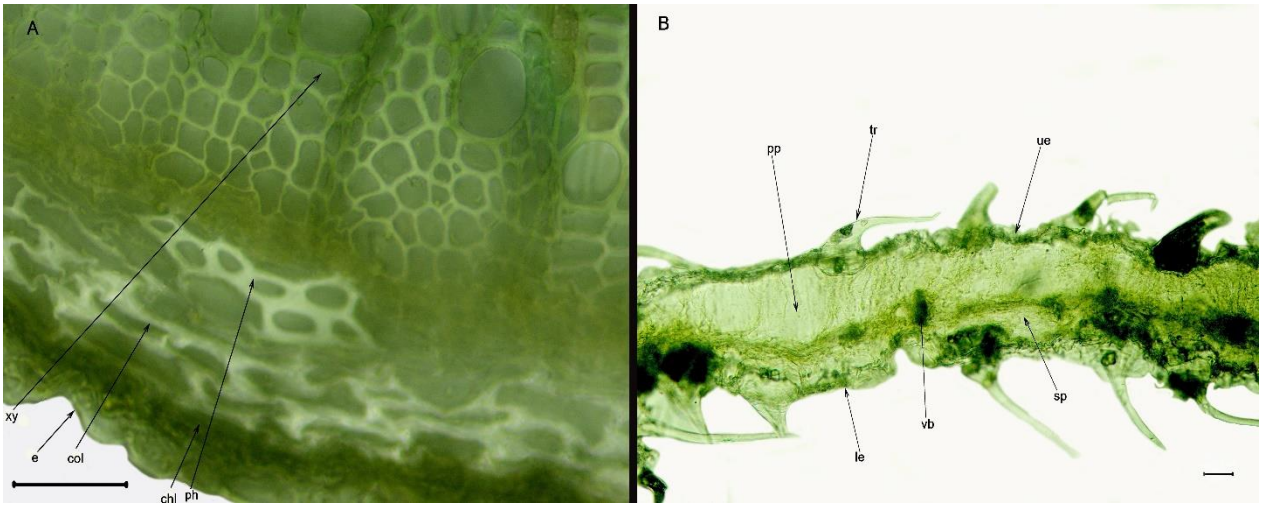

Fig. 3. *Heliotropium europeum.* A, cross-section of the stem; B, cross-section of the leaf. **vb**=vascular bundle. Scale bars: A=250 µm; B=50 µm.

Tournefortia sibirica

Stem. Due to differences in the degree of xylem development, the stem outline is irregularly rounded (Fig. 4A). The epidermis consists of nearly isodiametric cells with thickened outer walls; the inner periclinal walls are slightly thickened as well. The cuticle is thin and folded. Some epidermal cells contain dark contents. Epidermal hairs have a flask-shaped base and an elongated apical cell. Beneath the epidermis, 1–2 layers of chlorenchyma are composed of nearly isodiametric or tangentially elongated thin-walled cells. The remaining cortical layers are composed of thin-walled cortical parenchyma, within which solitary calcium crystals are observed. Small groups of primary phloem cells with thickened walls are also present. The phloem consists of 4–5 layers, its cells containing druse calcium crystals. Cambium is not distinguished. Xylem elements exhibit slight wall thickening. Vessels are arranged in radial rows, with their diameters gradually increasing. Cell walls thickening shows minor variation among the specimens. Radial rays are uniseriate. The pith consists of large, thin-walled cells containing druse crystals.

Leaf. Amphistomatic and isopalisade (Fig. 4B). Epidermal cells are slightly tangentially elongated or nearly isodiametric, with a thickened outer cell wall and a thin cuticle. Trichomes on both epidermises are similar. They may resemble stem trichomes, with a flask-shaped, expanded base and an elongated tip, or appear as simple unicellular hairs, or pyramid-shaped with a broad base and triangular apex. Beneath both epidermises, approximately two layers of low palisade tissue develop, with almost no intercellular spaces. The spongy mesophyll consists of tangentially elongated cells with small intercellular spaces. Druse crystals are noted in the leaf tissues. The vascular bundles are surrounded by chlorenchyma. In the area of the main vein, angular collenchyma develops above the lower epidermis, and numerous druse crystals are also observed there. The lower epidermis resembles the upper epidermis but consists of smaller cells.

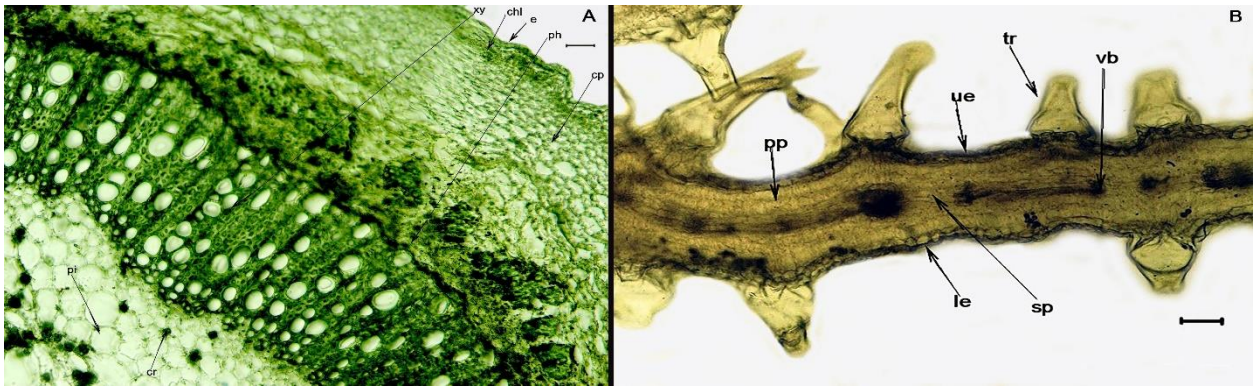

Fig. 4. *Tournefortia sibirica*. A, cross-section of the stem. B, cross-section of the leaf. **cr**-druse crystals; **vb**-vascular bundle. Scale bars: A=50 µm, B=50 µm.

Nonea polychroma

Stem. The epidermal cells have a significant thickening of the periclinal walls, and the cuticle is thin (Fig. 5A). Two types of epidermal trichomes are present: simple and podium. In one specimen, the base of a podium trichome is immersed into the inner stem layers. Beneath the epidermis lies a single layer of chlorenchyma composed of small, slightly tangentially elongated cells. This is followed by one to two layers of lamellar collenchyma. The cortical parenchyma comprises 4 layers of fairly large, thin-walled cells. The primary phloem consists of 1–2 cell layers with slight wall thickening; in some areas, this layer is discontinuous. The phloem consists of 2–3 layers of cells; the cambium is not detected. The xylem is few-layered and fascicular, with 1–2 rows of vascular elements clearly distinguishable. Mechanical cells of the xylem have slight wall thickening. The pith is composed of very large, thin-walled cells.

Leaf. Amphistomatic and isopalisade (Fig. 5B). The upper epidermis consists of small, almost isodiametric cells with thickened outer walls, slightly papillose and protruding. Trichomes are similar to those on the stem, with simple hairs predominating. Beneath the epidermis are 2 layers of palisade tissue, with almost no intercellular spaces, followed by 4 layers of spongy mesophyll with small intercellular spaces, and an additional 2 layers of palisade tissue. The lower epidermis is similar to the upper, but consists of somewhat larger cells and lacks papillose protrusions. Vascular bundles are surrounded by a chlorenchymatous sheath. In the area of the central vein, the thickening of the epidermal cell walls is more pronounced. Around the vascular bundle develops collenchyma, with slight thickening of the cell walls.

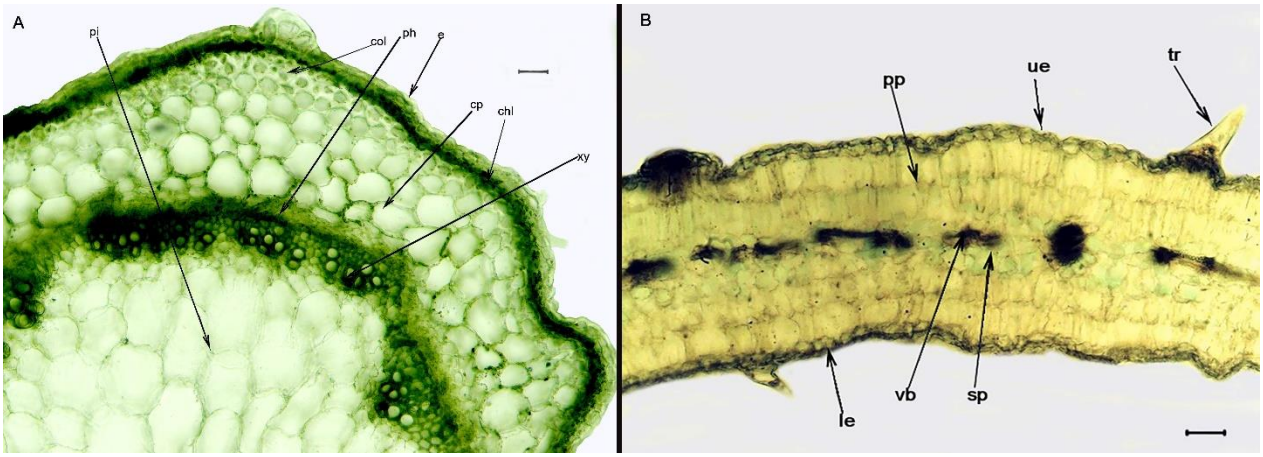

Fig. 5. *Nonea polychroma*. A, cross-section of the stem; B, cross-section of the leaf: **vb**-vascular bundle. Scale bars: A=50 µm, B=50 µm.

Alkanna orientalis

Stem. In cross-section exhibits a nearly triangular outline (Fig. 6A). The epidermal cells are small, nearly isodiametric, with significantly thickened cell walls, and are covered by a thin cuticle. There are three types of trichomes: simple unicellular, podium-type, and 2–3-celled trichomes. The terminal cell of 2–3-celled trichomes is cup-shaped, containing distinguishable granules. Beneath the epidermis, there are two layers of chlorenchyma and 2–3(-4) layers of large, thin-walled cortical parenchyma cells. The large-celled endodermis is clearly distinguishable. Primary phloem cells are absent. The phloem consists of several layers of cells; the cambium is indistinct. Xylem vessels are few in number and arranged in rows. The rays are uniseriate. Elements of mechanical tissue are sparse.

Leaf. Amphistomatic, isopalisade (Fig. 6B). The epidermal cells consist of nearly isodiametric cells with a well-developed thickening of the outer cell wall. The cuticle is thin. The trichomes are similar to those on the stem, with simple trichomes predominating. Beneath the upper epidermis, two layers of relatively tall palisade parenchyma cells are present. In the first layer, intercellular spaces are nearly absent, whereas in the second layer, they are small. These are followed by three layers of rounded spongy parenchyma cells with well-developed intercellular spaces. Next is a single layer of palisade tissue and the lower epidermis, which is similar to the upper epidermis. The vascular bundles are surrounded by a parenchymatous bundle sheath.

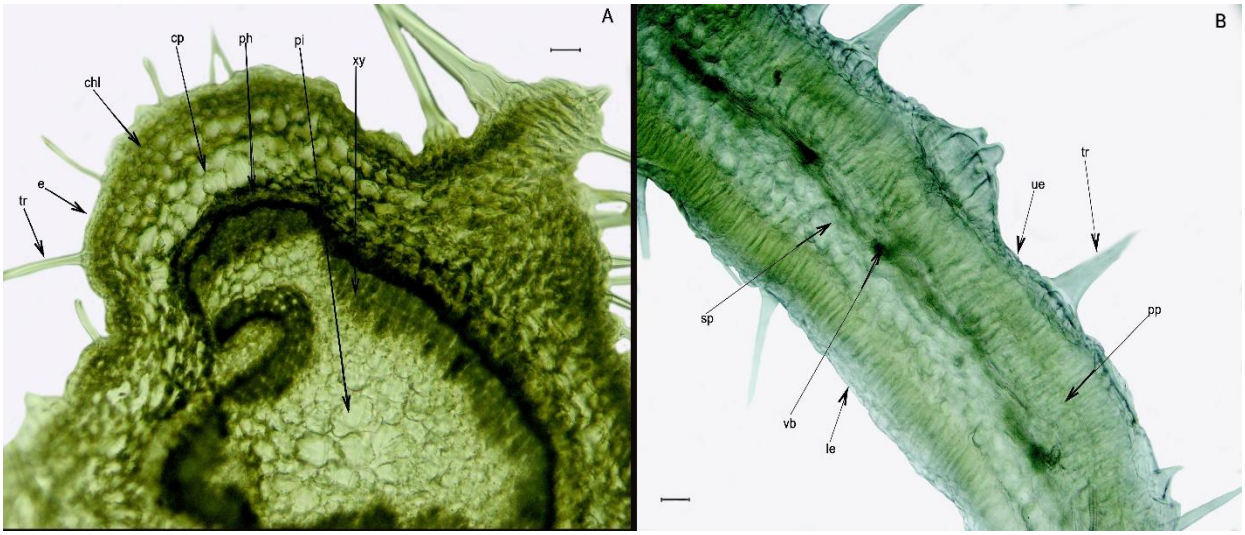

Fig. 6. *Alkanna orientalis*. A, cross-section of the stem; B, cross-section of the leaf. Scale bars: A=50 µm, B=50 µm.

Xerophytes

Nonea pulla

Stem. In cross-section, the stem exhibits an oval outline with pronounced ribs (Fig. 7A). The epidermal cells are small, nearly isodiametric, with thickened periclinal walls and a thin cuticle. Three distinct types of trichomes are present: simple erect unicellular trichomes, podium-type trichomes, and three-celled glandular trichomes terminating in a cup-shaped apical cell. Beneath the epidermis, there are two layers of chlorenchyma cells, which are partly absent in the ribs. The ribs themselves contain 2–3 layers of lamellar collenchyma, underlying the chlorenchyma in other parts of the stem. The cortical parenchyma is 1–2 layers thick and radially compressed. The primary phloem is 2–3 layers thick, intermittent in places, with slight thickening of the cell walls. The phloem is strongly compressed in the radial direction, and the cambium is indistinguishable. The xylem is fascicular – bundle outlines can be distinguished, and the spaces between them are filled with mechanical tissue. The vascular elements are unevenly developed. There are sections of the xylem with numerous relatively large vessels and sections where there are few in number, and the vessel lumens are very narrow. The parenchyma of the pith is thin-walled and in some areas destroyed.

Leaf. Isopalisade, amphistomatic (Fig. 7B). The upper epidermis consists of slightly tangentially elongated cells, with thickened periclinal walls and a thin cuticle. There are two types of trichomes: simple, unicellular, and pod-based. The cells of the podiums are larger than the other epidermal cells. Beneath the epidermis, there are 2 layers of palisade tissue with practically no intercellular spaces. Below them are 5-6 layers of slightly tangentially elongated cells of spongy tissue with small intercellular spaces. A chlorenchymatous bundle sheath surrounds the vascular bundles. Above the lower epidermis, there is an additional layer of palisade tissue with developed intercellular spaces. Their height is less than that of the cells in the upper palisade. The lower epidermis consists of cells morphologically similar to those in the upper epidermis, but slightly larger. The trichomes of the lower epidermis are similar to those of the upper epidermis. In the area of the central vein, a more significant thickening of the cell walls of both epidermises is observed compared to the rest of the leaf. In this area, up to 6 layers of angular collenchyma are noted above the lower epidermis. The sheath around the central vein consists of lamellar collenchyma.

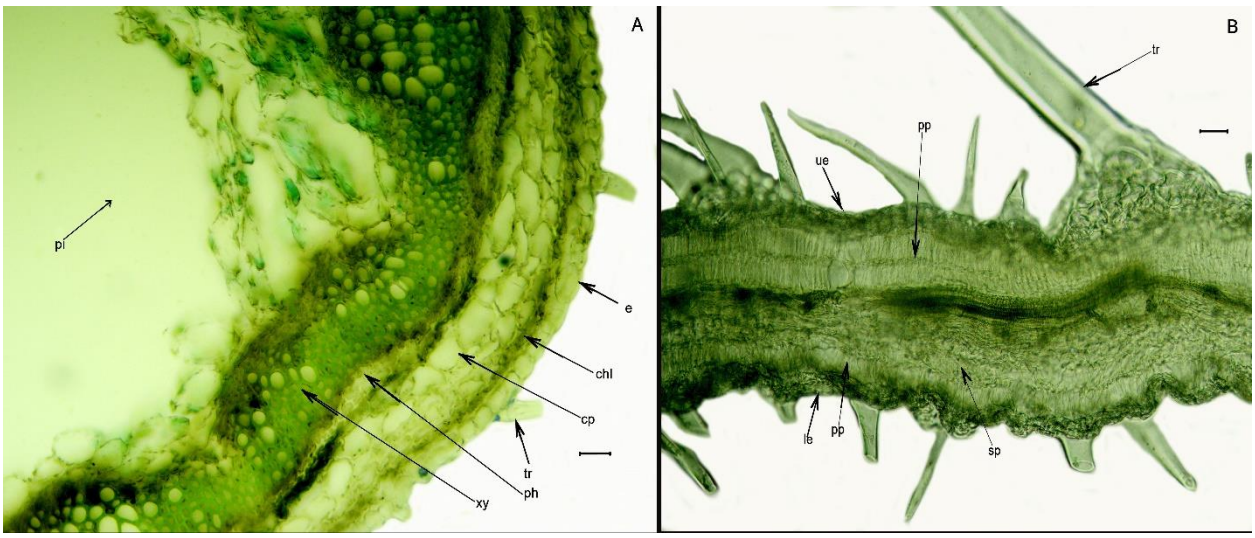

Fig. 7. *Nonea pulla.* A, cross-section of the stem; B, cross-section of the leaf. Scale bars: A=50 µm, B=50 µm.

Buglossoides tenuiflorum

Stem. The outline of the stem in cross-section is rounded (Fig. 8A). The epidermis consists of small, almost isodiametric cells with slight thickening of the outer cell wall, and the cuticle is thin. Epidermal trichomes are unicellular and simple. Beneath the epidermis are two layers of chlorenchyma, followed by approximately four layers of tangentially elongated, radially compressed parenchyma cells. The endodermis is distinguished by its relatively large cells. The phloem consists of highly compressed cells, the cambium is not distinguishable. Xylem cells are arranged in rows, and the total volume of xylem greatly exceeds that of the phloem. The pith is destroyed, with only individual large thin-walled cells remaining in some places.

Leaf. Amphistomatic, with a dorsiventral structure (Fig. 8B). The upper epidermis consists of trapezoidal-shaped cells with slight thickening of the cell walls and a thin cuticle. Trichomes have a podium, whose cells are much larger than other epidermal cells, with more developed thickening of the cell walls and small crystals. The palisade tissue is two-layered. The first layer has almost no intercellular spaces, while the second layer has well-developed intercellular spaces. Closer to the leaf edge, only one layer of palisade tissue remains. The spongy tissue consists of several layers of usually tangentially oriented cells with well-developed intercellular spaces. Compared to the upper epidermis, the lower epidermis has smaller cells, with slight thickening of the cell walls and a thin cuticle. The trichomes are the same as those on the upper epidermis. The vascular bundles are surrounded by a chlorenchyma sheath. In the main vein area, the lower epidermis has larger cells and more well-developed thickening of the outer cell wall than the epidermis of the lateral parts of the leaf—a clear combination of mesomorphic and xeromorphic features.

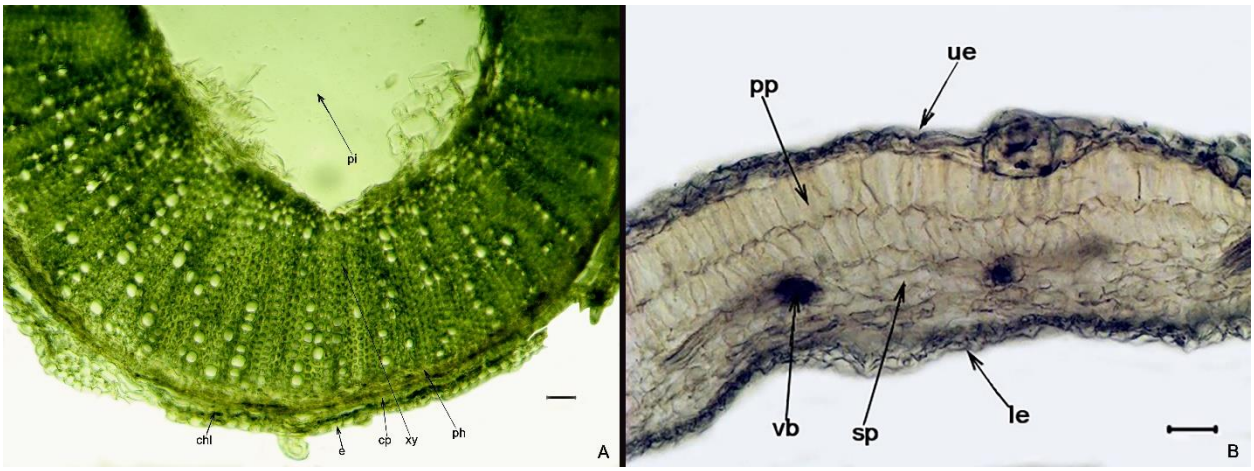

Fig. 8. *Buglossoides tenuiflorum*. A, cross-section of the stem; B, cross-section of the leaf. Scale bars: A=50 µm, B=50 µm.

Anchusa arvensis* subsp. *orientalis

Stem. Ribbed in outline**.** The epidermal cells are almost isodiametric in shape with thickened periclinal cell walls and a thin cuticle. Epidermal trichomes are simple and podium-type. Beneath the epidermis are 2 layers of thin-walled chlorenchyma and 1–2 layers of lamellar collenchyma. In the ribs, the collenchyma is more highly developed, forming up to 8 cell layers. The cortical parenchyma consists of 1–3 layers. The endodermis is constituted by relatively large, rectangular, tangentially oriented cells. The phloem is few-layered, consisting of about 3–4 layers. The xylem comprises 4–5 layers. Both xylem vessels and mechanical tissue show slight thickening of their cell walls. The pith parenchyma is large-celled and thin-walled.

Leaf. Amphistomatic and dorsiventral. The upper epidermis is composed of cells with slightly thickened periclinal walls, the central part of which is often papillately elongated. Trichomes are simple and unicellular. The palisade tissue is single-layered. Beneath it lies an additional layer of tightly packed isodiametric cells, with almost no intercellular spaces. The spongy tissue is 4–5-layered with well-developed intercellular spaces. The lower epidermis consists of small cells similar to those of the upper epidermis, with slight thickening of the outer cell wall. In addition to simple hairs, podium-type trichomes are also observed here.

Onosma gracilis

Stem. The epidermis is composed of isodiametric or slightly tangentially elongated cells with slightly thickened walls and a thin cuticle. Trichomes are of two types: simple and podium-type. 4–5 layers of lamellar collenchyma underlie the epidermis. The cortical parenchyma consists of large, tangentially oriented cells. The endodermis is somewhat distinguished by its larger cell size. The stele is ring-shaped. The primary phloem forms a layer of cells with significant wall thickening; the secondary phloem consists of 5–6 layers. The cambium is not distinct. The xylem vessels are evenly distributed in radial rows. Uniseriate radial rays are numerous. Mechanical elements of the xylem are abundant. Pith cells have a slightly thickened wall, and some contain starch grains.

Leaf. Amphistomatic and isopalisade. The upper epidermis consists of isodiametric cells with thickened periclinal walls and a thin cuticle. It has three types of

trichomes: simple, podium-type, and glandular. The podium trichomes are distinguished by their multicellular base, which is embedded in the mesophyll and filled with druse crystals. Rare glandular trichomes have a spherical apical cell and consist of four cells. Beneath the upper epidermis are 2, occasionally 3 layers of palisade tissue, almost devoid of intercellular spaces. The spongy tissue consists of 4–5 layers of rounded cells with intercellular spaces. Parenchymatous sheaths surround vascular bundles. Above the lower epidermis, there is one or sometimes two layers of palisade tissue. These cells are slightly shorter than those of the upper palisade layer, and intercellular spaces are present. The cells of the lower epidermis are tangentially elongated, small, with thickened periclinal cell walls and a thin cuticle. The trichomes of the lower epidermis are podium-type and simple.

Onosma sericea

Stem. Its structure is similar to that of the previous species. The epidermis is similar, except that in addition to podium trichomes, simple unicellular hairs are also present. Similarities between these species are noted in the structure of the collenchyma, cortical parenchyma, and phloem (Fig. 9). A distinctive feature of the xylem in this species is that vascular elements mainly formed at the beginning of the growing season. The pith consists of thin-walled cells.

Leaf. Structure is also similar to that of *O. gracilis*. Distinguishing features include predominantly thickened outer cell walls in the epidermal cells. In the area of the main vein, a mechanical sheath is well developed. Beneath the upper epidermis, there are several layers of collenchyma cells.

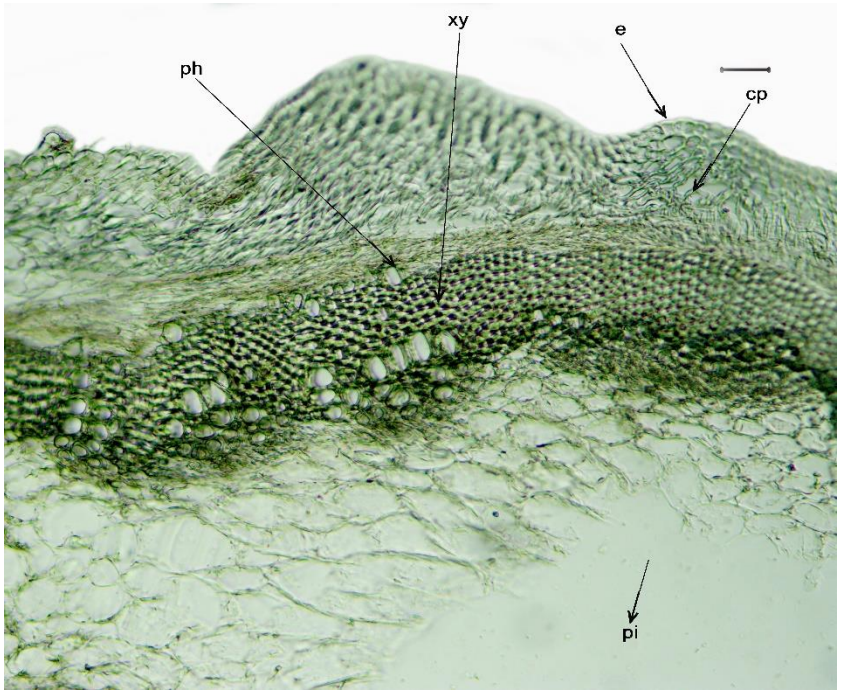

Fig. 9. *Onosma sericea*. Cross-section of the stem. Scale bar=50 µm

Summarizing the ecologically significant data of the studied species, the following observation can be made:
1. Trichomes of all examined Boraginaceae species represented by four distinct types: simple unicellular trichomes, unicellular trichomes with an expanded base, trichomes with a multicellular expanded base containing crystals (podium-type), and 2–3-celled trichomes with a rounded or cup-shaped apical cell containing crystals. Bristles are also present. Trichomes of various types typically cover the entire plant.

2. The annual stems of different species and genera within this taxonomic group exhibit significant structural similarity. Differences are primarily observed in the degree of development of vascular tissues, mechanical tissues, and the pith. The epidermis frequently exhibits thickening of the periclinal walls. A notable thickening of cell walls and the abundance of mechanical tissues are common features of the most xeromorphic species. These tissues include collenchyma, secondary phloem (forming either a

continuous ring or separate groups of cells above the usually thin primary phloem), various xylem elements, and pith cells with varying degrees of preservation and cell wall thickness.

3. The leaves of Boraginaceae species are diverse in size and function, including basal, rosette, cauline, and bract leaves. This study focused on cauline leaves. The main anatomical distinction among the studied species corresponds to two structural types: isopalisade and dorsiventral. Regardless of the anatomical type, leaf veins, including the main vein, are generally small and surrounded by chlorenchyma, although exceptions to this pattern are observed.

DISCUSSION

The investigation of plant adaptability has a history extending over a century. Metcalfe & Chalk (1965), in their review work on dicotyledons' anatomy, highlighted the Boraginaceae family's notable characteristic of exceptional hair covering development. The types of trichomes described by these authors, as well as those reported in other studies (Evert 2006; Nazari & Ghahremaninejad 2024, 2025), correspond closely to the trichomes observed in the present work, with one addition. In this study, we also used the term podium-type trichomes. These are trichomes that have a multicellular base, raising the trichome above the epidermal surface. Their contents are presented in the form of liquid or crystalline granules. Metcalfe & Chalk (1965) also noted that simple, unicellular, thick-walled trichomes may be either erect or lying along the epidermal surface. According to their observations, species exhibiting the greatest diversity of trichomes tend to be the most drought-resistant, as these trichomes fulfill multiple ecological functions. Specifically, they protect excessive insolation (simple trichomes), defend against grazing by livestock and insects (bristles, glandular trichomes, and those containing crystalline inclusions), and aid in the excretion of excess mineral substances from the plant organisms (trichomes with crystalline inclusions). Bristles are morphologically diverse; some forms, such as those equipped with anchor-like structures on fruits, actively contribute to species dispersal.

Tamanyan (2011), based on the ecological diversity of Boraginaceae species in Armenia, classified all species into three ecological types: mesophytes, mesoxerophytes, and xerophytes. According to her classification, among the species studied in the present work, the mesophyte group includes *Myosotis alpestris* and *Heliotropium supinum*. The mesoxerophyte group comprises *Alkanna orientalis*, *Heliotropium europaeum*, *Nonea polychroma*, and *Tournefortia sibirica*. The xerophyte group includes *Anchusa arvensis* subsp. *orientalis*, *Onosma sericea*, *O. gracilis*, *N. pulla*, and *Buglossoides tenuiflorum*. However, the present study shows that several species do not conform to Tamanyan's ecological groupings. According to the obtained data, the mesophyte group is characterized by the following anatomical features. The stem epidermal cells have thickened periclinal walls, or in some cases, only the outer wall is thickened. Trichomes are predominantly simple, rarely podium-type. Mechanical tissue (collenchyma) is absent or present in small amounts. The primary phloem is either absent or represented by small groups of cells. Xylem elements show substantial wall thickening; pith cells are thin-walled. The leaf is dorsiventral, with a typically two-layered palisade tissue.

Species exemplifying these features include *Myosotis alpinus*, *Heliotropium supinum* (with podium-type trichomes on the upper epidermis of the leaf and simple trichomes on the lower one), *H. europaeum* (with druse crystals in the xylem and pith of the stem), *Buglossoides tenuiflorum* (pith is disintegrated, its thin-walled cells are partially preserved, trichomes are podium-type), and *Anchusa arvensis* (with 1–2 layers of collenchyma in the stem, xylem elements with slight cell wall thickening, leaf has a dorsiventral structure and a single-layered palisade tissue).

Mesoxerophytes are characterized by the following features: the stem epidermis consists of cells with thickened periclinal walls, and trichomes are predominantly podium-type. The primary phloem may be continuous or discontinuous; the xylem elements exhibit slight cell wall thickening. The pith is thin-walled with druse crystals. The leaf is isopalisade, with both epidermal layers having thickened outer cell walls, trichomes are podium-type and/or simple palisade tissue beneath both epidermises is two-layered. Druse crystals are also present in the leaf tissues. This group includes *Nonea polychroma* (on the stem, both simple and podium-type trichomes are present; collenchyma is present; the xylem is arranged in bundles; crystals are absent. The leaf predominantly has simple trichomes. The palisade tissue beneath the upper epidermis is two-layered, and beneath the lower epidermis, it is single-layered. Collenchyma is present along the central vein), *Nonea pulla* (collenchyma is present in the stem and in the sheath of the main leaf vein, the palisade tissue is similar to that of *N. polychroma*), *Turnefortia sibirica* (both stem and leaf have only the outer cell wall thickened, stem trichomes have an expanded base and an elongated apical cell, primary phloem is discontinuous, xylem elements have slight thickening of cell walls. The leaf is isopalisade, trichomes are

either similar to those on the stem or simple unicellular, palisade tissue is two-layered, low in height; near the main vein, angular collenchyma and druse crystals of calcium are present).

Xerophytes are typically characterized by the presence of multiple trichome types and by a predominance of mechanical tissues over parenchymatous ones. For example, in *Onosma gracilis* and *O. sericea*, the stem bears at least two types of trichomes (simple and podium-type), while the leaf exhibits three types, including glandular trichomes with a rounded apical cell containing crystals and bristles. Collenchyma is developed in the cortex of *O. sericea*. The stele is ring-shaped, featuring a continuous layer of primary phloem with well-developed cell wall thickening, and the mechanical elements of the xylem are abundantly represented. Pith cells have slightly thickened cell walls. The leaves are isopalisade, with the palisade tissue being 2–3 layered. In *Alkanna orientalis*, the stem epidermis has significantly thickened cell walls. Trichomes are represented by three types: simple unicellular, podium-type, and glandular with a rounded apical cell containing granules, which may assume a cup-shaped form after disintegration. The primary phloem is absent. The mechanical elements of the xylem are few in number. The leaf is isopalisade. The epidermis shows well-developed thickening of the outer cell wall. The palisade tissue beneath the upper epidermis is two-layered and tall, whereas beneath the lower epidermis is single-layered.

In contrast to the ecological groupings proposed by Tamanyan (2011), the present study, based on both abiotic factors and detailed anatomical analyses of shoots, proposes a revised classification (Table 2). The mesophyte group comprises *Myosotis alpestris*, *Heliotropium europaeum*, *H. supinum*, *Buglossoides tenuiflorum*, and *Anchusa arvensis* subsp. *orientalis*. The mesoxerophyte group includes *Nonea polychroma*, *N. pulla*, and *Tournefortia sibirica*. Finally, the xerophyte group encompasses *Onosma sericea*, *O. gracilis*, and *Alkanna orientalis*. This revised classification reflects observed ecological and morphological traits that are closely associated with the species' habitat preferences.

Table 2. Comparison of ecological type assignments of studied species according to Tamanyan (2011) and the present study.

Taxa	**Ecological type by Tamanyan (2011)**	**Ecological type according to the present study**
Myosotis alpestris	mesophyte	mesophyte
Heliotropium europaeum	mesoxerophyte	mesophyte
H. supinum	mesophyte	mesophyte
Buglossoides tenuiflorum	xerophyte	mesophyte
Anchusa arvensis subsp. *orientalis*	xerophyte	mesophyte
Nonea polychroma	mesoxerophyte	mesoxerophyte
N. pulla	xerophyte	mesoxerophyte
Tournefortia sibirica	mesoxerophyte	mesoxerophyte
Onosma sericea	xerophyte	xerophyte
O. gracilis	xerophyte	xerophyte
Alkanna orientalis	mesoxerophyte	xerophyte

Thus, the functions of hair covering vary among different taxa. The variability of these functions is associated with the significant variation in the hair covering itself – its morphology, physiology, and location on the plant. It should also be noted that ecologically significant traits of different organs often complement one another, effectively adjusting the species' level of adaptation to their habitat and thereby contributing to their individual adaptive characteristics.

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