Turczaninowia 29, 2: 195–205 (2026)
https://www.doi.org/10.14258/turczaninowia.29.2.20
http://turczaninowia.asu.ru

ISSN 1560–7259 (print edition)
TURCZANINOWIA
ISSN 1560–7267 (online edition)

УДК 582.683.2:581.4+581.8+581.527.4(55)

Morphological, anatomical and micromorphological study of *Aethionema semnanense* (Brassicaceae), an endemic and endangered species from Iran

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***Keywords*:** *Aethionema arabicum, Aethionema cordatum,* anatomical structure of plants, endemic, rare species, SEM.

Summary. *Aethionema semnanense* is a rare, endemic, and endangered species of Iran, belonging to the earliest-diverging lineage of the family Brassicaceae. This study provides an integrated analysis of the morphological, anatomical, and micromorphological features of this species to clarify its taxonomic position and structural adaptations. Macromorphological traits such as ovate to orbiculate leaves, bilocular boat-shaped silicules, and winged filaments were documented. Anatomical observations revealed amphistomatic leaves with differentiated palisade and spongy tissues, idioblastic crystal-bearing cells, and well-developed vascular bundles. Micromorphological examination of seed surface patterns using scanning electron microscopy (SEM) demonstrated a distinct reticulate sculpturing that clearly differs from closely related species, including *A. arabicum* and *A. cordatum*. These combined characteristics reinforce the systematic distinctness of *A. semnanense* and contribute to understanding structural variation and adaptive strategies among early-diverging Brassicaceae taxa. The results also provide valuable information for future taxonomic, phylogenetic, and conservation-oriented studies on the genus *Aethionema*.

Морфологическое, анатомическое и микроморфологическое исследование *Aethionema semnanense* (Brassicaceae) – эндемичного и исчезающего вида из Ирана

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Ключевые слова: анатомическое строение растений, редкий вид, сканирующая электронная микроскопия, эндемик, *Aethionema arabicum, Aethionema cordatum*.

Поступило в редакцию 14.06.2025
Принято к публикации 16.07.2026

Submitted 14.06.2025
Accepted 16.07.2026

Аннотация. *Aethionema semnanense* – редкий и находящийся под угрозой исчезновения вид, эндемичный для Ирана, принадлежащий к наиболее рано дивергировавшей кладе семейства Brassicaceae. В данном исследовании представлено комплексное изучение морфологических, анатомических и микроморфологических признаков вида с целью уточнения его таксономического положения и структурных адаптаций. Макроморфологические признаки: листья овальные до округлых, двугнёздные лодочковидные стручочки и крылатые тычиночные нити. Анатомические наблюдения выявили амфистоматические листья с дифференцированными палисадной и губчатой паренхимами, идиобластами с кристаллами и хорошо развитыми проводящими пучками. Микроморфологический анализ поверхности семян с использованием сканирующей электронной микроскопии (СЭМ) выявил характерный сетчатый рисунок, значительно отличающийся от близкородственных видов, таких как *A. arabicum* и *A. cordatum*. Полученные данные подтверждают систематическую обособленность *A. semnanense* и дают представление о структурных адаптациях рано дивергировавших таксонов Brassicaceae. Результаты также представляют ценность для дальнейших таксономических, филогенетических и природоохранных исследований рода *Aethionema*.

Introduction

The genus *Aethionema* W. T. Aiton represents the earliest-diverging lineage within the Brassicaceae family and comprises approximately 60–70 species, predominantly distributed in the Irano-Turanian phytogeographical region (Moazzeni et al., 2018). These species are characterized by a wide diversity in morphology, including variations in leaf shape, fruit type (dehiscent vs. indehiscent), and floral structures. As the sister clade to the rest of the Brassicaceae, *Aethionema* has garnered attention for its phylogenetic importance and evolutionary distinctiveness (Al-Shehbaz, 2012; Edger et al., 2018).

Recent taxonomic and ecological studies have expanded the understanding of species diversity in *Aethionema*. According to Moazzeni et al. (2018), high-elevation habitats of Iran harbor underestimated diversity, and subsequent studies have led to the description of new species such as *A. alpinum* Moazzeni et Noroozi and *A. zagricum* Moazzeni et Mahmoodi. As noted by Moazzeni et al. (2018), many species of *Aethionema* are adapted to rocky and dry to alpine habitats, occurring from 500 to more than 3500 meters in elevation. These findings highlight the importance of continued floristic and systematic surveys in mountainous regions of Iran (Moazzeni et al., 2018, 2023).

Micromorphological traits, such as seed coat ornamentation and flower structure, have proven particularly valuable for taxonomic resolution within *Aethionema* (Pinar et al., 2007; Khosravi et al., 2009; Atceken et al., 2016). Recent studies have also demonstrated that anatomical characters of stems, leaves, and reproductive organs can effectively differentiate closely related taxa (Karaismailoğlu, 2019; Tekin, 2022). These characteristics, observed through techniques such as scanning electron microscopy (SEM), provide diagnostic tools that complement molecular data in resolving species boundaries and evolutionary relationships.

In Iran, *Aethionema* is represented by at least 18 species, some of which are very common, e. g., *A. grandiflorum* Boiss. et Hohen. and *A. carneum* (Banks et Sol.) B. Fedtsch., others are not so widely distributed. Six Iranian species of *Aethionema* are narrow endemics with distinct morphological features (Hedge, 1968; Moazzeni et al., 2018, 2023). These are *A. cephalanthum* Bornm., *A. erinaceum* (Boiss.) Khosravi et Mumm., *A. sabzevaricum* Khosravi et Joharchi, *A. semnanense* Mozaff., *A. stenopterum* Boiss., and *A. umbellatum* (Boiss.) Bornm. *Aethionema semnanense* is an endemic species of Iran that occurs on gravely slopes at the elevation between 2200 and 2900 m a. s. l. (Moazzeni et al., 2018). The genus is characterized by simple, entire leaves that are variable in shape and size in Iranian *Aethionema*. Some species have linear to narrowly oblong leaves 1–4 mm wide, e. g., *A. grandiflorum*, *A. transhyrcanum* (Czerniak.) N. Busch, and *A. virgatum* (Boiss.) Hedge, whereas others such as *A. cordatum* (Desf.) Boiss., *A. semnanense*, and *A. sabzevaricum* have ovate, elliptic, or cordate leaves 5–20 mm wide. All species do not produce basal rosettes.

Aethionema semnanense is perennial herbaceous plant 3 to 10 cm tall, without thorns, with broadly ovate leaves, silicules entire at margins, bilocular, cymbiform, 1–4-seeded, filaments winged. *Aethionema semnanense*, originally described by Mozaffarian (1996), is a rare endemic endangered perennial species confined to Semnan province (Iran). It is morphologically distinguished by its ovate leaves, bilocular cymbiform silicules, and winged filaments. Its anatomical and micromorphological features have not been thoroughly investigated yet, leaving a gap in understanding its taxonomic

placement within the genus. The present study aims to fill this gap by providing a comprehensive description of the anatomical and morphological structures of *A. semnanense*, including observations of leaf, stem, flower, and seed characteristics. These findings are expected to contribute to the taxonomy of *Aethionema* and enhance the knowledge of structural adaptations within early-diverging lineages of Brassicaceae.

In anatomical studies of Brassicaceae, specific structural traits such as idioblastic cells and amphistomatic leaves are considered informative for taxonomy and ecological interpretation. Amphistomatic leaves, characterized by the presence of stomata on both adaxial and abaxial surfaces, are generally associated with plants growing in high light or arid environments, as they enhance gas exchange efficiency (Salisbury, 1992). These features not only reflect adaptation to environmental pressures but also provide valuable taxonomic markers in species discrimination.

Materials and Methods

Based on the investigations conducted in the province and using the experiences of the authors of this article, based on different samplings in the province, the only habitat of *A. semnanense* species was identified around the villages of Eij and Javin of Sorkheh city. These localities are situated in the west of Semnan city. The type of the species was collected in the locality with geographical coordinates of 35°28′9″N, 52°53′33″E, at elevation 1336 m: "Semnan, Lastjerd, Eij to Javin, 1900 m, Taherian and Maddah 850" (TARI; iso – Research Center of Semnan). Some collected samples were dried, according to standard herbarium techniques, and stored in the Trakya University Faculty of Pharmacy Herbarium. For morphological measurements, herbarium and fresh plant samples were used, and at least 20 measurements were taken for each character from as many different individual plants as possible. Gypsum and limestone plant communities are especially visible in this area. However, the mining and construction of factories in the region have led to irreparable damage to the vegetation of the region and the destruction of many habitats. The species was sampled from rocky, gypsum-rich slopes in Semnan province. The villages of Eij and Jovin have beautiful natural landscapes, which are located on the southern slope of Miantigh Mountain on the southern edge of the Alborz Mountains (Fig. 1). Fresh plant material of *A. semnanense* was collected during the growing season from the natural population. For morphological analyses, both herbarium and fresh specimens were used. At least 20 measurements were taken for each character (e. g., leaf, petal, fruit, seed) from multiple individuals to ensure statistical validity.

Anatomical studies were conducted on hand-made cross sections of leaves and stems. Fifteen leaf samples (five per individual from three individuals) were fixed, stained with Carmen Zaji and Methylene Blue (Sotoodehnia-Korani, 2020), and observed using a light microscope (Leitz Wetzlar) equipped with a Nikon Coolpix camera.

Trichome characteristics and seed surface ornamentation were examined using scanning electron microscopy (SEM; Tescan Vega-3 LMU). Samples were mounted on aluminum stubs, sputter-coated with a 25 nm gold layer, and analyzed at 15–22 kV acceleration voltage at the SEM Laboratory of Semnan University.

Anatomical traits (e.g., epidermis thickness, stomatal length, palisade cell dimensions) were measured using calibrated image analysis software. Statistical analyses were conducted using SPSS software (version 15.0). All morphological and anatomical measurements were tested for normality using the Shapiro-Wilk test. One-way Analysis of Variance (ANOVA) was applied to evaluate significant differences among measured traits (e. g., leaf thickness, stomatal length, seed size). When significant differences were observed ($p < 0.05$), post hoc comparisons were made using Tukey's HSD test to determine which groups differed significantly. All data are presented as mean ± standard deviation (SD).

Results

Morphological Characteristics

Aethionema semnanense is a perennial herbaceous plant with a woody base and prostrate, glabrous stems. Leaves are ovate to bicuculate, coriaceous, sessile, entire-margined, exhibiting a distinct greenish-blue coloration. Leaf apices rounded; the surfaces may be slightly mucronulate to emucronulate. Inflorescences densely spicate and racemose, measuring approximately 8–9 mm in length and 4–5.4 mm in width during flowering and fruiting stages.

Petals are yellowish-purple, obdeltoid with a truncate apex, and clawed at the base, 3.5–7 × 0.7–1.2 mm. Sepals are elliptic-obovate, with membranous margins and a subacute apex, 2.0–2.5 × 1.1–1.3 mm.

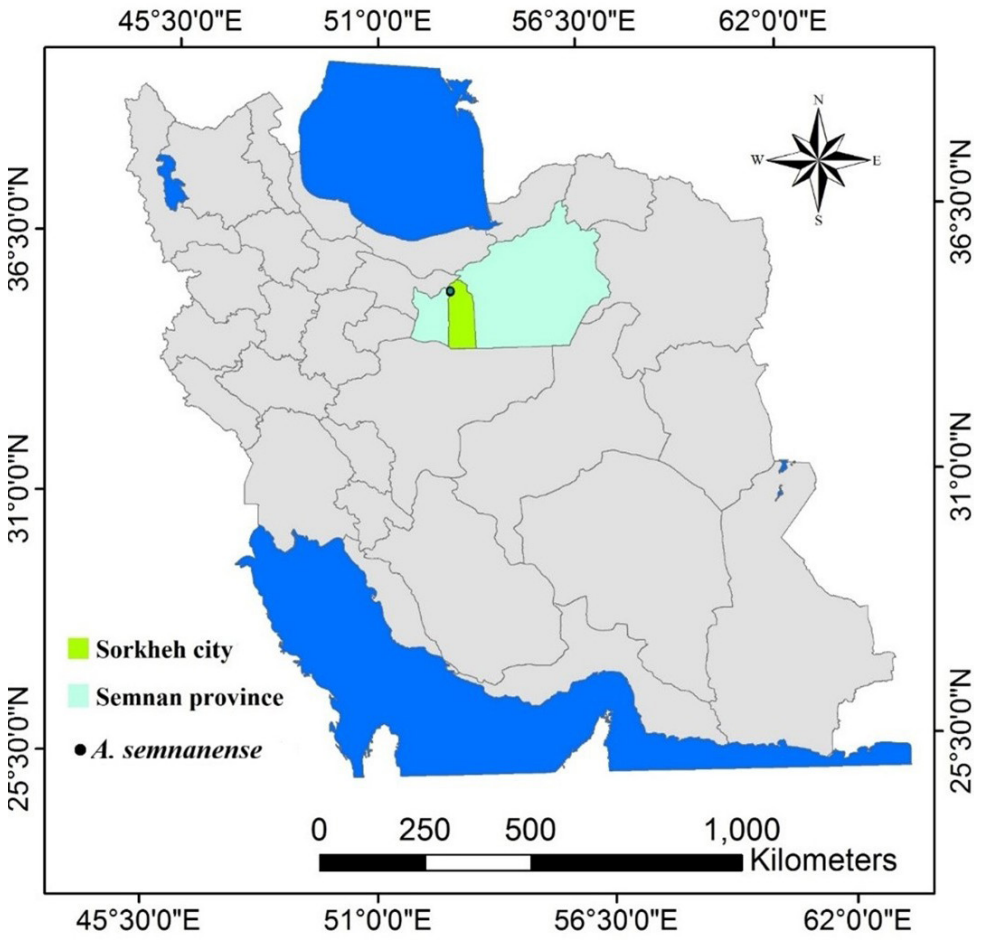

Fig. 1. The distribution of *Aethionema semnanense.*

Androecium is tetradynamous, consisting of four long (2.4–3.1 mm) and two short (1.7–2.2 mm) filaments, all winged. Anthers approximately 0.8–1.0 mm long and equal in both stamen types.

Ovary bilocular, with each locule containing two ovules. Styles are short (0.2–0.3 mm), terminating with a capitate stigma. Fruiting pedicels thin, glabrous, 2–4 mm long, with an erect to recurved orientation. Siliques are orbicular-elliptic, dehiscent, greenish, with entire margins, 14.3–16.1 × 20–25.1 mm. Each fruit typically contains four ovoid seeds 2–2.5 mm long and 0.8–1.5 mm wide, exhibiting a distinctive reticulate surface ornamentation.

The combination of coriaceous, orbicular leaves and large, winged fruits makes *A. semnanense* easily distinguishable from other species within the genus *Aethionema* (Fig. 2, Table 1).

Anatomical Characteristics

Cross-sections of the stem reveal three types of epidermal cells: square, rectangular, and rectangular-oval. The cortex is composed of circular to oval parenchymatous cells arranged in seven to nine layers beneath the epidermis. A distinct layer of cells is observed just beneath the phloem and above the collateral vascular bundles. The regions between these vascular bundles are reinforced by bands of sclerenchyma fibers, and the central pith consists of parenchymatous cells with circular to polygonal shapes (Fig. 3A–C).

Leaf anatomy exhibits a well-defined upper and lower epidermis, both composed of unicellular, rectangular to oval cells devoid of trichomes. The mesophyll is differentiated into palisade and spongy parenchyma, arranged symmetrically, giving the leaf a mesomorphic and amphistomatic structure. Amphistomatic leaves, characterized by the presence of stomata on both adaxial and abaxial surfaces, are generally associated with plants growing in high light or arid environments, as they enhance gas exchange efficiency (Salisbury, 1992). The palisade parenchyma, present on both adaxial and abaxial surfaces, consists of 3–5 layers of primarily cylindrical cells. The spongy parenchyma, located

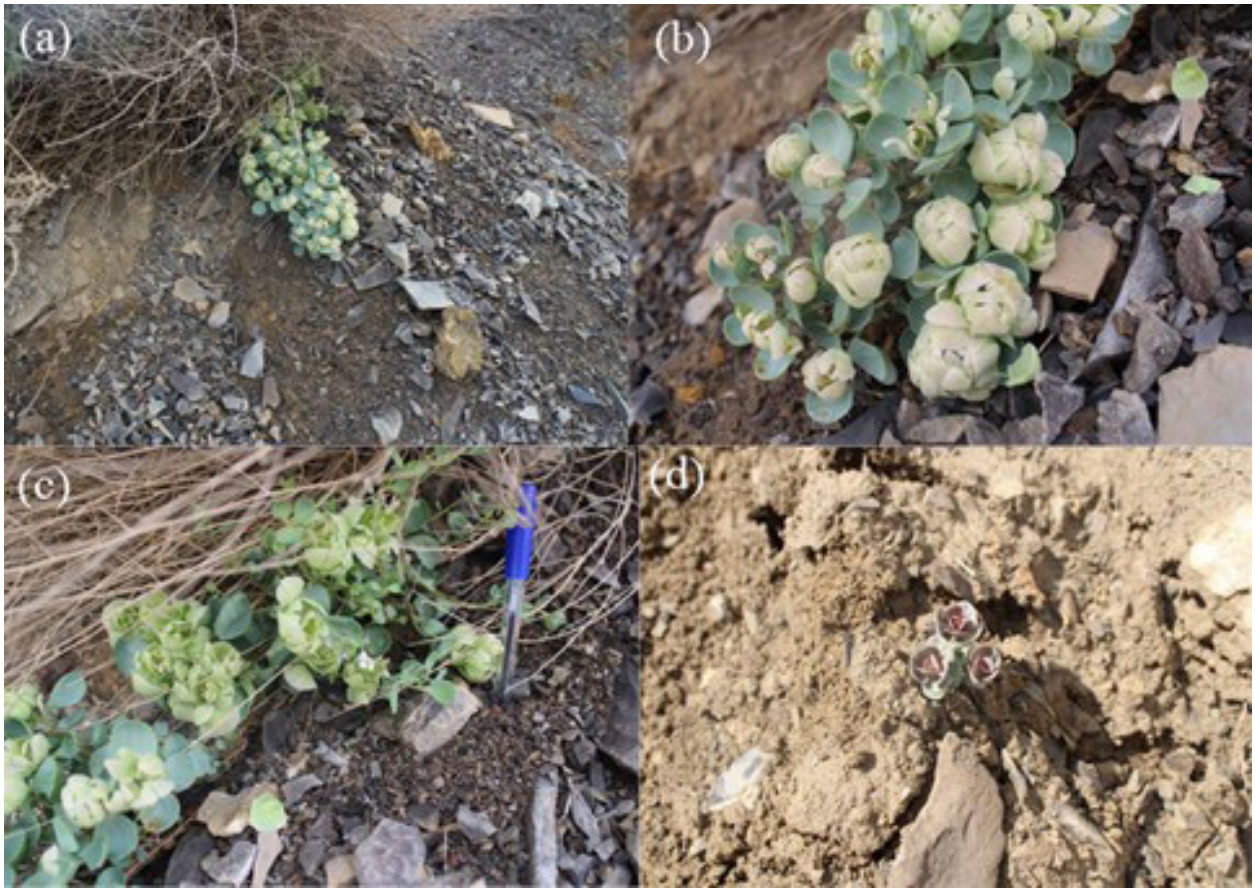

Fig. 2. *Aethionema semnanense* in its natural habitat at Eij and Javin (Semnan, Iran).

Table 1. Measurements of morphological organs of *Aethionema semnanense*

Morphological organ	Mean
Plant height (cm)	20.13
leaf (mm)	19.35 (length) × 17.33 (width)
Inflorescence (cm)	8.5 (length) × 4.7 (width)
Petal (mm)	5.25 (length) × 0.95 (width)
Stamen filament (mm)	1.95 short, 2.75 long
Ovule (mm)	1.65 (length) × 1.1 (width)
Fruiting pedicel (mm)	3.14
Silicule (mm)	22.55 × 15.2

between the palisade layers, comprises 1–3 layers of oval to irregular cells. A prominent midvein is centrally located within the mesophyll (Fig. 3E–F).

Idioblastic cells which are specialized plant cells that often contain crystals or secondary metabolites and may contribute to defense, mechanical strength, or storage (Fahn, 1982), containing crystals are observed in all examined tissues, including the stem, leaf, and seed coat (Fig. 3F). The stomata are anisocytic (cruciferous type), positioned flush with the epidermis. Quantitative measurements of anatomical tissues are summarized in Table 2.

In stem cross-sections, epidermal cells measured approximately 24.3 ± 2.4 µm in length and 21.4 ± 5.4 µm in width, while pith cells are the largest, averaging 73.4 ± 17.2 µm in length and 66.3 ± 12.2 µm in width. Tracheary elements exhibit diameters of 31.1 ± 3.7 µm by 53.3 ± 2.1 µm. In leaf tissue, palisade parenchyma cells are notably elongated, with average dimensions of 88.4 ± 18.1 µm in length and 26.2 ± 11.1 µm in width, while spongy parenchyma cells are smaller and more irregular (32.3 ± 14.4 µm in length). Epidermal cells of the leaf measured 26.5 ± 2.1 µm in

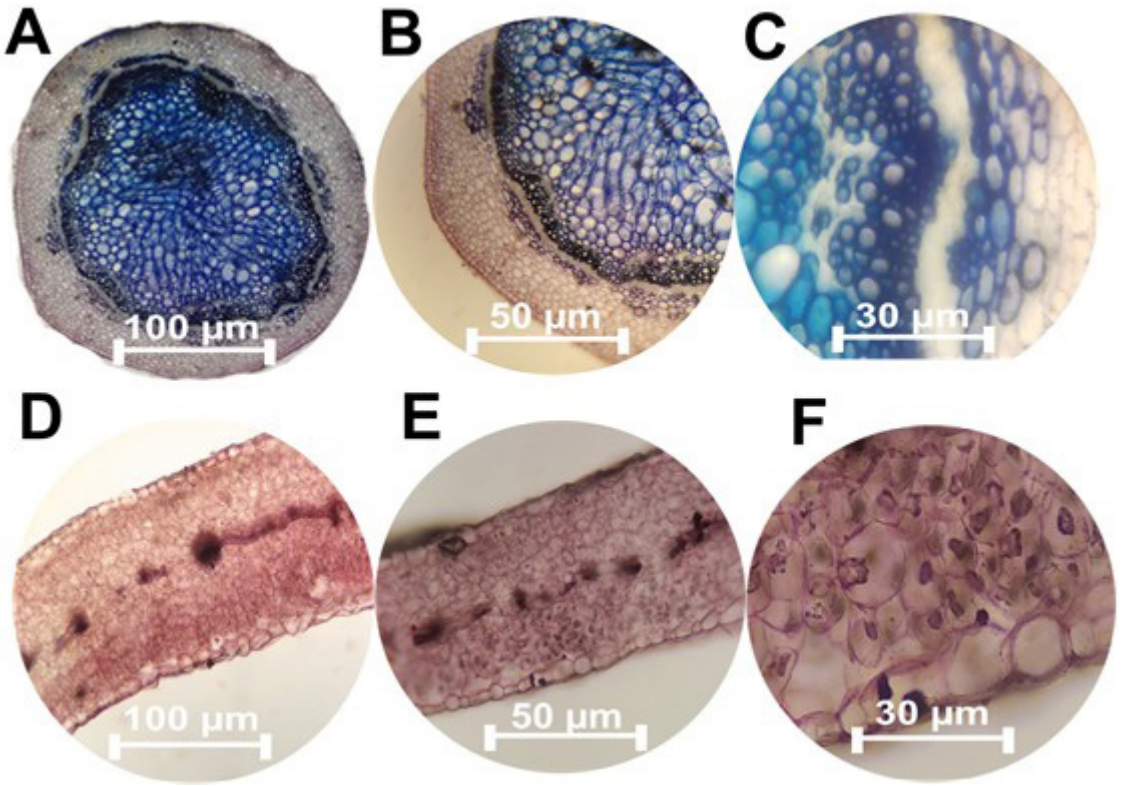

Fig. 3. Cross sections of *Aethionema semnanense*: A–C – stem sections; D–F – leaf sections.

Table 2. Measurements of anatomical tissues of *Aethionema semnanense*

Anatomical tissue	Mean Width (µm) ± SD	Mean Length (µm) ± SD
Stem		
Epidermis cell	21.4 ± 5.4	24.3 ± 2.4
Trachea cell	53.3 ± 2.1	31.1 ± 3.7
Pith cell	66.3 ± 12.2	73.4 ± 17.2
Colenchyma	32.4 ± 2.6	32.4 ± 39.3
Leaf		
Idioblast	88 ± 8.8	
Palisade cell	26.2 ± 11.1	88.4 ± 18.1
Spongy cell	32.3 ± 14.4	
Epidermis cell	23.6 ± 3.7	26.5 ± 2.1
Stomatat cell	5.1 ± 1.4	11.42 ± 3.6

length and 23.6 ± 3.7 µm in width. Stomatal length and width average 11.42 ± 3.6 µm and 5.1 ± 1.4 µm, respectively, with an interstomatal distance of 111.11 µm. These measurements provide a detailed anatomical profile of *A. semnanense* and serve as valuable diagnostic characters for comparison with related species.

Idioblastic cells with distinctive morphology are observed in all examined tissues of *Aethionema semnanense*, including leaves, stems, and seeds (Fig. 3F). The stomata are of the anisocytic (cruciferous) type and are located flush with the surrounding epidermal cells. No epidermal hairs are detected on either surface. Quantitative measurements indicate that the average distance between stomata is 111.11 µm, with an average stomatal length of 11.42 µm and width of 5.01 µm (Fig. 4).

The combination of these anatomical features – including epidermal cell types, idioblast distribution, stomatal characteristics, and seed coat morphology – provides valuable diagnostic traits for the taxonomic delineation of *Aethionema semnanense*.

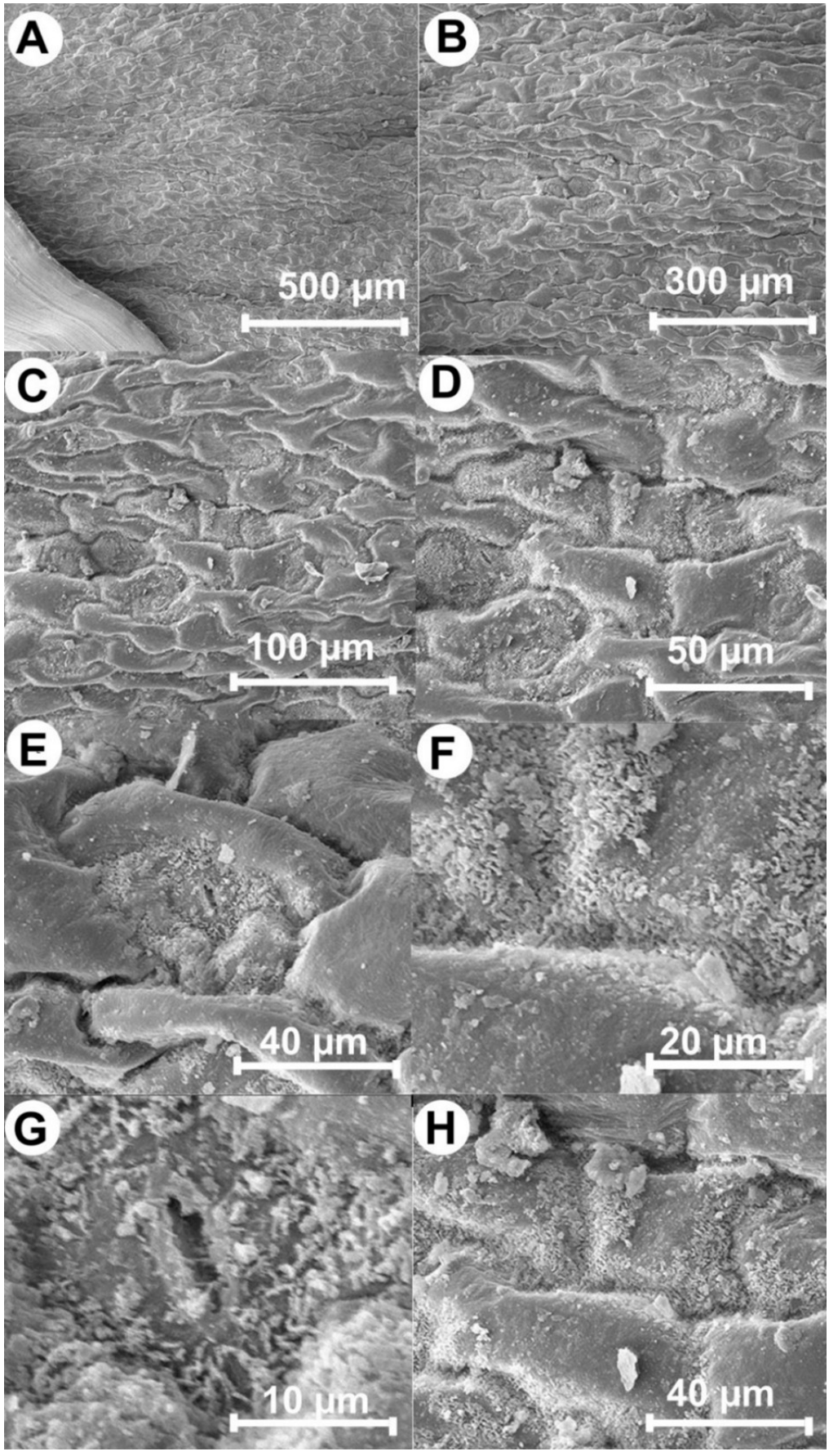

Fig. 4. The abaxial leaf surface of *Aethionema semnanense* was examined using scanning electron microscopy (SEM).

Although the seed coat appears smooth under the stereomicroscope and to the naked eye, SEM reveals a distinct reticulate surface ornamentation. The seeds are ovoid in shape and exhibit well-defined sculpturing patterns characteristic of the species (Fig. 5, Table 2).

SEM analysis of seed surface ornamentation shows a well-defined reticulate pattern, with ovoid seeds exhibiting a sculptured testa. These micromorphological traits are clearly visible under SEM imaging and contribute to species-level identification (Fig. 5, Table 2).

Discussion

This study presents the first comprehensive morphological and anatomical characterization of *Aethionema semnanense*. The results provide valuable insights into its diagnostic traits and support its systematic placement within the genus *Aethionema*.

Morphologically, *A. semnanense* is readily distinguished by its coriaceous, orbicular leaves. While large fruits are noted, the specific morphology and dimensions of the wings, in conjunction with other features, are significant taxonomic markers. These traits, along with the floral morphology including clawed petals, a bilocular ovary, and winged filaments, further support the unique identity of this species, differentiating it from closely related species such as *A. sabzevaricum*, *A. cordatum*, and *A. saxatile*, as documented by Moazzeni et al. (2018, 2023).These characteristics align with traits used in traditional Brassicaceae classifications, reinforcing the taxonomic utility of reproductive structures. A central highlight of this study is the micromorphological analysis of seed surface ornamentation via SEM. The reticulate sculpturing observed in *A. semnanense* is pronounced and ovoid in pattern, with deep brown coloration. Such features are not only distinctive but also critical for species-level delimitation in the genus. While reticulate patterns have also been documented in species like *A. stylosum* DC., *A. eunomioides* (Boiss.) Bornm., and *A. dumanii* Vural et Adıgüzel (Pinar et al., 2007; Atçeken et al., 2016), the specific characteristics of *A. semnanense* – notably the depth, direction, and density of the seed testa network – set it apart. Compared to *A. arabicum* (L.) Andrz. ex Reichenb. and *A. cordatum*, whose seeds often exhibit verrucate or verrucate-reticulate patterns with lighter brown coloration (Atçeken et al., 2016), *A. semnanense* presents a more uniform and well-defined reticulate sculpturing. These contrasts further emphasize the value of seed micromorphology as a robust tool for infrageneric classification in *Aethionema* and more broadly in Brassicaceae (Kaya et al., 2011; Karaismailoğlu, 2019). The seed surface ornamentation of *A. semnanense*, as observed under SEM, displays a well-defined and uniform reticulate pattern with deeply impressed anticlinal walls and smooth periclinal surfaces. This sculpturing is distinct from that of *A. arabicum*, which typically exhibits a verrucate-reticulate or papillate pattern with more

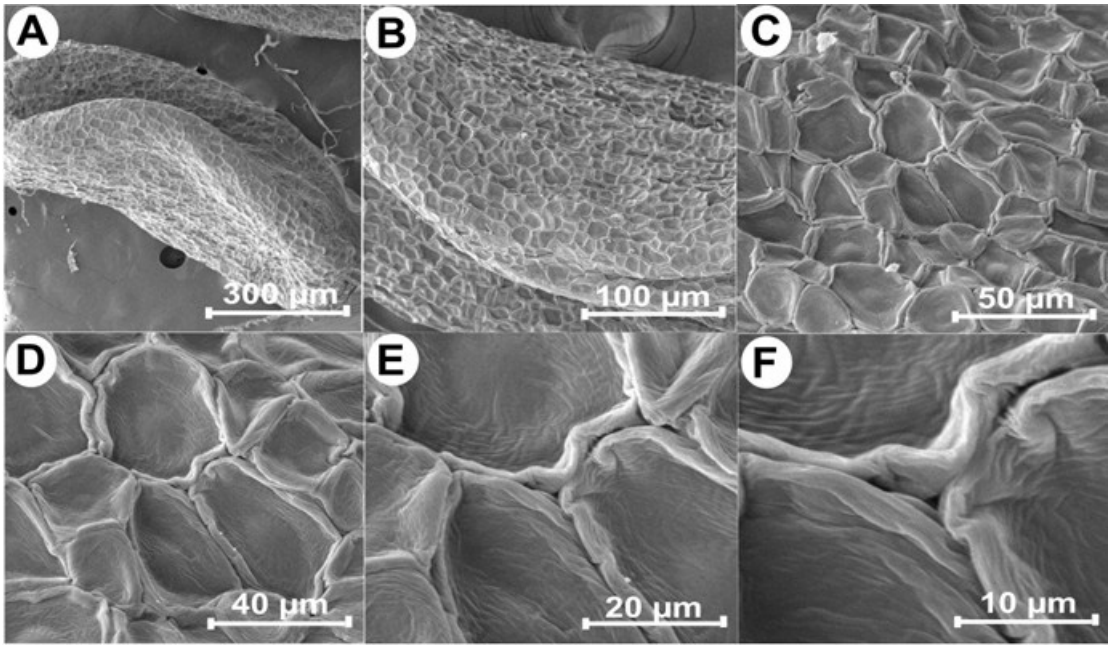

Fig. 5. The surface of *Aethionema semnanense* 's seed-coat as viewed by scanning electron microscopy (SEM).

irregular and less continuous ridges (Atceken et al., 2016). In contrast, *A. cordatum* tends to show a lighter coloration and a less densely reticulate testa, with occasional undulate cell boundaries (Pinar et al., 2007). These micromorphological distinctions – particularly in the uniformity, depth, and directionality of the reticulate network – further support the taxonomic uniqueness of *A. semnanense* and highlight the diagnostic value of seed coat traits within the genus.

Anatomically, several features observed in *A. semnanense* are consistent with general Brassicaceae characteristics. These include amphistomatic and equifacial leaves, anisocytic (cruciferous) stomata, and the presence of idioblastic cells. The stomata, level with the epidermis, measured on average 11.42 μm in length and 5.01 μm in width, with an interstomatal distance of 111.11 μm. While such stomatal configurations have been documented in many Brassicaceae species (Metcalfe, Chalk, 1950), the symmetrical palisade arrangement observed here – with 3–5 layers of cylindrical cells on both adaxial and abaxial surfaces – may represent a species-specific adaptation, possibly related to the environmental conditions of its high-altitude, sun-exposed habitats.

One particularly interesting finding is the widespread presence of idioblastic cells in all organs examined, including leaves, stems, and seeds. These specialized cells, often containing crystals, are believed to play roles in mechanical support, detoxification, and defense (Tekin, 2022). In *A. semnanense*, idioblasts were abundant and uniformly distributed across tissues, suggesting their functional significance may be heightened in this species. The prevalence of idioblasts aligns with the structural adaptations of other Brassicaceae taxa that inhabit harsh or nutrient-limited environments, where crystal storage or defensive function is advantageous.

In the stem cross-sections, the relatively reduced pith diameter compared to other *Aethionema* species may also be noteworthy. The proportionally thicker cortex and sclerenchyma rings surrounding vascular bundles indicate structural reinforcement, possibly supporting the plant's prostrate growth form in rocky slopes. Such anatomical patterns, combined with its morphological distinctiveness, underscore the evolutionary divergence of *A. semnanense* within the genus.

Although *A. semnanense* was previously listed as "Data Deficient (DD)" by Moazzeni et al. (2018), our field observations suggest that the species may be under increasing threat due to habitat degradation caused by mining, overgrazing, and industrial development in the Eij and Javin areas. Given that our study was limited to a single known population, we acknowledge that this assessment may not represent the full range of the species. Therefore, while we tentatively refer to it as "endangered" due to its narrow distribution and observed environmental pressures, a comprehensive conservation status assessment based on broader sampling is urgently needed.

Altogether, the morphological and anatomical findings presented here not only reinforce the systematic distinctness of *A. semnanense* but also contribute to a broader understanding of character diversity in *Aethionema*. These results provide a strong basis for future phylogenetic studies and could assist in resolving taxonomic uncertainties within this underexplored group. Given the endemic and endangered status of *A. semnanense*, further studies focusing on population variability, conservation priorities, and potential phylogeographic patterns are highly recommended.

Conclusion

This study provides the first comprehensive analysis of the morphological, anatomical, and micromorphological features of *Aethionema semnanense*, a rare and endemic species in Iran. Detailed examination of the stem, leaf, fruit, and seed revealed a combination of distinctive traits, including coriaceous ovate leaves, cymbiform and winged fruits, and winged filaments of stamens. The micromorphological characteristics of the seeds, particularly their reticulate ornamentation and ovoid shape observed under SEM, further support the taxonomic distinctness of this species.

From a conservation perspective, this study underscores the vulnerability of narrowly endemic species to habitat disturbance. We recommend extended field surveys across all known populations and suggest ex-situ conservation strategies such as seed banking and cultivation trials under controlled conditions. Such actions would support long-term preservation and potentially allow the use of *A. semnanense* in rock gardens or alpine plant collections, given its morphological appeal.

Acknowledgements

We would like to thank the Semnan Agricultural and Natural Resources Research and Education Center (Semnan, Iran) for their support and valuable contributions. We also express our sincere appreciation to Amir Maddah for his essential assistance in the identification and collection of plant specimens.

REFERENCES / ЛИТЕРАТУРА

Al-Shehbaz I. A. 2012. A generic and tribal synopsis of the Brassicaceae (Cruciferae). *Taxon* 61(5): 931–954. https://doi.org/10.1002/tax.615002

Al-Shehbaz I. A., Beilstein M. A., Kellogg E. A. 2006. Systematics and phylogeny of the Brassicaceae (Cruciferae): an overview. *Plant Syst. Evol.* 259(2–4): 89–120. https://doi.org/10.1007/s00606-006-0415-z

Appel O., Al-Shehbaz I. A. 2003. Cruciferae. In: K. Kubitzki (ed.). *The Families and Genera of Vascular Plants*. Vol. 5. Berlin: Springer. Pp. 75–174. https://doi.org/10.1007/978-3-662-07255-4_17

Arshad W., Steinbrecher T., Wilhelmsson P. K., I., Fernandez-Pozo N., Pérez M., Mérai Z., Rensing S. A., Chandler J. O., Leubner-Metzger G. 2024. *Aethionema arabicum* dimorphic seed trait resetting during transition to seedlings. *Front. Plant Sci.* 15: 1358312. https://doi.org/10.3389/fpls.2024.1358312

Atceken M. M., Dural H., Yilmaz Citak B. 2016. Morphological, anatomical and palynological investigations on some taxa of *Aethionema* W. T. Aiton (Brassicaceae). *Biodicon* 9: 55–68.

Barthlott W. 1981. Epidermal and seed surface characters of plants: systematic applicability and evolutionary aspects. *Nord. J. Bot.* 1(3): 345–355. https://doi.org/10.1111/j.1756-1051.1981.tb00704.x

Beilstein M. A., Al-Shehbaz I. A., Kellogg E. A. 2006. Brassicaceae phylogeny and trichome evolution. *Am. J. Bot.* 93(4): 607–619. https://doi.org/10.3732/ajb.93.4.607

Beilstein M. A., Al-Shehbaz I. A., Mathews S., Kellogg E. A. 2008. Brassicaceae phylogeny inferred from phytochrome A and *ndhF*. *Am. J. Bot.* 95(10): 1307–1327. https://doi.org/10.3732/ajb.0800065

Beilstein M. A., Nagalingum N. S., Clements M. D., Manchester S. R., Mathews S. 2010. Dated molecular phylogenies and Miocene origin of *Arabidopsis thaliana*. *PNAS* 107(43): 18724–18728. https://doi.org/10.1073/pnas.0909766107

Chandler J. O., Wilhelmsson P. K., Fernandez-Pozo N., Graeber K., Arshad W., Pérez M., et al. 2024. Dimorphic diaspore model *Aethionema arabicum*. *Plant Cell* 36(7): 2465–2490. https://doi.org/10.1093/plcell/koae085

Couvreur T. L. P., Franzke A., Al-Shehbaz I. A., Bakker F. T., Koch M. A., Mummenhoff K. 2010. Molecular phylogenetics and diversification in Brassicaceae. *Mol. Biol. Evol.* 27(1): 55–71. https://doi.org/10.1093/molbev/msp202

Edger P. P., Hall J. C., Harkess A., Tang M., Coombs J., Mohammadin S., et al. 2018. Brassicales phylogeny inferred from 72 plastid genes. *Am. J. Bot.* 105(3): 463–469. https://doi.org/10.1002/ajb2.1040

Franzke A., Lysak M. A., Al-Shehbaz I. A., Koch M. A., Mummenhoff K. 2011. Evolutionary history of Brassicaceae. *Trends Plant Sci.* 16(2): 108–116. https://doi.org/10.1016/j.tplants.2010.11.005

Hall J. C., Sytsma K. J., Iltis H. H. 2002. Phylogeny of Capparaceae and Brassicaceae. *Am. J. Bot.* 89(11): 1826–1842. https://doi.org/10.3732/ajb.89.11.1826

Hedge I. C. 1968. *Aethionema* R. Br. In: *Flora Iranica*. Vol. 57. Graz: Akad. Druck- und Verlagsanstalt. Pp. 100–110.

Hohmann N., Wolf E. M., Lysak M. A., Koch M. A. 2015. *A time-calibrated road map of Brassicaceae species radiation and evolutionary history. Plant Cell* 27(10): 2770–2784. https://doi.org/10.1105/tpc.15.00482

Huang C.-H., Sun R., Hu Y., Zeng L., Zhang N., Cai L., et al. 2016. Brassicaceae phylogeny using nuclear genes. *Mol. Biol. Evol.* 33(2): 394–412. https://doi.org/10.1093/molbev/msv226

Karaismailoğlu M. C. 2019. Comparative seed morphology in *Aethionema*. *Bangladesh J. Plant Taxon*. 26(1): 1–12 https://doi.org/10.3329/bjpt.v26i1.41911.

Khosravi A. R., Jacquemoud F., Mohsenzadeh S., Menke M., Mummenhoff K. 2009. Phylogenetic position of *Aethionema trinervium*. *Ann. Mo. Bot. Gard.* 96(4): 564–574. https://doi.org/10.3417/2007004

Khosravi A. R., Mohsenzadeh S., Mummenhoff K. 2008. Phylogeny of *Acanthocardamum erinaceum*. *Nord. J. Bot.* 26(1–2): 25–30. https://doi.org/10.1111/j.1756-1051.2008.00205.x

Koch M. A., Kiefer C., Ehrich D., Vogel J., Brochmann C., Mummenhoff K., Hurka H., Brysting A. K. 2006. Phylogeography of *Arabis alpina*. *Mol. Ecol.* 15(3): 825–839. https://doi.org/10.1111/j.1365-294X.2005.02848.x

Lenser T., Graeber K., Cevik Ö. S., Adigüzel N., Dönmez A. A., Grosche C., et al. 2016. Fruit and seed dimorphism in *Aethionema arabicum*. *Plant Physiol.* 172(3): 1691–1707. https://doi.org/10.1104/pp.16.00838

Manafzadeh S., Staedler Y. M., Conti E. 2017. Irano-Turanian region in evolutionary studies. *Biol. Rev.* 92(3): 1365–1388. https://doi.org/10.1111/brv.12287

Moazzeni H., Al-Shehbaz I. A., German D. A., Zarre S., Mummenhoff K., Koch M. A., et al. 2018. Revision of *Aethionema* s. l. in Iran. *Phytotaxa* 356(4): 241–266. https://doi.org/10.11646/phytotaxa.356.4.1

Mohammadin S., Peterse K., van de Kerke S. J., et al. 2017. Anatolian origins of *Aethionema*. *Am. J. Bot.* 104(7): 1042–1054. https://doi.org/10.3732/ajb.1700076

Mozaffarian V. 1996. Flora of Iran: new species and combinations. *Iran J. Bot.* 7(1): 127–142. [In Persian]

Öztürk D. 2022. *Aethionema gypsicola*, a new crucifer. *Phytotaxa* 539(2): 175–185. https://doi.org/10.11646/phytotaxa.539.2.5

Pinar N. M., Bayrak N., Geven F. 2007. Seed coat sculpturing in *Aethionema*. *Pak. J. Bot.* 39: 1025–1036.

Prantl K. 1891. Cruciferae. In: *Die natürlichen Pflanzenfamilien*. Vol. 3(2). Leipzig: Engelmann. Pp. 145–206.

Rechinger K. H. 1988. *Gypsophila*. In: *Flora Iranica*. Vol. 163. Graz: Akad. Druck- und Verlagsanstalt. Pp. 206–246.

Tekin M. 2022. Morphological and anatomical study of *Aethionema lepidioides*. *Acta Bot. Croat.* 81(1): 70–79. https://doi.org/10.37427/botcro-2022-006

Williams J. G., Hanafey M. K., Rafalski J. A., Tingey S. V. 1993. Genetic analysis using RAPD. *Methods Enzymol.* 218: 704–740. https://doi.org/10.1016/S0076-6879(08)70213-6

Wolfe A. D., Liston A. 1998. PCR-based methods in plant systematics. In: *Molecular Systematics of Plants II*. Springer. Pp. 43–86. https://doi.org/10.1007/978-3-642-58457-2_2