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Research Paper

Integrative biosystematics study of *Seseli staurophyllum* Rech.f. (Apiaceae), an endemic gypsophyte from Iran

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Abstract

Seseli staurophyllum Rech.f. (\equiv *Lomatopodium staurophyllum* (Rech.f.) Rech.f.) is a narrowly distributed endemic species of Apiaceae, restricted to gypsum–marl and serpentine substrates in northeastern Iran. Formerly treated as the sole representative of the monotypic genus *Lomatopodium*, this taxon exhibits distinctive morphological traits and a high degree of ecological specialization. Despite its taxonomic and ecological significance, comprehensive biosystematics studies integrating morphology, micromorphology, and habitat characteristics have remained limited. In this study, fresh field material and herbarium specimens were examined to document vegetative morphology, micromorphological structures, and ecological parameters. The species develops woody, highly branched subterranean stems covered with waxy and farinose layers, bears one to two pairs of cuneate to flabellate leaves, and produces compound umbels with predominantly two to three rays. Scanning electron microscopy revealed specialized epidermal features, including persistent epicuticular wax, sunken stomata, and simple multicellular trichomes, which are commonly associated with drought tolerance in gypsum-adapted plants, high solar radiation, and edaphic stress. Ecological analyses confirm that *S. staurophyllum* is strictly confined to gypsum-rich and serpentine substrates across a limited elevational range in northern Iran. The updated distributional data, assessment of habitat specialization, and identification of key adaptive traits presented here provide essential information for taxonomic clarification, ecological interpretation, and conservation-oriented studies of gypsum-associated endemic plants.

Keywords: Endemic species; gypsum habitats; micromorphology; serpentine soils; conservation; morphology

Introduction

The family Apiaceae is one of the largest and most taxonomically complex families of flowering plants, comprising approximately 430 genera and 3,700–3,800 species worldwide (Calviño et al., 2008). The subfamily Apioideae represents the largest lineage within the family and exhibits remarkable morphological and ecological diversity (Clarkson et al., 2021). Most members are herbaceous annuals or perennials, ranging from small, short-lived herbs to robust species exceeding three meters in height. A defining diagnostic feature of Apiaceae is the characteristic inflorescence, typically arranged in simple or compound umbels, which has long served as a key trait in taxonomic and evolutionary studies (Clarkson et al., 2021). Iran constitutes one of the principal centers of diversity for Apiaceae in the Irano–Turanian region, hosting numerous endemic taxa that contribute to its unique floristic composition (Ghahremaninejad et al., 2025). Numerous taxa have diversified in arid and semi-arid ecosystems and exhibit a wide range of morphological, anatomical, and physiological adaptations, including finely dissected leaves, thickened stems, pubescence, and specialized secretory structures. These traits facilitate survival under harsh environmental conditions such as high solar radiation, drought, alkaline soils, and pronounced temperature fluctuations (Clarkson et al., 2021). In addition to their ecological importance, many Apiaceae species possess significant ethnobotanical, medicinal, and industrial value owing to their essential oils and diverse bioactive secondary metabolites (Wang et al., 2022). Several genera of Apiaceae, including *Ferula*, *Dorema*, *Bunium*, *Heracleum*, and *Prangos*, are of particular ecological and economic importance and are widely used in traditional Iranian medicine for the treatment of gastrointestinal, respiratory, and neurological disorders (Calviño et al., 2008; Mousavi et al., 2020). In contrast to these species-rich and economically prominent genera,

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Seseli staurophyllum Rech.f. represents a narrowly distributed endemic taxon with a highly restricted ecological niche. Anatomical studies within the Apiaceae have proven valuable for taxonomic and systematic investigations. For instance, Khajepiri et al. (2010) described detailed fruit anatomical traits in *Pimpinella* species from Iran, highlighting diagnostic features useful for species delimitation. In parallel, molecular phylogenetic analyses have consistently provided robust insights into relationships within the family; a notable example is the work by Fereidounfar et al. (2016) on the phylogeny of Southwest Asian *Pimpinella* and related genera. These studies underscore the importance of integrating morphological, anatomical, and molecular evidence in elucidating species boundaries and evolutionary history in Apiaceae. This species was formerly treated as the sole representative of the monotypic genus *Lomatopodium* Rech.f., but recent taxonomic treatments and global databases recognize it within the genus *Seseli* based on nomenclatural priority and phylogenetic evidence (Pimenov & Leonov, 1993; Cai et al., 2022; Plants of the World Online, 2026). *Seseli staurophyllum* Rech.f. (\equiv *Lomatopodium staurophyllum* (Rech.f.) Rech.f.; \equiv *Eriocyclus staurophyllum*) is a perennial species endemic to northeastern Iran and primarily associated with gypsum-rich and serpentinic substrates. It is locally known as “Pāpehan” and is recognized as a highly localized Iranian endemic with a fragmented distribution restricted to specific edaphic conditions (Mozaffarian, 1996). Morphologically, the species exhibits a distinctive combination of traits, including woody, thick, and intensely branched subterranean stems often bearing persistent basal leaf remnants from previous growing seasons. The leaves typically consist of one to two pairs of cuneate to flabellate segments, and the inflorescences are compound umbels with two to three (occasionally four) rays (Pimenov & Leonov, 1993). These vegetative and reproductive characteristics clearly distinguish *S. staurophyllum* from morphologically related taxa and reflect adaptation to arid and edaphically stressful environments. Micromorphological investigations using scanning electron microscopy (SEM) have revealed specialized epidermal features, including sunken stomata, thick epicuticular wax layers, and protective trichomes. Together, these traits contribute to reduced transpiration, enhanced reflectance of solar radiation, and increased tolerance to drought and soil-related stressors. Preliminary phytochemical studies further suggest the presence of aromatic and biologically active compounds, indicating potential medicinal and industrial relevance (Sefidkon, 2001). Despite its pronounced ecological specialization and distinctive structural traits, integrative biosystematic studies combining morphology, micromorphology, and ecological parameters for *S. staurophyllum* remain scarce. Understanding the relationships between its structural adaptations and highly specialized habitat is essential for taxonomic clarification, conservation planning, and broader insights into plant adaptation to extreme environments. Accordingly, the present study provides a comprehensive biosystematic assessment of the morphology, micromorphology, and ecological characteristics of *Seseli staurophyllum*, with the aim of clarifying its adaptive strategies and ecological specialization. Gypsum ecosystems, which constitute the primary habitat of this species, are increasingly recognized as natural evolutionary laboratories. These environments impose intense selective pressures—such as extreme soil chemistry, limited water availability, and high ion concentrations—that promote the evolution of highly specialized, locally adapted flora. Gypsophile plants often exhibit elevated levels of endemism, pronounced ecological specialization, and distinctive morphological and physiological traits, making them valuable systems for investigating adaptation, speciation, and biogeographical processes (Palacio et al., 2012; García-Fayos et al., 2013; Llinares et al., 2015; Escudero et al., 2017; Sánchez-Martín et al., 2021).

Materials and Methods

Study area and sample collection

Field sampling of *Seseli staurophyllum* Rech.f. (\equiv *Lomatopodium staurophyllum* (Rech.f.) Rech.f.) was conducted in known populations in northern Semnan Province, mainly around the villages of After and Arvaneh. Geographic coordinates (decimal degrees) and elevation (m a.s.l.) were recorded at each site using a Garmin GPSMAP 64s device. Sampling date and vegetative condition were documented in field datasheets. Six geographically distinct populations were surveyed, and 5–10 representative individuals were collected per population (total $n = 42$ individuals). Voucher specimens of *S. staurophyllum* Rech.f. were collected during field surveys in northern Semnan Province and deposited in the Herbarium of Farzanegan Campus, Semnan University, and the Herbarium of the Semnan Provincial Agricultural and Natural Resources Research Center. All specimens were confirmed and registered under the voucher code FGU 385.

Sampling design and vegetation assessment

Vegetation sampling was conducted using plot-based methods. Quadrat size was adjusted according to vegetation structure: 1 m² plots for herbaceous stands and 10 m² plots for shrub-dominated areas. Plots were placed randomly or systematically within each site. Within plots, cover and frequency of associated species were recorded, and surface soil samples (0–20 cm) were collected. Vegetation cover was estimated visually following standard phytosociological practice. A minimum of three plots was surveyed per site to ensure representative sampling of local vegetation structure.

Morphological (morphometric) analyses

Morphological traits measured included plant height, leaflet length and width, petiole length, number of leaf pairs per stem, number of umbel rays, and trichome density and length. Measurements were performed using a digital caliper (accuracy 0.01 mm) and a stereomicroscope (10–40 \times). Macrophotographs were taken with a Canon EOS 80D camera equipped with a 100 mm macro lens, and ImageJ software was used for precise measurements. For each quantitative trait, measurements were obtained from at least 30 organs per population, allowing assessment of both intra- and inter-population variation.



Scanning electron microscopy (SEM)

Leaf samples were prepared for SEM to examine epidermal surfaces and trichome structure. Fresh material was stored in silica gel in the field, air-dried or critical-point dried, mounted on aluminum stubs, and sputter-coated with gold–platinum (10–20 nm). Observations were carried out using a Hitachi S-4800 or JEOL JSM-6510LV microscope at accelerating voltages of 5–15 kV and magnifications ranging from 50× to 10,000×. Representative micrographs were selected based on consistency across individuals and populations.

Microanatomical analysis

Leaf and stem microanatomy were investigated using transverse thin sections stained with Fast Green/Safranin or Coomassie Blue. Measurements of epidermal thickness, number and thickness of mesophyll layers, spongy parenchyma thickness, and vascular bundle diameter were conducted under a light microscope at magnifications of 100–400×. At least ten sections from different individuals were examined for each organ to ensure anatomical consistency.

Soil analysis

Surface soil samples (0–20 cm) were analyzed for physicochemical properties. Soil pH and electrical conductivity (EC) were measured in soil–water suspensions (1:2.5 and 1:5, respectively). Soil texture was determined using the hydrometer method and classified according to USDA criteria. Organic matter content was measured by the Walkley–Black method. Gypsum content was quantified gravimetrically and, where possible, confirmed by X-ray diffraction (XRD). Major cations (Ca^{2+} , Mg^{2+} , Na^+ , K^+) were analyzed by atomic absorption spectroscopy, and sulfate and chloride concentrations were determined using standard ionic methods. All soil analyses were conducted in triplicate, and mean values were used for statistical analyses.

Ecological data and associated vegetation

Environmental variables recorded at each site included elevation, slope, aspect, substrate type (gypsum, serpentine, or marl), and surface cover of stones and gravels. Associated plant species were identified and classified according to Raunkiaer life-form categories. Species co-occurrence and habitat structure were evaluated to characterize ecological relationships within gypsum-associated plant communities. Plant material of *Seseli staurophyllum* was collected from all known populations in northern Semnan Province during the growing seasons of 2023–2025. Sampling followed standard protocols for morphological and micromorphological analysis. Ecological and soil data were recorded in situ. Our previous studies on gypsum-associated flora in Semnan Province provide a valuable framework for designing the sampling strategy and contextualizing the observed ecological patterns (Rabizadeh et al., 2019; Rabizadeh & Nasrollahi 2022; Rabizadeh et al., 2023).

Statistical analyses

Morphometric, anatomical, and ecological data were summarized using descriptive statistics. Differences among populations were evaluated using analysis of variance (ANOVA) or the Kruskal–Wallis test when assumptions of normality and homoscedasticity were not met. Soil physicochemical parameters were analyzed descriptively to characterize habitat conditions across populations. All statistical analyses were conducted in R (version 4.x), with statistical significance set at $p < 0.05$. Raw morphological, ecological, and soil datasets, together with statistical outputs and R scripts, are provided in the Supplementary Materials to ensure analytical transparency and reproducibility.

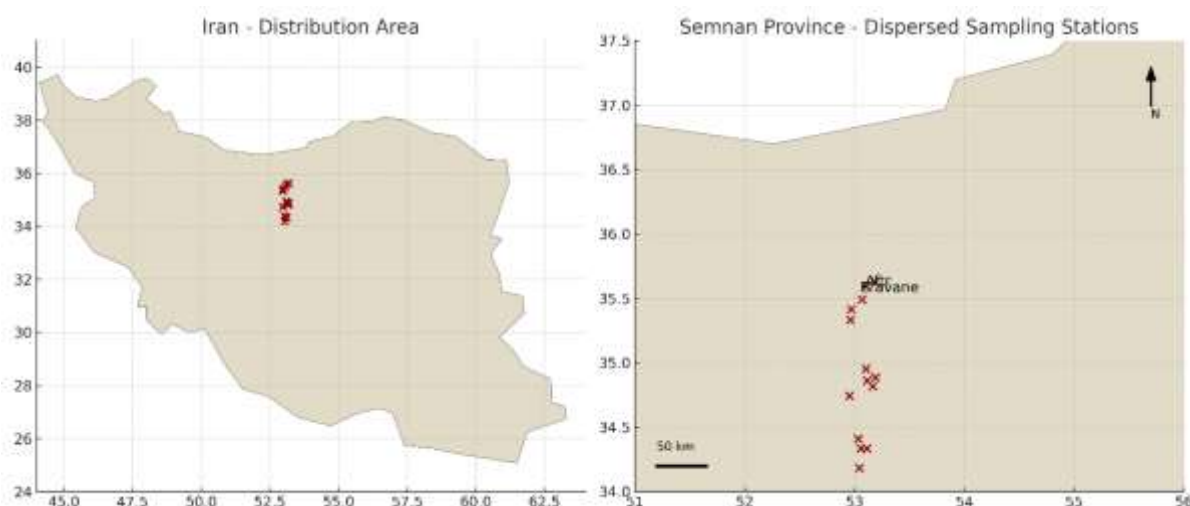


Figure 1. Geographic distribution map of *Seseli staurophyllum* in Semnan Province, Iran. Red dots indicate the sampling sites in the Arvaneh and After regions. The map is provided at an approximate scale of 76 km.



Results

Morphological study of *Seseli staurophyllum* in its natural habitat

Seseli staurophyllum Rech.f. is a perennial species characterized by a woody, multi-headed subterranean stem. At the beginning of the growing season, individuals form a compact basal rosette of leaves at the soil surface (Figure 2A–B). With stem elongation during the reproductive phase, plants develop an erect to sub-erect, bushy habit, reaching heights of approximately 25–70 cm in the examined populations (Figure 2C–D). Leaves are cuneate to flabellate (wedge-shaped to fan-shaped) and typically divided into one to two pairs of lobes, occasionally appearing trifoliate. The leaf surfaces are covered by a conspicuous waxy and farinose layer, giving the plant a grayish to silvery appearance under field conditions. Inflorescences consist of compound umbels positioned terminally on the stems. During anthesis, umbels bear predominantly two to three rays, rarely four (Figure 2E–F). Bracts and bracteoles are reduced or absent, and flowers are small and actinomorphic, consistent with general patterns observed in Apiaceae. No marked qualitative differences in gross morphological traits were observed among populations; however, quantitative variation was detected in plant height, leaf dimensions, and umbel ray number, as summarized in Supplementary Dataset S1.

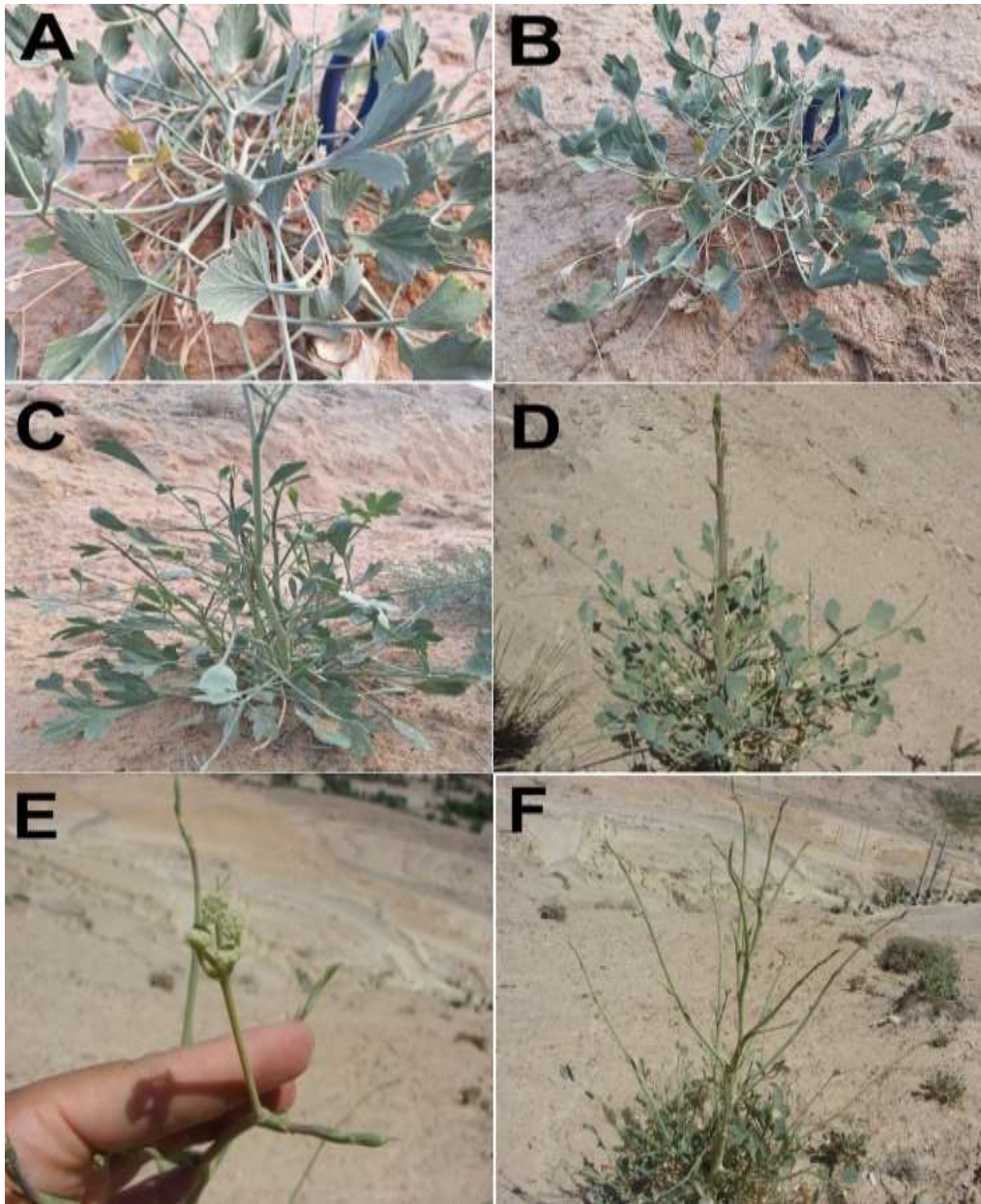


Figure 2. Morphology of *Seseli staurophyllum* in its natural habitat. (A–B) Compact leaf rosette at the soil surface at the beginning of the growing season. (C–D) Erect, bushy habit of the plant with stem elongation and onset of flowering. (E–F) Dense compound umbels with 2–3 (occasionally 4) rays during the flowering stage.



Anatomical study of *Seseli staurophyllum*

Transverse sections of stems and leaves of *Seseli staurophyllum* Rech.f. revealed a well-developed protective and supporting tissue system (Figure 3). In stem cross-sections (Figure 3A–B), the epidermis is covered by a conspicuously thick cuticle, beneath which several continuous layers of sclerenchyma are present in the peripheral region. The central portion of the stem consists predominantly of parenchymatous tissue with large intercellular spaces. Vascular bundles are arranged in a ring and exhibit well-developed xylem and phloem tissues. Secretory canals were consistently observed in the cortical region adjacent to the vascular bundles (Figure 3C). Leaf cross-sections (Figure 3D) show a uniseriate epidermis on both adaxial and abaxial surfaces, covered by a thick cuticle. The mesophyll is differentiated into palisade and spongy parenchyma, with the latter being relatively well developed. Secretory ducts were present near the vascular bundles within the mesophyll tissue. The leaf margin (Figure 3E) and petiole cross-sections (Figure 3F) display prominent collenchyma tissue and U-shaped vascular bundles embedded in parenchyma. These anatomical features were consistently observed across examined individuals. Quantitative anatomical measurements, including epidermal thickness, mesophyll thickness, and vascular bundle diameter, are summarized in Supplementary Table 1. To further evaluate the taxonomic distinctiveness of *Seseli staurophyllum*, key morphological and anatomical traits were compared with closely related Iranian species, including *Semenovia eriocarpa* (formerly *Seseli elbursense*) and *S. libanotis* (Table 2). The comparison highlights several diagnostic features of *S. staurophyllum*, such as its cuneate–flabellate leaves with 1–2 pairs of lobes, thick epicuticular wax layer, simple non-glandular trichomes, and reduced umbel ray number (mostly 2–3 rays). In contrast, *S. libanotis* exhibits pinnate leaves with numerous umbel rays, while *Semenovia eriocarpa* differs in leaf morphology and has unresolved fruit characteristics. These differences, together with anatomical features described above (Figure 3), support the distinct taxonomic position of *S. staurophyllum* within the genus *Seseli*.

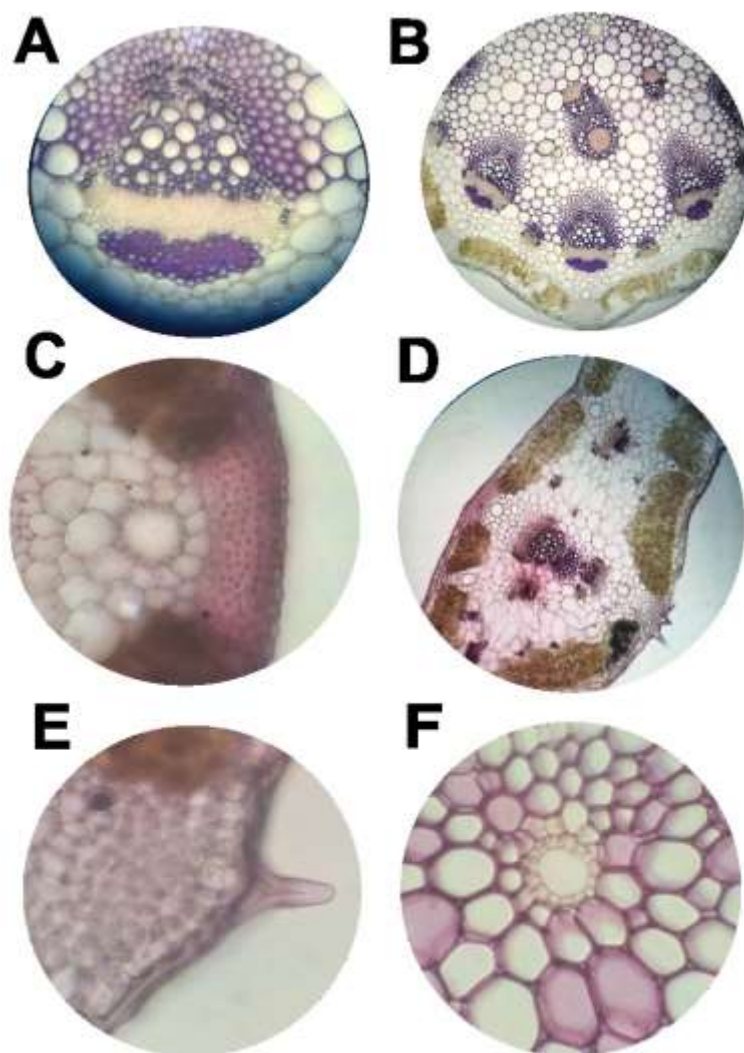


Figure 3. Anatomical characteristics of the stem and leaf of *Seseli staurophyllum* in transverse sections. (A–B) Stem cross-sections showing a thick cuticle and multiple peripheral sclerenchyma layers. (C) Xylem–phloem region with prominent peripheral secretory canals. (D) Leaf cross-section displaying a well-developed spongy parenchyma and secretory ducts. (E) Trichome structure along the leaf margin. (F) Secretory duct within the leaf tissue.

Table 1. Micromorphological features of leaves, stems, and fruits of *Seseli staurophyllum* observed by SEM and their ecological/adaptive significance.

Observed Feature (SEM)	Ecological/Adaptive Role	Structure
Thick and continuous waxy layer on the epidermis	Reduces transpiration and reflects sunlight, protecting tissues from excessive heat	Leaf surface
Sunken stomata within epidermal tissue	Minimizes water loss under dry conditions	Stomata
Non-glandular, simple, short, multicellular trichomes, semi-dense	Reduces surface temperature, reflects light, protects against radiation stress	Trichomes
Long and sunken grooves between ribs	Stores aromatic and essential compounds for defense	Secretory ducts in vegetative organs

Caption: Scanning electron microscopy (SEM) observations of leaves and stems of *Seseli staurophyllum* highlighting key micromorphological adaptations to gypsum–marl habitats and their ecological significance.

Table 2. Morphological and anatomical comparison of *Seseli staurophyllum* with closely related Iranian species in the genus *Seseli* (including *Semenovia eriocarpa*, formerly *Seseli elbursense*, and *S. libanotis*). Key diagnostic traits, including leaf shape, trichome type, epicuticular wax, umbel ray number, and fruit characters, are highlighted to clarify the taxonomic distinctiveness of *S. staurophyllum*. Data sources: *Seseli staurophyllum* – present study; *Semenovia eriocarpa* – Lyskov et al., (2020); *Seseli libanotis* – Cai et al., (2022).

Feature / Species	<i>Seseli staurophyllum</i>	<i>Semenovia eriocarpa</i> (≡ <i>Seseli elbursense</i>)	<i>Seseli libanotis</i>	Reference
Habit	Woody, thick subterranean stems	Erect herbaceous perennial	40–120 cm, erect branching stems	Present study; Lyskov et al. 2020; Cai et al., 2022
Leaf type	Cuneate–flabellate, 1–2 pairs lobes	Limited data; leaves described; fruits unknown	Lower leaves stalked, upper sessile, pinnate	Present study; Lyskov et al. 2020; Cai et al., 2022
Leaf surface	Thick epicuticular wax, greyish appearance	Not fully documented	Compound, pinnate leaves, bluish green	Present study; Lyskov et al. 2020; Cai et al., 2022
Trichomes	Simple, non-glandular	Not evaluated	Not reported	Present study; Lyskov et al. 2020; Cai et al., 2022
Umbel rays	Mostly 2–3 rays, rarely 4	Unknown	Many rays, up to 60 flowers per umbel	Present study; Lyskov et al. 2020; Cai et al., 2022
Fruit	Well-developed schizocarps	Mature fruits not known	Ovoid/ellipsoid, brown, slightly hairy	Present study; Lyskov et al. 2020; Cai et al., 2022
Habitat	Gypsum & serpentine soils, narrow endemic	Northern Iran endemic, limited data	Dry, rocky terrain across Eurasia	Present study; Lyskov et al. 2020; Cai et al., 2022
Key taxonomic traits	Leaf lobation, epicuticular wax, trichomes, fewer umbel rays	Leaf morphology, unresolved fruits, molecular data moved to <i>Semenovia</i>	Typical <i>Seseli</i> morphology	Present study; Lyskov et al. 2020; Cai et al., 2022

Micromorphological characteristics (SEM)

Scanning electron microscopy revealed distinct micromorphological features on the vegetative organs of *Seseli staurophyllum*. Both adaxial and abaxial leaf surfaces are covered by a continuous epicuticular wax layer (Figures 4–5). The wax layer appears as irregular platelets and granules distributed over the epidermal cells. Stomata are predominantly elliptical and sunken below the level of surrounding epidermal cells, occurring mainly on the abaxial leaf surface (Figure 4). Mean stomatal dimensions measured from SEM images were approximately 12.3 μm in length and 6.2 μm in width (Figure 5). Simple, non-glandular, multicellular trichomes of variable length were observed on leaf and stem surfaces (Figures 4–6). Trichomes are sparsely to moderately distributed and arise directly from epidermal cells. No glandular trichomes were detected. SEM observations of the stem surface (Figure 6) revealed a similar wax-covered epidermis with scattered stomata and simple trichomes. Micromorphological features were consistent among individuals sampled from different populations.

SEM–EDS elemental analysis

SEM–EDS analysis in this study reflects only surface deposition of mineral elements on the leaf epidermis; internal absorption or physiological uptake of these elements was not assessed. Analysis of leaf surfaces revealed the presence of multiple mineral elements (Figures 7–8), with elemental spectra and mapping showing relatively high surface concentrations of Ca, S, and O, together with detectable amounts of Mg, Na, Cl, K, Si, and Al. The spatial distribution of Ca and S was largely coincident, consistent with the occurrence of calcium sulfate (gypsum) particles deposited on the leaf surface. Elemental weight percentages derived from EDS analysis are presented in Figure 8. EDS measurements were performed on multiple regions of interest per sample, and representative spectra are shown; full raw EDS datasets are provided in Supplementary Materials (Dataset S2). Since leaf samples were not washed prior to analysis and cross-sectional EDS observations were not conducted, the detected elements should be interpreted as surface deposition from the gypsum-rich environment, rather than unequivocal evidence of internal uptake.



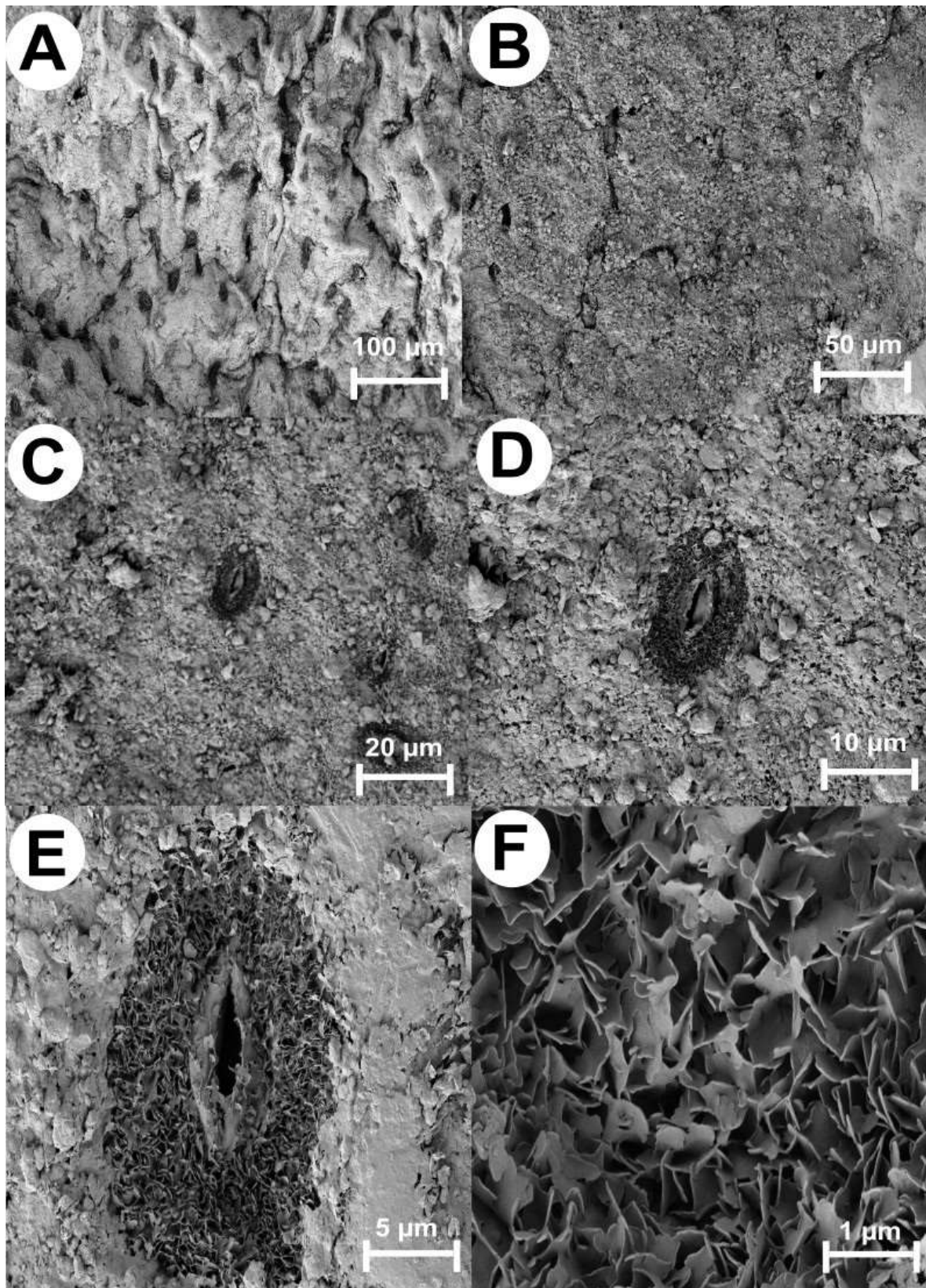


Figure 4. Surface structure of the abaxial leaf of *Seseli staurophyllum* as observed by SEM. Continuous waxy layer, sunken stomata, and simple multicellular trichomes are visible.

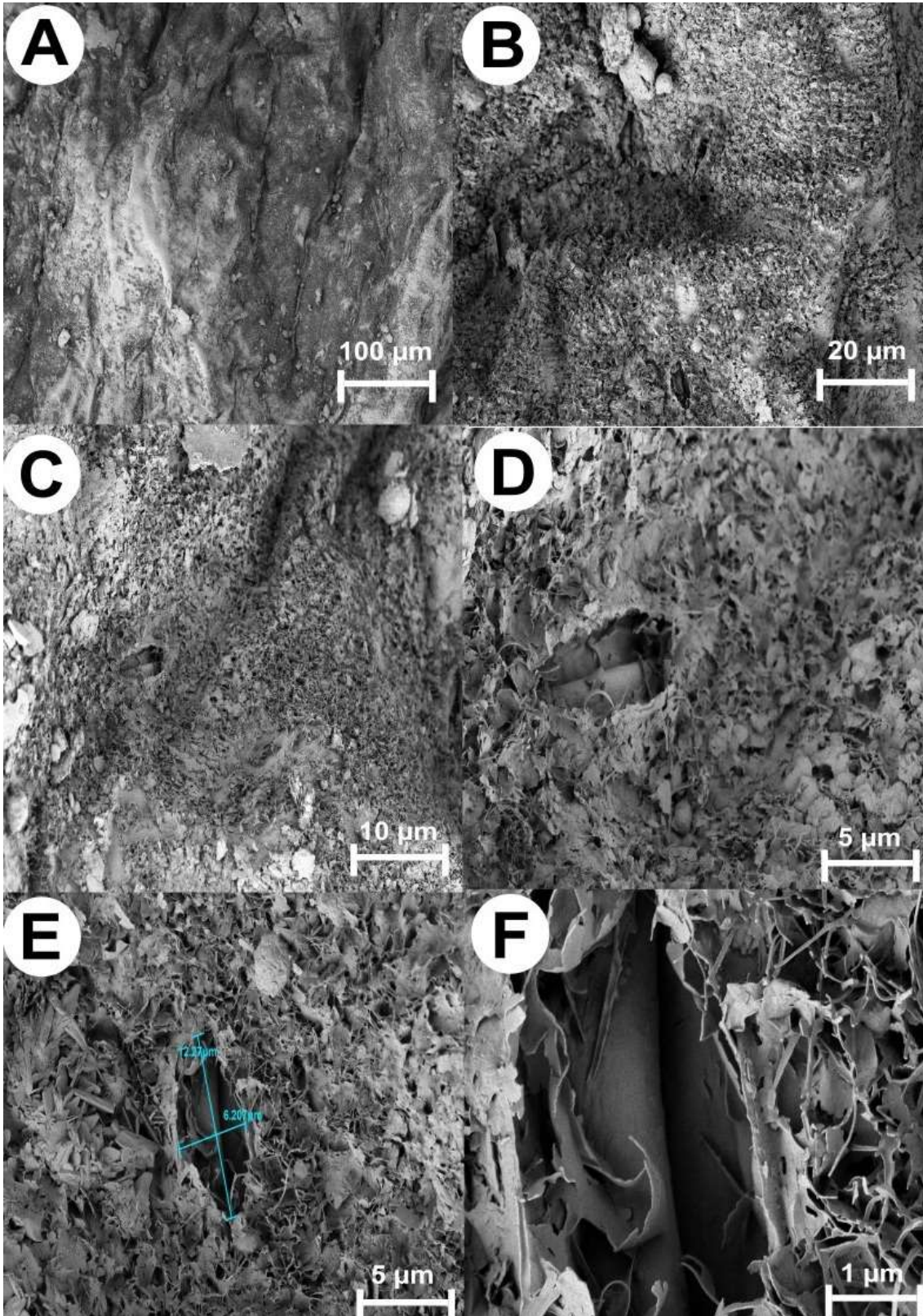


Figure 5. Adaxial leaf surface of *Seseli staurophyllum* observed by SEM. The epidermis is covered with a thick waxy layer, and elliptical stomata are clearly visible. The waxy layer reflects light and reduces transpiration. The stomata have an average length of 12.27 μm and width of 6.20 μm .



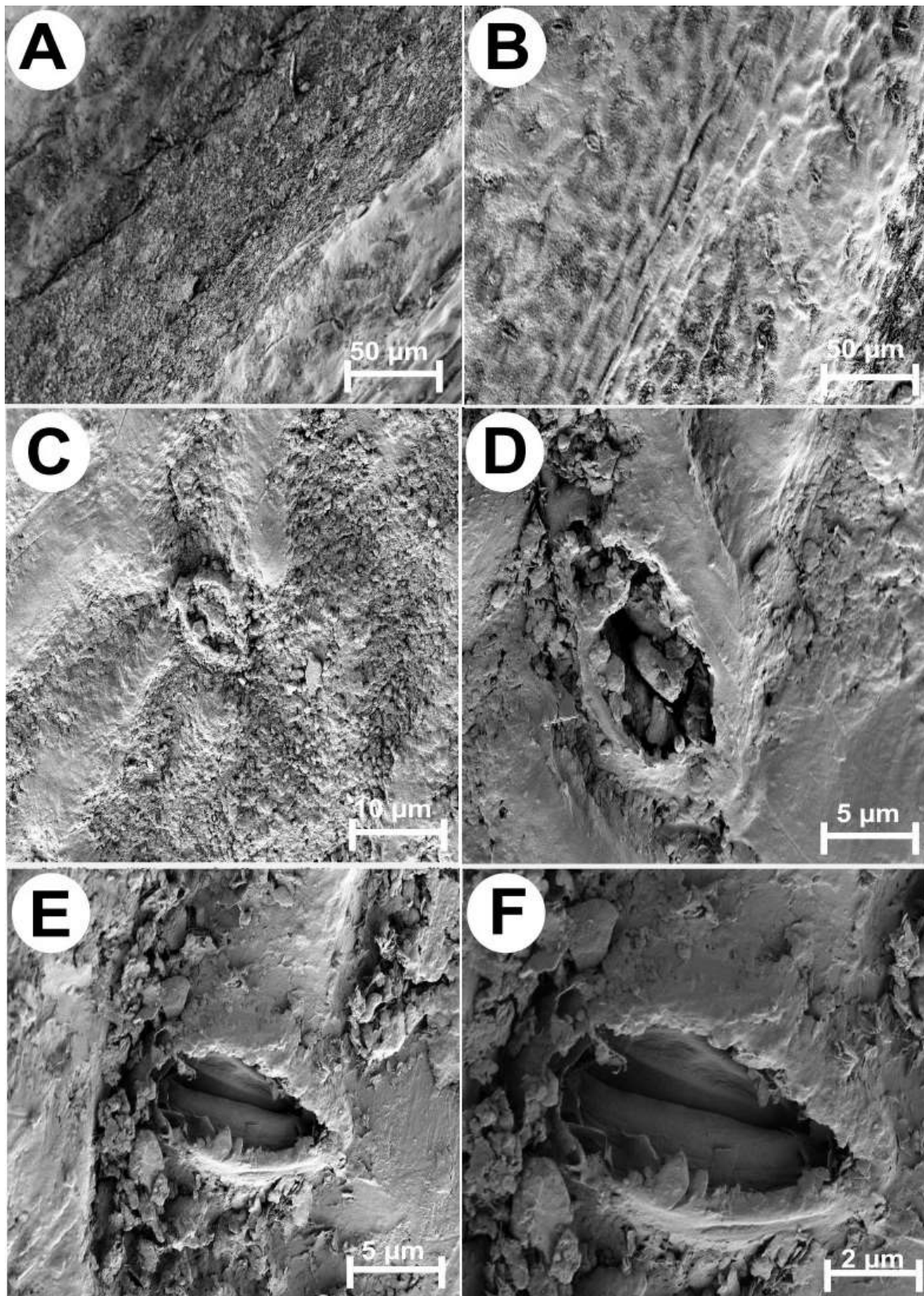


Figure 6. Adaxial stem surface of *Seseli staurophyllum* observed by SEM. The epidermis exhibits a waxy layer, scattered stomata, and simple trichomes, which contribute to moisture retention and protection against heat stress.

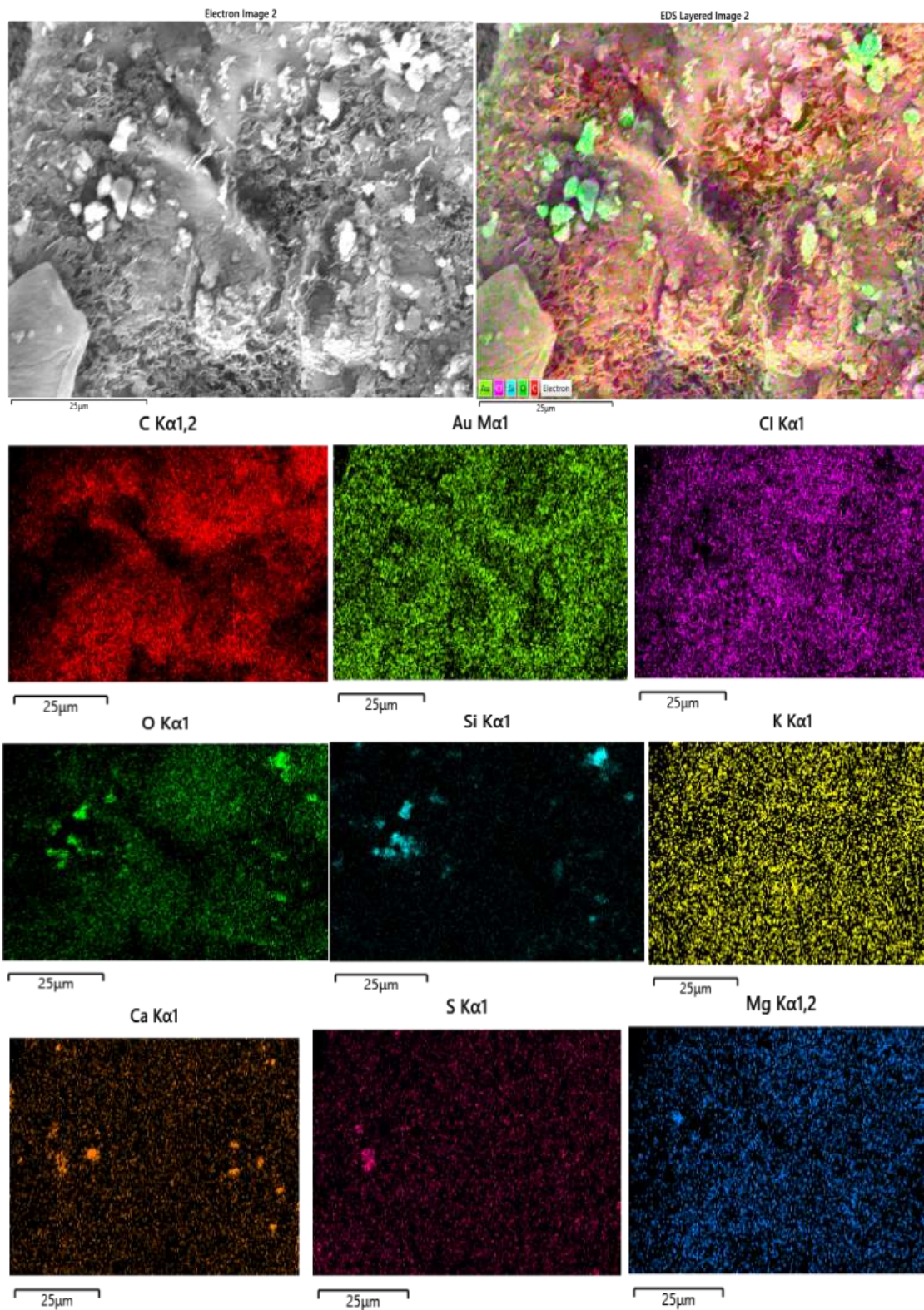


Figure 7. SEM–EDS analysis of the leaf surface of *Seseli staurophyllum*. The SEM image shows mineral particles and salt accumulations deposited on the epidermal surface. Elemental mapping illustrates the spatial distribution of major elements including C, O, Mg, Na, Al, Si, S, Cl, K, and Ca. High surface concentrations of Ca and S are consistent with gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) deposition from the surrounding gypsum–marly environment, while Na, Cl, and K likely reflect surface-associated soluble salts.



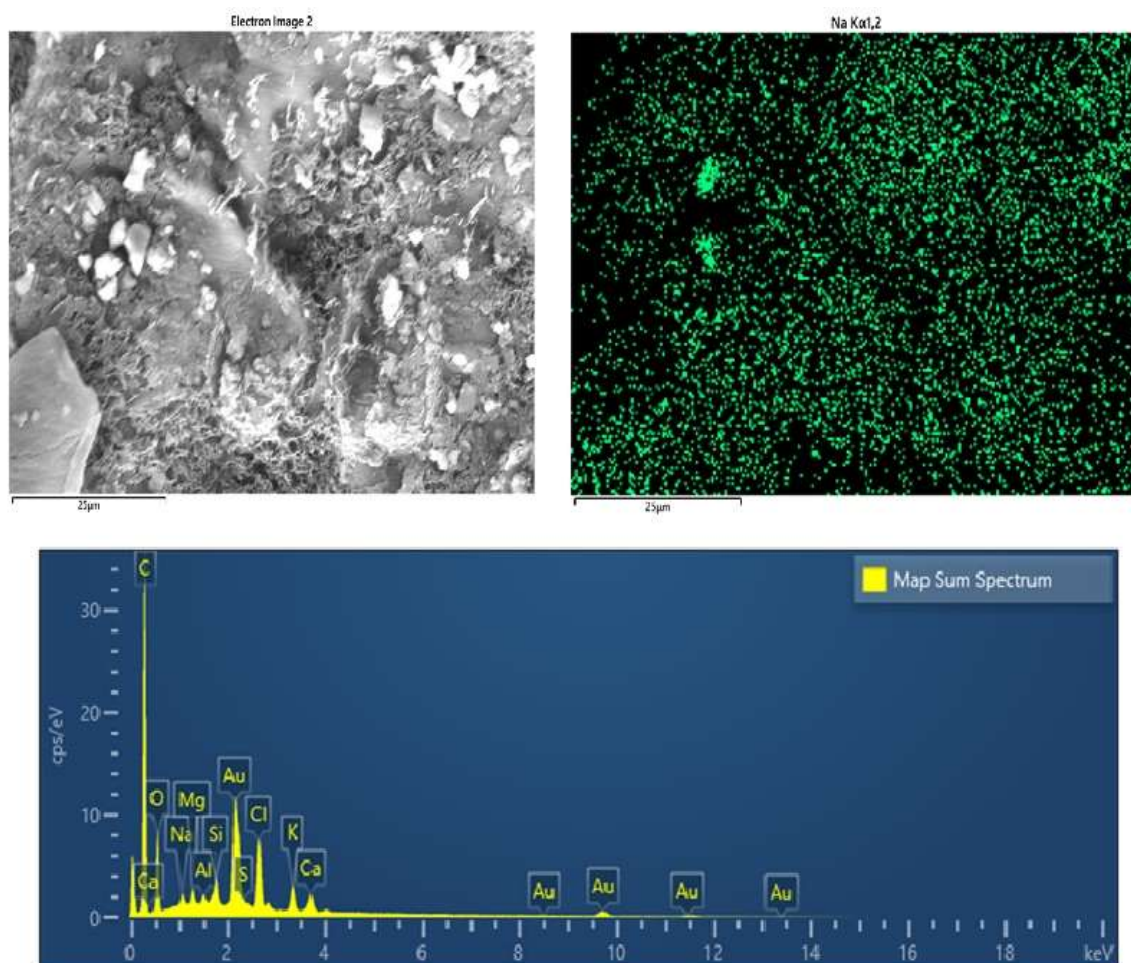


Figure 8. Relative elemental composition detected on the leaf surface of *Seseli staurophyllum* by SEM–EDS analysis. The highest weight percentages correspond to Ca, S, and O, indicating the predominance of surface-associated gypsum deposits, followed by Na, Cl, and K, reflecting the chemical characteristics of the gypsum–marl habitat.

Ecological characteristics and habitat conditions

Seseli staurophyllum was recorded exclusively from open habitats characterized by gypsum- and serpentine-rich substrates in northern Semnan Province (Figure 9). The species occurs at elevations ranging from 1,420 to 1,690 m a.s.l. across the surveyed populations (Table 3). All populations were located on south- to southwest-facing slopes with inclination values between 12° and 38°. Surface substrates consisted predominantly of gypsum–marl or serpentine materials, with high surface cover of stones and gravels (45–75%). Soil physicochemical analyses showed alkaline conditions across all sites, with pH values ranging from 7.8 to 8.4 (Table 3). Electrical conductivity (EC) values varied between 1.9 and 4.6 dS m⁻¹. Soil texture was classified mainly as loam to sandy loam, with relatively low organic matter content (0.4–1.2%). Gypsum content of surface soils ranged from 18.5% to 42.3%. Concentrations of calcium (Ca²⁺) and sulfate (SO₄²⁻) ions were consistently higher than other measured ions, whereas sodium (Na⁺), potassium (K⁺), and magnesium (Mg²⁺) occurred at lower concentrations (Table 3).

Associated vegetation

Vegetation accompanying *S. staurophyllum* was sparse and discontinuous. A total of 23 vascular plant species belonging to 14 families were recorded across the studied plots (Supplementary Table 3). The most frequent associated taxa included *Acantholimon* spp., *Zygophyllum eurypterum*, *Gypsophila* spp., *Artemisia* spp., and *Noaea mucronata*. Life-form analysis indicated the dominance of chamaephytes (43%) and hemicryptophytes (35%), followed by therophytes and geophytes. Species richness per plot ranged from 4 to 9 species, and total vegetation cover varied between 15% and 38%.



Table 3. Ecological and soil characteristics of habitats of *Seseli staurophyllum* Rech.f. in northern Semnan Province. Values are presented as mean \pm standard error (SE) or observed range based on field and laboratory measurements.

Category	Unit	Ecological / Soil factor	Value
Topographic factors	m	Elevation	1420–1690
	°	Slope	12–38
	—	Aspect	South–Southwest
Soil physical properties	cm	Soil depth	0–50
	%	Sand	76.81 \pm 0.90
	%	Silt	14.80 \pm 1.10
	%	Clay	9.40 \pm 0.11
Soil chemical properties	—	pH	7.8 \pm 0.08
	dS m ⁻¹	Electrical conductivity (EC)	2.62 \pm 0.08
	meq L ⁻¹	Na ⁺	2.82 \pm 0.18
	meq L ⁻¹	Mg ²⁺	5.45 \pm 0.72
	meq L ⁻¹	Ca ²⁺	31.22 \pm 1.33
	mg kg ⁻¹	K	95.55 \pm 28.52
	mg kg ⁻¹	P	2.48 \pm 0.60
	%	Total nitrogen (N)	0.011 \pm 0.00
	%	Organic carbon (OC)	0.20 \pm 0.01
	—	Sodium adsorption ratio (SAR)	0.66 \pm 0.01
	%	Calcium carbonate (CaCO ₃)	3.40 \pm 2.05
	%	Gypsum (CaSO ₄)	18.5–42.3

Discussion

Ecological specialization and endemism

Seseli staurophyllum Rech.f. is a monotypic taxon within Apiaceae, strictly endemic to gypsum–marl and serpentine substrates of Semnan Province, Iran. Its highly restricted geographic distribution, together with distinct morphological and micromorphological traits documented in this study, indicates a strong association with edaphically extreme habitats. Gypsum and serpentine soils are characterized by elevated salinity, high concentrations of Ca²⁺ and SO₄²⁻, low water-holding capacity, and pronounced thermal fluctuations, which collectively act as strong environmental filters permitting only a limited set of specialized taxa to persist (Palacio et al., 2012; Escudero et al., 2017; Sánchez-Martín et al., 2021). The combination of narrow endemism and monotype in *S. staurophyllum* suggests a history of long-term geographic and ecological isolation. This pattern is consistent with hypotheses proposing persistence of specialized taxa within edaphically stable refugial habitats, such as gypsum outcrops, while surrounding populations may have been reduced or eliminated through climatic fluctuations or competitive exclusion (García-Fayos et al., 2013; Llinares et al., 2015).

Morphological and micromorphological adaptations

Scanning electron microscopy revealed a continuous epicuticular wax layer covering leaf surfaces, producing a silvery–gray appearance. Such wax layers have been frequently reported in plants inhabiting arid and gypsum-rich environments and are commonly associated with increased reflectance and reduced heat absorption under intense solar radiation (Palacio et al., 2012; Escudero et al., 2017). Sunken stomata observed on the abaxial leaf surfaces were located within shallow epidermal depressions. This stomatal arrangement is widely described in xerophytic plants and is considered to reduce direct exposure to dry air, thereby limiting transpirational water loss (García-Fayos et al., 2013). In *S. staurophyllum*, this feature likely contributes to maintaining leaf water balance under conditions of limited soil moisture availability. Leaves and young aerial organs were further characterized by the presence of simple, multicellular, non-glandular trichomes. Such trichomes are known to influence boundary-layer properties at the leaf surface and may contribute to reduced leaf temperature and moderated transpiration rates (Sánchez-Martín et al., 2021). The coexistence of epicuticular waxes and trichomes in *S. staurophyllum* suggests a multi-layered structural strategy associated with persistence in dry, high-radiation habitats.

Taxonomic differentiation within *Seseli*

Comparative analysis of key morphological and anatomical traits of *S. staurophyllum* with closely related Iranian species, including *Semenovia eriocarpa* (formerly *Seseli elbursense*) and *S. libanotis* (Table 2), highlights several diagnostic features that support its distinct taxonomic status. *S. staurophyllum* can be distinguished by its cuneate–flabellate leaves with 1–2 pairs of lobes, thick epicuticular wax layer, simple non-glandular trichomes, and relatively reduced umbel ray number (mostly 2–3 rays). In contrast, *S. libanotis* exhibits pinnate leaves with numerous umbel rays, whereas *Semenovia eriocarpa* differs in leaf morphology and presents unresolved fruit characteristics. These morphological differences, in combination with the anatomical traits described above (Section 3.2, Figure 3), indicate that *S. staurophyllum* is a distinct species within the genus *Seseli*. The table-based comparison provides a clear framework for distinguishing this species from closely related taxa, supporting its classification as a narrow endemic and reinforcing the importance of integrating both morphological and micromorphological evidence in taxonomic assessments. This comparison also



underscores the value of documenting minor but consistent structural traits, such as wax layer thickness and trichome type, which may be overlooked in floristic surveys but are critical for accurate species identification and understanding evolutionary relationships within Apiaceae.

Ion management and physiological strategies

Although direct physiological measurements such as leaf water potential, ion compartmentalization, or gas exchange were not performed in the present study, the interpretation of adaptive traits is based on well-established structure–function relationships documented in gypsum-adapted plants. Micromorphological features such as sunken stomata, thick epicuticular wax layers, and trichome development have repeatedly been linked to drought resistance and reduced transpirational water loss in gypsophytes (Palacio et al., 2012; Escudero et al., 2017; Sánchez-Martín et al., 2021). Therefore, the adaptive interpretations proposed here should be regarded as ecologically informed inferences rather than direct physiological evidence. Future studies integrating physiological measurements would be necessary to confirm these functional mechanisms. EDS analysis revealed the presence of Ca, S, and Na on the leaf surface. Similar patterns of foliar mineral accumulation have been documented in other gypsophytes and are often interpreted as mechanisms for coping with high ionic concentrations in the substrate (Palacio et al., 2012; Escudero et al., 2017). In *S. staurophyllum*, the coexistence of surface mineral deposits with protective anatomical features suggests an integrated structural response to edaphic stress. Although the present study did not investigate physiological processes directly, these observations are consistent with previously reported strategies of ion compartmentalization and exclusion in gypsum-associated plants. Accordingly, SEM–EDS data in the present study are interpreted as evidence of surface mineral deposition related to habitat conditions, rather than direct proof of physiological uptake or internal accumulation of elements.

Comparison with other gypsum-associated taxa

Gypsum specialists from different phylogenetic lineages, such as *Gypsophila struthium* and *Herniaria fruticosa*, exhibit convergent morphological and micromorphological traits, including thick epicuticular wax layers, sunken stomata, trichome development, and sulfur-rich surface deposits (Palacio et al., 2012; Llinares et al., 2015). Comparable anatomical and micromorphological adaptive features have been documented in gypsum-associated taxa of Iran, including several endemic and gypsophilic species, such as *Astragalus* spp., *Acantholimon cymosum*, and other gypsophytes from central Iran (Rabizadeh et al., 2019; Rabizadeh & Nasrollahi, 2022; Rabizadeh et al., 2023), supporting the functional convergence observed in *S. staurophyllum*. The occurrence of comparable features in *S. staurophyllum* highlights functional convergence driven by similar environmental constraints, despite its isolated phylogenetic position within Apiaceae.

Conservation implications and future directions

Seseli staurophyllum is strictly associated with gypsum and serpentine substrates. Its narrow geographic range and monotypic status suggest that it may be highly sensitive to habitat disturbances. Anthropogenic activities such as gypsum extraction, grazing pressure, and land-use change may pose risks to its limited populations. Future research should aim to investigate physiological mechanisms of ion regulation and water-use strategies, conduct demographic studies to assess population stability, and integrate molecular phylogenetic approaches to further clarify the evolutionary history and taxonomic placement of this species. Such efforts would contribute valuable information for both biodiversity conservation and the broader understanding of plant adaptation to extreme edaphic environments (Palacio et al., 2012; García-Fayos et al., 2013). It should be noted that SEM–EDS analysis reflects surface elemental composition and does not allow discrimination between internally absorbed elements and those deposited externally on the leaf surface. Since the leaf samples were not washed prior to analysis and cross-sectional observations were not performed, the detected Ca, S, and Na cannot be unequivocally interpreted as resulting from physiological uptake. Nevertheless, the occurrence of these elements on the leaf surface is consistent with the gypsum-rich environments in which the species grows, where mineral dust deposition and salt accumulation are common. Such surface deposits may contribute to protective or adaptive functions in plants inhabiting arid and gypsum ecosystems, as previously reported for other gypsophilous species.

Conservation assessment

Based on the restricted geographic distribution, limited number of populations, and ongoing habitat threats, *Seseli staurophyllum* qualifies as a threatened species under the IUCN Red List criteria. Its Extent of Occurrence (EOO) and Area of Occupancy (AOO) are both highly restricted, and the species occurs in a small number of locations exposed to gypsum extraction, grazing, and land-use changes. According to the IUCN criteria B1 and B2, and considering the continuing decline in habitat quality, *S. staurophyllum* can be preliminarily assessed as Endangered (EN). This structured evaluation highlights the urgent need for conservation measures, including habitat protection, population monitoring, and restriction of anthropogenic disturbances. Further studies integrating population size, reproductive success, and potential threats are recommended to refine the assessment and support evidence-based conservation planning.



Conclusion

Seseli staurophyllum Rech.f. is a monotypic and narrowly endemic taxon restricted to gypsum–marl and serpentine substrates of Semnan Province, Iran. The species is characterized by a distinctive set of morphological, anatomical, and micromorphological features documented in this study, including thick epicuticular wax layers, sunken stomata, multicellular non-glandular trichomes, and surface mineral deposition. Together, these traits are consistent with persistence in habitats characterized by limited water availability, high solar radiation, and elevated concentrations of soil salts typical of gypsum-rich environments (Palacio et al., 2012; Escudero et al., 2017). SEM and EDS observations revealed the presence of calcium- and sulfur-rich deposits on leaf surfaces; these elements were detected at the surface level and may reflect environmental deposition. Although physiological processes were not directly assessed, the coexistence of surface mineral accumulation and protective anatomical traits highlights the ecological relevance of micromorphological characteristics in plants occurring on extreme edaphic substrates. Given its highly restricted distribution, monotypic status, and strict habitat association, *S. staurophyllum* may be sensitive to anthropogenic disturbances such as gypsum extraction, grazing, and land-use change. Conservation efforts focusing on the protection of gypsum habitats, combined with further integrative biosystematic, ecological, and physiological studies, are essential for safeguarding this endemic taxon and for advancing our understanding of plant adaptation to extreme soil conditions. Future studies incorporating a broader range of sampling sites and site-specific environmental data would allow the application of multivariate ordination approaches to further quantify habitat–trait relationships.

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Author Contributions

Fatemeh Rabizadeh: Conceptualization; fieldwork and specimen collection; methodology; morphological and micromorphological analyses; ecological data collection; data curation; formal analysis; writing—original draft preparation; writing—review and editing; visualization. The author has read and agreed to the published version of the manuscript.

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Data Availability Statement

All data generated or analyzed during this study are included in this article. Additional raw data (SEM–EDS files, high-resolution images, and soil analysis data) are available from the corresponding author upon reasonable request.

Conflicts of Interest

The author declares no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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