Leaf, Seed and Pollen Micromorphology in *Datura innoxia* and *Datura stramonium*: Implications for Taxonomy and Species Delimitation

Maryam Keshavarzi[1*], Majid Eskandari[2], Soma Marofi[1]

Received: 2025-07-15 Accepted: 2025-09-19

Abstract

The genus *Datura* (Solanaceae) comprises medicinal and toxic plants with a wide global distribution, two of which are native to Iran. In the present study, populations of *D. innoxia* and *D. stramonium* were collected from different regions of Iran. Microscopic and micromorphological traits were examined using light microscopy and scanning electron microscopy. Quantitative and qualitative data were analyzed by multivariate statistical methods, to determine the differential value of micromorphological traits of leaves, seeds, and pollen grains to better distinguish *Datura* species in Iran. The results revealed that leaf surface features, as well as seed traits and pollen morphology provided clear distinctions between the two species. *Datura innoxia* exhibited dense leaf trichomes, smoother seed surfaces, and striato-reticulate pollen ornamentation, whereas *D. stramonium* had nearly glabrous leaves, rougher seed surfaces, and rugulate-reticulate pollen ornamentation. The type, length and density of epidermal trichomes, exine ornamentation, lumen type, muri arrangement, exine thickness, length of pollen axes and seed shape and size were of diagnostic importance. The findings demonstrate that micromorphological traits of leaves, seeds, and pollen are of high taxonomic value in distinguishing *Datura* species in Iran and can serve as complementary tools in systematic studies and identification keys. Nevertheless, research gaps remain, including the need for more extensive population sampling, precise quantitative measurements, statistical comparisons across different geographical regions, and integration of micromorphological data with molecular phylogeny.

Keywords: *Datura*, Micromorphology, Pollen grain, Seed surface, Taxonomy

Introduction

The genus *Datura* (Solanaceae) comprises 14 species worldwide, with two of these species growing naturally in Iran (Luna-Cavazos and Bye, 2011; POWO, 2025). These plants are widely distributed in temperate and tropical regions of both the Old and New Worlds and characterized by large, trumpet-shaped flowers that range from

1-Department of Plant Sciences, Faculty of Biological Sciences, Alzahra University
2-Department of Botany, Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization (AREEO), Tehran, Iran
*Corresponding author email address: m.keshavarzi@alzahra.ac.ir
Doi: 10.48308/pae.2026.242023.1125

white to purple, and spiny capsules. The leaves are simple or may have sinuate or dentate margins, and the bisexual flowers are borne on long pedicels. The calyx persists until fruit maturity, while the corolla is funnel-shaped with 5–12 lobes or teeth. Capsules dehisce either by longitudinal slits or irregular openings (Khatamsaz, 1998).

Members of this genus occur naturally in almost all parts of the world except extremely cold regions (Nandini et al., 2015). *Datura* is a well-known weed, with its long seed longevity contributing to its success as an invasive plant (Bonde, 2001). It is both medicinal and poisonous, and in some cases also cultivated as an ornamental. The genus is mainly distributed in the southern parts of North America, with its center of diversity located in the Western Hemisphere (Symon and Haegi, 1991). Medicinal uses are primarily based on the leaves and seeds (Shah et al., 2013), while hallucinogenic properties have also been reported (Arefi et al., 2016).

Previous studies on *Datura* have emphasized its medicinal and toxic properties. Investigations of trichomes in *Lycium* species revealed the presence of glandular and non-glandular hairs of diagnostic value (Joubert et al., 1984). Similarly, trichome type and structure are useful for differentiating genera within Solanaceae (Harisha and Switu, 2013). Leaf trichome distribution is widely applied in taxonomy and anatomy, occurring as unicellular, bicellular, non-glandular, or glandular with bulbous bases.

Seed micromorphology also exhibits variation across genera in traits such as size, shape, color, texture, ornamentation, and hilum position (Khafagi et al., 2018). Seed traits such as length, width, and thickness are taxonomically important, while main ornamentation patterns include irregular- , regular-, and warty-reticulate types (Khafagi et al., 2018).

Pollen grains in Solanaceae are generally symmetrical and predominantly isopolar, exhibiting a range of shapes including prolate-spheroidal, oblate-spheroidal, sub-oblate, and sub-prolate forms. Apertures are typically tricolporate, with tetracolporate pollen occurring only rarely (Perveen and Qaiser 2007). The tectal surface shows considerable variation, encompassing scabrate, verrucate, striate, and reticulate patterns, and less commonly rugulate-fossulate or rugulate-reticulate ornamentation. Among these characters, pollen shape, aperture configuration, and exine surface ornamentation represent the most taxonomically informative traits (Perveen and Qaiser 2007). Based on these features, Perveen and Qaiser (2007) distinguished several pollen types in their comparative study of seven genera of Solanaceae. Within *Datura*, pollen grains are commonly characterized by a striato-reticulate exine and three zonocolporate apertures, although rugulate patterns may also occur, reflecting a notable degree of palynological variation within the genus (Dhanya and Devipriya 2016).

Ibrahim et al. (2016) emphasized the diagnostic importance of trichome diversity, while Timmerman (1927) had earlier referred to the differential value of trichomes in *Datura*. In this genus, the size, distribution, and ornamentation of surface trichomes appear to contribute to species delimitation. Many studies have relied mainly on qualitative descriptions of leaf, seed, and pollen traits, while quantitative data (precise measurements of dimensions, trichome density, pollen wall thickness, etc.) remain scarce. Comparative statistical analyses across populations that could separate environmental from genetic variation are lacking. Most studies have been geographically restricted, highlighting the need to investigate additional populations from different climatic zones, altitudes, and border regions of Iran to better assess spatial diversity. Furthermore, ultrastructural studies (SEM) of pollen and seeds are limited. Although some international studies have addressed pollen structure, detailed data specific to Iranian populations—such as exine, granule, and pore structures analyzed through electron microscopy and light sectioning—are still missing.

It should be noted that most identification keys rely on macromorphological traits, while micromorphological features of seeds and pollen are rarely included. Demonstrating the diagnostic value of these traits could lead to more accurate species identification. Despite the presence of *Datura* species in various habitats across Iran, comprehensive studies remain scarce. The few existing reports are limited to chemical composition and pharmacological or toxicological effects. Given the medicinal and toxic significance of these plants and the lack of sufficient information on micromorphological diversity, the present study aims to determine the differential value of micromorphological traits of leaves, seeds, and pollen grains to better distinguish *Datura* species in Iran.

Material and methods

For taxonomic investigations, several populations and plant specimens of the genus *Datura* were collected from its distribution areas in Iran (Fig. 1). Although some local floras of Iran have recorded *Datura innoxia* mainly from the southern parts of the country, herbarium records and recent field and laboratory studies indicate that this species has a wider distribution in Iran and has also been observed and sampled in the northern and northwestern regions (includ-

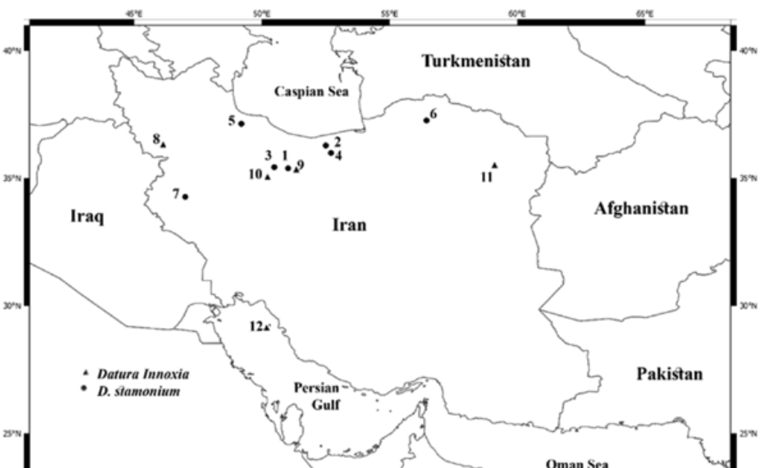

Fig. 1. Map of sample collection points studied in this study

ing the provinces of West Azerbaijan, Ardabil, Mazandaran, etc.). In Iran, *D. innoxia* occurs mostly in disturbed and human habitats (roadsides, abandoned lands, around settlements, and gardens). As a result, its distribution pattern is partly affected by cultivation and escape from cultivation (Maslo and Šarić, 2019). After transfer to the herbarium of Alzahra University (ALUH), the specimens were identified using regional floras (Khatamsaz, 1998; Schonbeck-Temesy, 1972) (Table 1).

For micromorphological studies of seeds, all populations were examined with a Dino-Lite digital stereomicroscope. For each species at each location, 3–5 individuals were sampled. Micromorphological measurements for leaf, seed and pollen grains were carried out using ImageJ 1.54r, based on 10 replicates per accession. Quantitative and qualitative seed characters evaluated are listed in Table 2. For the study of leaf surface traits, the approaches of Munien et al. (2015) and Aworinde et al. (2014) were applied. The wax features on seed surfaces were examined based on the methods of Barthlott et al. (1998), Kaya et al. (2016), and Junlakitjawat et al. (2010).

For palynological investigations, flowers were boiled in hot water for 5 minutes, and pollen grains were separated from anthers under a stereomicroscope and transferred to slides. Pollen grains were initially studied under a light microscope (×100 magnification). For palynological trait assessment, the studies of Mohsen and Badr (2019), Bhat et al. (2018), and Basak et al. (2017) were consulted.

For Scanning Electron Microscopy (SEM), samples of leaves, seeds, and pollen grains

Table 1. Geographical information and voucher numbers of sampled species

Species	Voucher details	Population no.
Datura innoxia	Azarbaijan, Boukan, Maroofi, S98771ALUH	8
	Tehran, Vanak, Alzahra University Campus, Mardani, 38778ALUH	9
	Markazi, Saveh, Narjesi, 22ALUH	10
	Khorassan, Birjand, Ghamami, 75622IRAN	11
	Bushehr, Kharg Island, Sangari, and Tehrani, 26458IRAN	12
D. stramonium	Tehran, Shahryar, Sayahpour, 38770ALUH	1
	Mazandaran, Ghaemshahr, Ahmadian, 38780ALUH	2
	Alburz, Karaj, Mahdasht, Keshavarzi, S98772ALUH	3
	Mazandaran, Savadkouh, Zirab, Eskandari, Bakhshi, and Ghamami, 74715IRAN	4
	Gilan, Fouman, Eskandari, and Ghamami, 74649Iran	5
	Khorassan, 40 km to S. Ashkhaneh, Darkesh, Eskandari, and Ghamami, 71827IRAN	6
	Kermanshah, Sahneh, Nowrooz Abad, Eskandari and Torabi, 65376IRAN	7

were mounted on aluminum stubs, coated with gold, and examined with a VEGA3 TESCAN SEM. To evaluate interspecific relationships and the taxonomic value of traits, multivariate statistical methods were applied. Mean values of quantitative traits were used, while qualitative traits were coded as binary or multistate variables. Relationships among species and studied populations were analyzed using cluster analysis and ordination based on principal component analysis (PCA) derived from factor analysis. Statistical analyses were performed with the software PAST ver. 4.03 (Hammer et al, 2020) and factor analysis by SPSS ver. 26. Average taxonomic distances and squared Euclidean distances are applied as dissimilarity coefficients in the cluster analysis of micromorphological data.

Results and discussion

Leaf surface analysis

Stomatal length and width showed variation among the studied species (Table 3). The stomatal type in all populations of both species was anomocytic and anisocytic. Epidermal cell walls were sinuous. In populations of *D. stramonium*, trichomes were absent, whereas in *D. innoxia* they were abundant. Three types of trichome (simple, glandular, and multicellular) were observed in *D. innoxia* species: simple long and short uniseriate and non-glandular hairs (Fig. 2 a, d & g), simple multicellular non-glandular hairs (Fig. 2. e & c), capitate glandular trichomes (Fig. 2. f) with short stalk (Fig. 2. b). In *D. innoxia*, covering (non-glandular) trichomes were long, dense, and clearly visible, while short-stalked glandular trichomes with swollen

Table 2. Quantitative and qualitative traits used in the micromorphological study of *Datura* species

Quantitative traits	
Stomata Length of leaf surface (μm)	Seed width (mm)
Stomata width of leaf surface (μm)	Seed length (mm)
Length to the width of the seed (mm)	Trichome length of leaf surface (μm)
Length of Polar axis (μm)	Length of equatorial axis (μm)
p/e ratio	Exine thickness (μm)
Qualitative traits	
Hair on leaf surface (present 1/absent 2)	Seed surface ornamentation (verrucate 1/verrucate-reticulate 2)
Hair of the leaf surface (unicellular 1/multicellular 2, glandular 3, all types 4)	Seed Wax type (granules 1/threads 2)
Stomata type (Anomocytic 1/Anisocytic 2/both 3)	Exine ornamentation (regulate 1/reticulate 2/striate-reticulate 3)
Seed shape (reniform 1/circular 2)	Muri arrangement (long parallel 1, short irregular 2)
Muri (long 1/short 2)	Lumen type (large 1/small 2)
	Leaf surface (smooth 1/rough 2)

heads were present in some areas.

In general, the leaf surface of *D. stramonium* appeared smoother, with clearer stomatal visibility and more uniform epidermal folds, whereas *D. innoxia* showed a wavy epidermis with dense trichome coverage, obscuring stomatal distribution. Thus, the main distinguishing feature between the two species is the type and density of epidermal trichomes.

Seed surface analysis

Qualitative traits of seeds revealed clear differences between the two species (Table 3). In *D. innoxia*, surface wax was of the Threads type, while in *D. stramonium* it was Granular. The hilum position in both species was subterminal (Fig. 3. a & f). Seed shape was reniform in *D. innoxia* (Fig. 3. a) and rounded/reniform in *D. stramonium* (Fig. 3. F). Surface ornamentation in both species was verrucate–reticulate (Fig. 3. b & g). Seeds of *D. innoxia* appeared smoother with elongated, more regular epidermal cells and weakly undulating boundaries, while those of *D. stramonium* were rougher, with irregular, thickened cell margins and prominent granules (Fig. 3. i) . Overall, *D. innoxia* seeds had a more regular surface, whereas *D. stramonium* seeds were markedly rugose and granular.

Pollen grain analysis

Qualitative variation in pollen traits was evi-

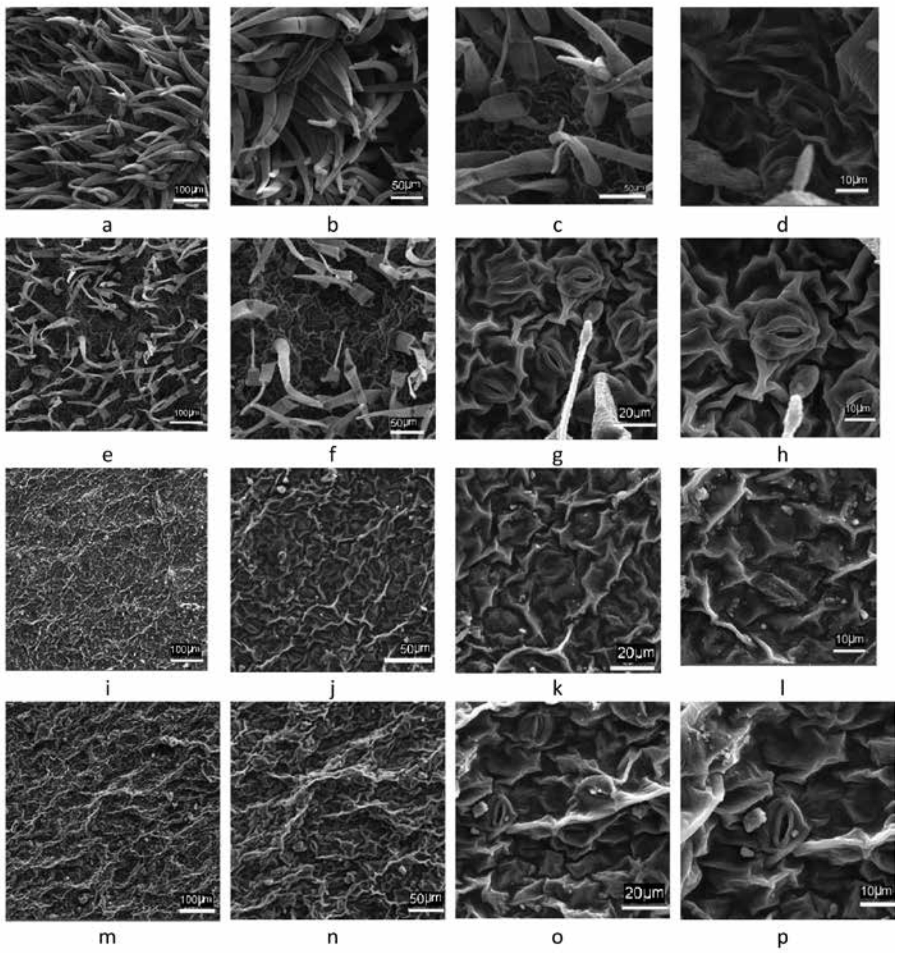

Fig. 2. Scanning electron micrographs of leaf surface of *D. innoxia*: a-d) Boukan population (no. 8), e-h) Saveh population (no. 10); *D. stramonium:* i-l) Ghaemshahr population (no. 2), m-p)Shahryar population (no. 1)

dent (Table 3). The general pollen shape was oblate-spheroidal. In an equatorial view, grains were rounded to elliptical (Fig. 4. c & o), while in a polar view, they were rounded-trilobed (Fig. 4. b, f, j & n). Apertures were colporate (Fig. 4 f & j), and all studied populations showed narrow muri. Exine ornamentation in *D. innoxia* was striato-reticulate (Fig. 4. C & g), while in *D. stramonium* it was rugulate-reticulate (Fig. 4. K & o). In *D. innoxia*, muri were long, parallel (Fig. 4. d & h), and longer, whereas in *D. stramonium* they were shorter, irregular, and less elevated (Fig. 4. L & p).

Pollen grains of *D. innoxia* were generally larger, sub-spheroidal, and exhibited reticulate patterns with larger lumina and thinner muri. In contrast, *D. stramonium* had smaller, sometimes ellipsoid pollen with rugulate to reticulate ornamentation, narrower lumina, and thicker muri. In both species, pollen was predominantly tricolpate, but grooves in *D. innoxia* were narrower and more regular compared with the deeper and irregular furrows of *D. stramonium*.

Statistical analysis

Quantitative micromorphological traits were evaluated with a one-way ANOVA. Levene's test indicated unequal variances, hence Welch's ANOVA was also performed, revealing highly significant differences among species ($F(42.8, 249.9) = 249.9$, $p < 0.001$). These findings demonstrate notable interspecific variation in quantitative traits, supporting subsequent multivariate analyses (e.g., cluster analysis and ordination). Post-hoc pairwise differences were assessed with Tukey's test.

Qualitative traits were coded binarily or categorically. Distributions across species were examined for each character using Chi-square tests or Fisher's exact test, as appropriate. To evaluate overall variation in qualitative traits, a Jaccard-based similarity matrix was constructed, and group separation was tested using PERMANOVA, allowing for the assessment of whether qualitative traits differentiate *Datura* species.

The UPGMA dendrogram based on Euclidean distance showed clear clustering of individuals by species, with short inter-cluster distances indicating high

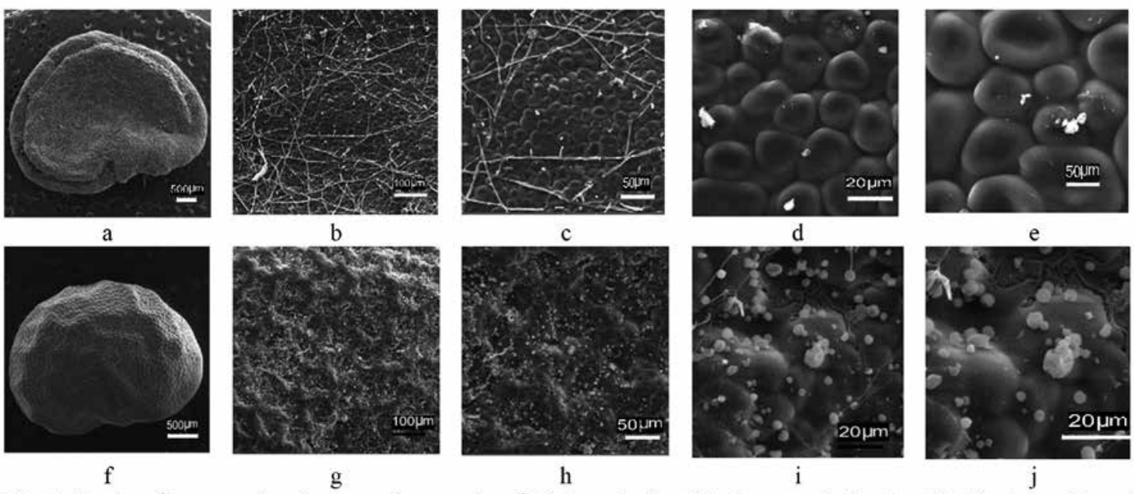

Fig. 3. Seed surface scanning electron micrographs of *D. innoxia*: (a-e)Boukan population (no. 8); *D. stramonium:* f-j) Mahdasht population (no. 3)

similarity within species and longer inter-cluster distances indicating substantial differentiation between species. Notably, species A and B cluster together before joining other groups, suggesting closer similarity in micromorphological traits (Fig. 5). PCoA based on micromorphological traits showed clear separation between *Datura* species studied. The two species clustered in distinct regions of the plot, indicating divergence in micromorphological characters. The degree of overlap between species was limited, suggesting that the measured traits reliably discriminate between *D. innoxia* and *D. stramonium* (Fig. 6).

To determine the most variable characters, a factor analysis based on PCA was performed. It revealed that the first three factors accounted for 93% of the total variation. In the first factor, approximately

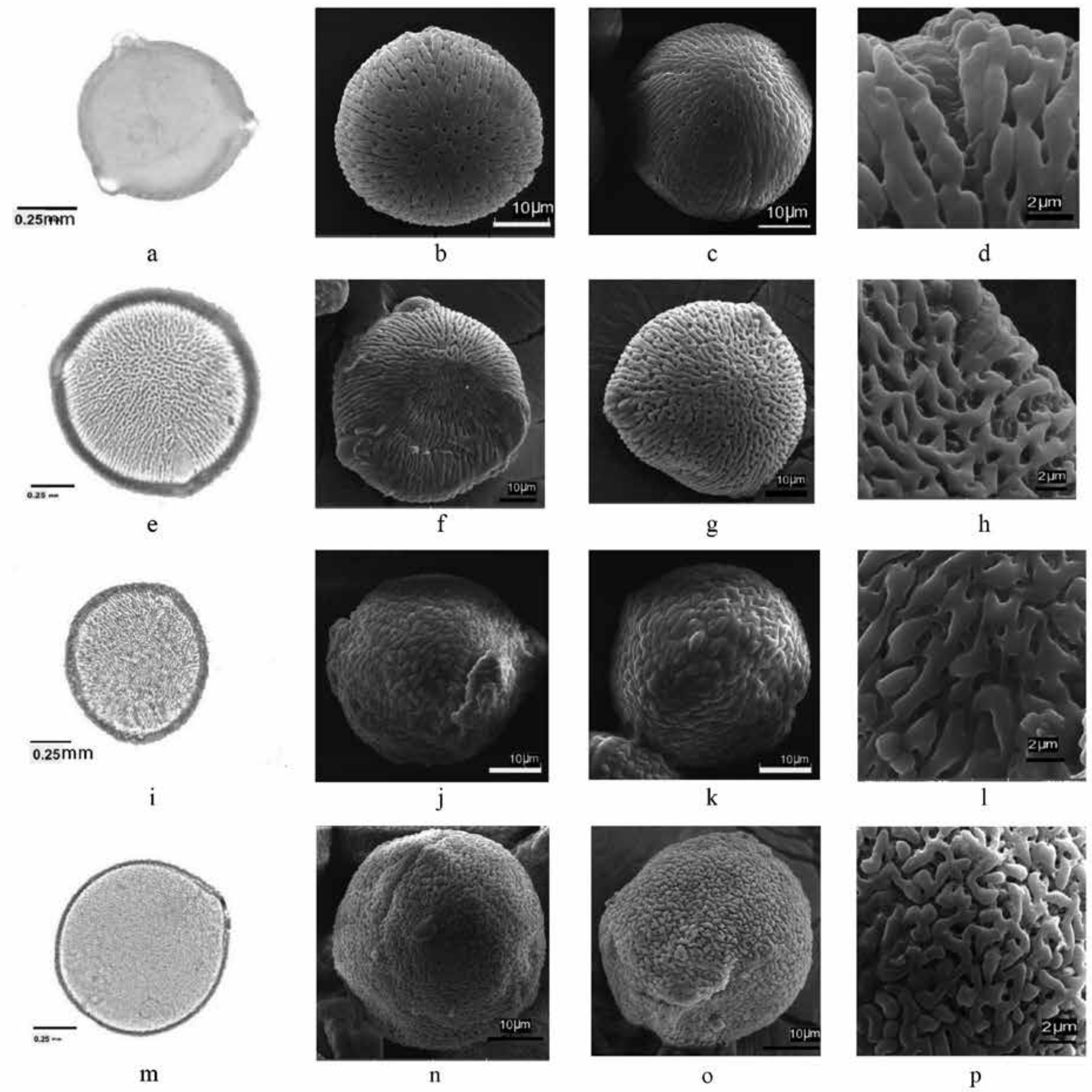

Fig. 4. Pollen surface scanning electron micrographs of *D. innoxia*: a-d) Vanak population (no. 9), e-h) Kharg island population (no. 12); *D. stramonium:* i-l) Nowrooz abad population (no. 7), m-p) Zirab population (no. 4). The left column is images from a light microscope, and the next three columns are electron micrographs

77 % of the total variation was accounted for 17 characters that exhibited the highest correlation (≥ 0.7) (Table 4). In the second factor, exine thickness showed the highest correlation, contributing about 9 % of the total variation. The most significant character in the third factor was the ratio of seed length to width .

Previous studies have reported variation in stomatal types within the genus *Datura*. Gaire (2008) recorded anisocytic stomata in *D. stramonium*, while Gómez-Nucamendi et al. (2016) observed anisocytic stomata. In contrast, Hasan and Amer (2019) identified anomocytic stomata, and Ibrahim et al. (2016) reported the presence of both anomocytic and anisocytic stomata on the adaxial and abaxial leaf surfaces. In the present study, both stomatal types were consistently observed in all populations of both *D. innoxia* and *D. stramonium*. In addition, the epidermal cell walls were undulate in both species, corroborating earlier observations (Wallis and Konjovic 1963; Gaire 2008; Gómez-Nucamendi et al. 2016; Ibrahim et al. 2016). These results indicate that the type of stomata alone may not be adequate for species delimitation in *Datura*; however, it gains taxonomic value when combined with other micromorphological characters.

Trichome morphology showed clearer interspecific differentiation. In the present study, populations of *D. stramonium* lacked trichomes, whereas *D. innoxia* exhibited abundant glandular and non-glandular, predominantly multicellular trichomes. This finding stands in contrasts to several earlier reports that described both covering and glandular trichomes in *D. stramonium* (Gaire 2008; Gómez-Nucamendi et al. 2016; Hasan and Amer 2019). Such discrepancies may reflect geographic variation, environmental influences, or differences in sampling strategy and developmental stage. Our results suggest that trichome presence, type, and abundance may exhibit considerable intraspecific variability, yet still provide useful diagnostic characters at the population or regional level.

Seed micromorphology also proved to be informative. Seeds of *D. innoxia* were reniform, whereas those of *D. stramonium* were rounded to reniform, both with ornamented seed coats. These observations are aligning with previous studies (Gaire 2008; Gaire and Subedi 2013; Nandini et al. 2015; Kh-

Table 3. The summary of micromorphological measured and evaluated data for two *Datura* species in the present study

	Location	Leaf stomata length(µm)	Leaf stomata width(µm)	Seed length to width	Seed length(mm)	Seed width(mm)	Leaf hair length(µm)	Polar axis length(µm)	Equatorial axis length(µm)	p/e	Exine Thickness(µm)	Stomata type	Leaf surface	Leaf hair	Leaf hair type	Seed surface	Seed shape	Exine ornamentation	Lumen type	Seed wax type	Long or short muri	Muri arrangement
D. stramonium	Shahryar	4	3	1.33	17.16	13.89	0	36.81	39.43	0.93	50	3	1	2	-	2	2	1	1	1	1	2
	Ghaemshahr	3	2	1.5	16.22	14.51	0	36.81	39.43	0.93	50	3	1	2	-	2	2	1	1	1	1	2
	Mahdasht	3.36	2.57	1.33	17.16	13.89	0	38.98	35.33	1.1	20	3	1	2	-	2	2	1	1	1	1	2
	Zirab	4	2.9	1.37	16.22	14.51	0	38.98	35.33	1.1	20	3	1	2	-	2	2	1	1	1	1	2
	Fouman	3.3	2.5	1.32	17.16	13.89	0	36.81	39.43	0.93	50	3	1	2	-	2	2	1	1	1	1	2
	Darkesh	3.9	2.4	1.63	16.22	14.51	0	38.98	35.33	1.1	20	3	1	2	-	2	2	1	1	1	1	2
	NowroozAbad	3.6	2.5	1.44	17.1	14.01	0	36.81	39.43	0.93	50	3	1	2	-	2	2	1	1	1	1	2
D. innoxia	Boukan	5.43	4.25	1.27	22.78	14.85	162.3	39.38	37.86	1.04	30	3	2	1	2	1	1	2	2	2	2	1
	Vanak	5.5	3.7	1.48	23	15.6	156	39.38	37.86	1.04	30	3	2	1	2	1	1	2	2	2	2	1
	Saveh	4.5	3.1	1.45	22.82	19.9	152.3	56.26	47.62	1.18	60	3	2	1	2	1	1	2	2	2	2	1
	Birjand	5.2	3.9	1.33	24.2	17	162	56.26	47.62	1.18	60	3	2	1	2	1	1	2	2	2	2	1
	Kharg	5.5	3.9	1.33	24.1	16.13	165	56.26	47.62	1.18	60	3	2	1	2	1	1	2	2	2	2	1

Table 4. Component matrix of factor analysis based on micromorphological characters of *Datura* populations

Component Matrix			
	Component		
	1	2	3
Leaf hair length	0.993	-0.095	0.005
Exine ornamentation	0.992	-0.087	0.022
Leaf hair presence	-0.992	0.087	-0.022
Seed surface	-0.992	0.087	-0.022
Lumen type	0.992	-0.087	0.022
Seed shape	-0.992	0.087	-0.022
Seed wax type	0.992	-0.087	0.022
Muri arrangement	-0.992	0.087	-0.022
Long or short Muri	0.992	-0.087	0.022
Leaf hair type	0.992	-0.087	0.022
Seed length	0.992	-0.036	-0.071
Leaf stomata length	0.900	-0.336	-0.004
Leaf stomata width	0.867	-0.378	-0.222
Leaf surface	0.854	-0.005	-0.084
Polar axis length(μm)	0.801	0.484	0.122
Seed width	0.767	0.456	0.318
Equatorial axis length(μm)	0.726	0.655	-0.180
p/e	0.650	0.100	0.481
Exine thickness	0.409	0.758	-0.450
Seed length to width	-0.253	0.169	0.798

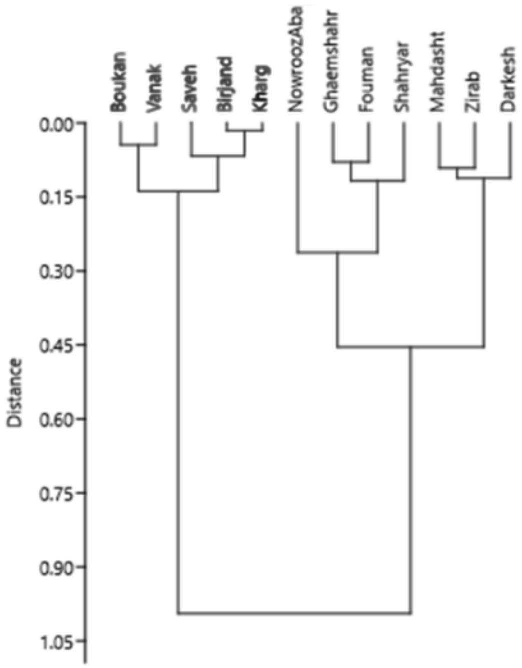

Fig. 5. UPGMA dendrogram based on Euclidean distance for two *Datura* species studied. Two separate clusters are formed

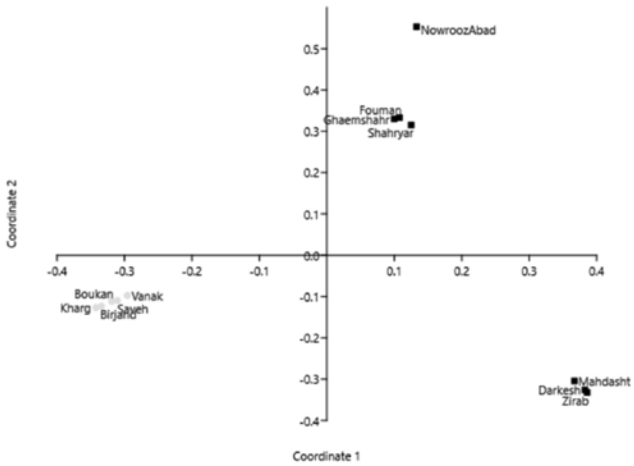

Fig. 6. PCoA scatter diagram of two *Datura* species studied. blue dots stand for *D. innoxia* and black squares for *D. stramonium*

afagi et al. 2018; Barakat et al. 2019). The epicuticular wax appeared as threads in *D. innoxia* and granules in *D. stramonium*, and the hilum was subterminal in both species, in agreement with Khafagi et al. (2018). Although surface ornamentation was generally verrucate–reticulate in both taxa, subtle differences were evident, with ocellate patterns in *D. innoxia* and more distinctly reticulate patterns in *D. stramonium*, as also reported by Barakat et al. (2019). Anticlinal walls were undulate in both species, further confirming earlier findings.

Palynological characters were largely consistent with previous reports but nonetheless contributed to species discrimination. The pollen grains of both species exhibited an oblate-spheroidal, which was similarly reported by Dhanya and Devipriya (2016), and Rajurkar and Tidke (2017) for *D. innoxia*.Earlier descriptions of prolate-spheroidal pollen in *D. stramonium* suggest some degree of variation (Adedeji and Akinniyi 2015). In an equatorial view, pollen grains were rounded to elliptical, while in a polar view, they appeared rounded-trilobed, which is in agreement with Perveen and Qaiser (2008), Dhanya and Devipriya (2016), and Rajurkar and Tidke (2017). The aperture type was consistently colporate, as reported in previous palynological studies of the genus and muri were narrow in both species, matching the observations of Dhanya and Devipriya (2016).

Exine ornamentation varied between the two species, being striato-reticulate in *D. innoxia* and rugulate-reticulate in *D. stramonium*. These patterns are in accordance with earlier investigations (Perveen and Qaiser, 2008; Dhanya and Devipriya, 2016; Rajurkar and Tidke, 2017), as does the general arrangement of muri.

Conclusion

Molecular phylogenetic studies have divided the genus *Datura* into three sections, *Ceratocaulis*, *Datura*, and *Dutra,* based on phylogenetic relationships and fruit morphology. According to fruit position on the branch, capsule dehiscence, and seed margin structure, *D. stramonium* and *D. innoxia* belong to two distinct clades (Bye and Sosa, 2013). The present study demonstrates that these macromorphological distinctions are reinforced by micromorphological traits, which proved to be reliable for separating the two species in Iran.

Leaf epidermal features, including stomatal type and trichome morphology, showed considerable taxonomic value, supporting earlier conclusions by Ibrahim et al. (2016). In addition, palynological characters, particularly pollen shape, aperture type, and exine ornamentation, contributed to species delimitation, consistent with broader trends observed in Solanaceae (Al-Quran 2004). Seed micromorphology further provided stable and diagnostic traits, as previously emphasized for the family (Kong et al. 2011; Khafagi et al. 2018). Collectively, these micromorphological features successfully differentiated *D. innoxia* and *D. stramonium*.

Overall, this study highlights the importance of integrating leaf, seed, and pollen micromorphology in the systematics of *Datura*. These characters offer valuable tools for identification keys and taxonomic revisions of the genus in Iran. However, further research is needed to strengthen these conclusions. Future studies should incorporate detailed quantitative analyses (e.g., pollen size, trichome density, and exine thickness) and statistical comparisons across a wider range of populations. Expanding sampling efforts across diverse ecological and climatic regions of Iran would aid clarify patterns of intraspecific variation. Furthermore, the integration of micromorphological data with molecular phylogenetic analyses is also essential for achieving a more comprehensive understanding of inter- and intraspecific relationships. Finally, investigating the ecological and chemical correlates of micromorphological traits, as well as their developmental plasticity, would provide deeper insights into the adaptive significance of these characters. This study provides an important step toward understanding intraspecific variation and the systematic application of micromorphological traits in the genus *Datura*.

Acknowledgements

The authors are thankful to the anonymous referees for improving the manuscript.

References

Adedeji, O., and Akinniyi, T.A., 2015. Pollen morphology of some species in the family Solanaceae. *Journal of Advanced Laboratory Research in Biology*, 6(4), 124-128.

Al-Quran, S., 2004. Pollen morphology of Solanaceae in Jordan. *Pakistan Journal of Biological Sciences*, 7(9), 1586-1593.

Arefi, M., Barzegari, N., Asgari, M., Soltani, S., Farhidnia, N., and Fallah, F., 2016. *Datura* poisoning, clinical and laboratory findings. Report of five cases. *Romanian Journal of Legal Medicine*, 24(4), pp308-311. DOI: https://doi.org/10.4323/rjlm.2016.308.

Aworinde, D.O., Ogundele, A., and Ogundairo, B.O., 2014. Morphological and Leaf Epidermal Features of Some *Capsicum* Species (Solanaceae) from Nigeria. Pertanika *Journal of Tropical Agricultural Science*, 37(1), 65 – 72.

Barakat, N.A., Soliman, M.S.A., and Zahran, F.A., 2019. Macro-and micromorphometrical seed characters in seven species of Egyptian *Datura* and *Nicotiana* (Solanaceae). *Phytotaxa*, 413(2), 149-158. DOI: https://doi.org/10.11646/phytotaxa.413.2.4

Barthlott, W., Neinhuis, C., Cutler, D., Ditsch, F., Meusel, I., Theisen, I., and Wilhelmi, H., 1998. Classification and terminology of plant epicuticular waxes. *Botanical Journal of the Linnean Society*, 126(3), 237-260. DOI: https://doi.org/10.1111/j.1095-8339.1998.tb02529.x.

Basak, M., Sonar, A. S., and Chowdhury, M., 2017. Phenetic study of some Indian Solanaceae based on foliar micromorphology, palynology and reproductive potentiality. *Plant Archives*, 17(2), 1267-1273.

Bhat, N. A., Jeri, L., Mipun, P., and Kumar, Y., 2018. Systematic studies (micromorphological, leaf architectural, anatomical and palynological) of genus *Physalis* L. (Solanaceae) in northeast India. *Plant Archives*, 18(2), 2229-2238.

Bonde, K., 2001. The genus *Datura*: from research subject to powerful hallucinogen, *Ethnobotanical Leaflets*, 1998(1), 10.

Bye, R. and Sosa, V., 2013. Molecular phylogeny of the jimsonweed genus *Datura* (Solanaceae). *Systematic Botany*, 38(3), pp.818-829. DOI: https://doi.org/10.1600/036364413X670278.

Dhanya, C. and Devipriya, V., 2016. Pollen morphological studies on two Solanaceous genera *Brugmansia* Pers. and *Datura* L. L. *International Journal of Advanced Research*, 4, pp.1879-1887.

Gaire, B.P. and Subedi, L., 2013. A review on the pharmacological and toxicological aspects of *Datura stramonium* L. *Journal of integrative medicine*, 11(2), pp.73-79. DOI: https://doi.org/10.3736/jintegrmed2013016.

Gaire, B.P., 2008. Monograph on *Datura stramonium*. The School of Pharmaceutical and Biomedical Sciences, Pokhara University, Nepal.

Gómez-Nucamendi, O.L., Hernández-Sandoval, L., Figueroa-Cabañas, M., and Martínez, M., 2016. Leaf anatomy of four species and one variety of *Datura* (Solanoidea, Solanaceae). *Journal of Plant Biology Research*, 5(2),37-47.

Hammer, O., Harper, D. and Ryan, P., 2020. PAST: Paleontological Statistics Software Package for Education and Data Analysis version. 4.03. *Palaeontologia Electronica*, 4, 1-9.

Harisha, C.R. and Jani, S., 2013. Pharmacognostical study on trichomes of Solanaceae and its significance. *Univers J Pharm*, 2, pp.100-104.

Hassan, R.A. and Amer, W.M., 2019. Biosystematic study of the Egyptian *Datura stramonium* (Solanaceae). *Phytotaxa*, 408(3), pp.178-194. DOI: https://doi.org/10.11646/phytotaxa.408.3.3.

Ibrahim, H.M., Abdo, N.A., Al Masaudi, E.S., and Al-Gifri, A.N.A., 2016. Morphological, epidermal, and anatomical properties of *Datura* Linn. Leaf in Sana'a City-Yemen and its taxonomical significance. *Asian Journal of Plant Science and Research*, 6(4), pp.69-80.

Joubert, A.M., Verhoeven, R.L. and Venter, H.J.T., 1984. An anatomical investigation of the stem and leaf of the South African species of *Lycium* L.(Solanaceae). *South African Journal of Botany*, 3(4), pp.219-230. DOI: https://doi.org/10.1016/S0022-4618(16)30033-X

Junlakitjawat, A., Thongpukdee, A. and Thepsithar, C., 2010. Seed coat micromorphology of some *Solanum* species in Thailand. *Journal of the Microscopy Society of Thailand*, 24(1), pp.13-16.

Kaya, A., Satıl, F. and Aslan, M., 2016. Seed morphology of the genus *Hyoscyamus* L. in Turkey and its systematic significance. *Acta Microscopica*, 25(2), pp.48-55.

Khafagi, A., El-Ghamery, A., Ghaly, O. and Ragab, O., 2018. Fruit and seed morphology of some species of Solanaceae. *Taeckholmia*, 38(1), pp.123-140. DOI: https://doi.org/10.21608/taec.2018.13520.

Khatamsaz, M., 1998. Flora of Iran (Solanaceae), no. 24. -Tehran.

Kong, M.J., Lee, J.S. and Hong, S.P., 2011. Comparative seed morphology of Solanaceae in Korea. *Korean Journal of Plant Taxonomy*, 41(1), pp.35-46. DOI: https://doi.org/10.11110/kjpt.2011.41.1.035.

Luna-Cavazos, M. and Bye, R., 2011. Phytogeographic analysis of the genus *Datura* (Solanaceae) in continental Mexico. *Revista mexicana de biodiversidad*, 82(3), pp.977-988.

Maslo, S. and Šarić, Š., 2019. *Datura innoxia* Mill.(Solanaceae), a new alien species in the flora of Bosnia and Herzegovina. *Thaiszia*, 29, pp.225-230. DOI: https://

doi.org/10.33542/TJB2019-2-07.

Mohsen, L. and Badr, A., 2019. Description of seed and pollen micromorphology and their taxonomic impact in some *Solanum* L. species. *Taeckholmia*, 39(1), pp.1-17. DOI: https://doi.org/10.21608/taec.2019.11353.1003.

Munien, P., Naidoo, Y. and Naidoo, G., 2015. Micromorphology, histochemistry and ultrastructure of the foliar trichomes of *Withania somnifera* (L.) Dunal (Solanaceae). *Planta*, 242(5), pp.1107-1122. DOI: https://doi.org/10.1007/s00425-015-2341-1.

Nandini, D., Ravikumar, B.S. and Prasanna, R.K.K., 2015. Morphometric analysis of *Datura* plant to understand variation and similarities among four major species. *Med Aromat Plants*, 4(209), pp.2167-0412.

Perveen, A. and Qaiser, M., 2007. Pollen morphology of family Solanaceae from Pakistan. *Pak. J. Bot*, 39(7), pp.2243-2256.

POWO, 2025. (Plants of the World Online), *Datura* L. Facilitated by the Royal Botanic Gardens, Kew. Plants of the World Online | Kew Science. (Accessed 26 September 2025)

Rajurkar, A. and Tidke, J., 2019. Pollen morphodiversity in some genera of family Solanaceae. *International Journal of Applied Research*, 3(3), pp.113-115.

Schonbeck-Temesy, E., 1972. Solanaceae. In: Rechinger, K.H. (ed). Flora Iranica 100:1-82.

Shah, V.V., Shah, N.D. and Patrekar, P.V., 2013. Medicinal plants from Solanaceae family. *Research journal of pharmacy and technology*, 6(2), pp.143-151.

Symon, D. and Haegi, L., 1991. *Datura* (Solanaceae) is a New World genus. Solanaceae. III. Taxonomy, chemistry, evolution. Royal Botanic Gardens Press, Kew, UK, pp.197-210.

Timmerman, H., 1927. *Datura*: the nomenclature of the species used in medicine. *Pharmaceutical Journal Pharmacist*.118, 64, 571.

Wallis, T.E. and Konjovic, M., 1963. *Datura sanguinea* R. and P., its Stem and Leaves. *Journal of Pharmacy and Pharmacology*, 15(Supplement_1), pp.170T-179T. DOI: https://doi.org/10.1111/j.2042-7158.1963.tb11207.x.