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Seed morphological diversity of Egyptian *Allium* L. (Amaryllidaceae) and its taxonomic significance

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Running title: *ALLIUM* SEED MACRO- AND MICROMORPHOLOGY

Abstract – *Allium* L. (Amaryllidaceae, Allioideae, Allieae) has disputed generic delimitation and species boundaries, compounded by the proliferation of the species' synonyms. This study provides for the first time a comprehensive description of the seed morphology of native, endemic, and near-endemic species in Egypt and addresses the significance of seed traits for infrageneric classification. Twenty-two *Allium* taxa belonging to four subgenera and six sections were investigated using fresh or dry materials from their mature seeds. Thirty-eight quantitative and qualitative traits of the seeds' dorsal and ventral sides were investigated using stereomicroscopy and scanning electron microscopy (SEM). Statistical and multivariate analyses were performed. This work provides the first description of the seeds of 13 *Allium* taxa, including *A. artemisietorum* Eig & Feinbrun, *A. barthianum* Asch. & Schweinf., *A. blomfieldianum* Asch. & Schweinf., *A. crameri* Asch. & Boiss., *A. desertorum* Forssk., *A. erdelii* Zucc., *A. mareoticum* Bornm. & Gauba, *A. papillare* Boiss., *A. roseum* subsp. *tourneuxii* Boiss., *A. sativum* L., *A. sinaiticum* Boiss., *A. spathaceum* Steud. ex A.Rich., and *A. trifoliatum* Cirillo. This study reports for the first time a comparative investigation of dorsal seed surface traits against ventral traits, revealing conspicuous differences for most species and highlighting the most informative diagnostic seed traits for distinguishing taxa. *Allium* subg. *Allium* L. has a broader range of variation than any of the other subgenera.

Keywords: *Allium*, endemic and near-endemic, macro- and micromorphology, multivariate analysis, scanning electron microscope, seed, taxonomy.

Introduction

Allium L. (Amaryllidaceae, Allioideae, Allieae) has a disputed generic delimitation and species boundaries, which is compounded by the proliferation of its synonyms (Choi et al. 2012, Nour et al. 2022). It is one of the most taxonomically complex and species-rich genera, with approximately 1063 species (Sennikov and Lazkov 2023). Members of the genus exhibit high morphological diversity in their floral parts (Friesen et al. 2006). *Allium* is a bulbous plant with a short rhizome, membranous tunics, and linear leaves. Its inflorescence is a multiflowered umbel, and the floral parts are strongly withered once the capsules have matured. Capsules are trigonous and typically contain ovate to drop-shaped seeds; however, the shape of the seeds varies greatly depending on the characteristics of the capsule (Fritsch 2001). The genus is dispersed across Africa; southwestern, middle, and central Asia; Europe; and North and South America (Friesen et al. 2006, Khassanov 2018). *Allium* was classified into 15 subgenera and 67 sections using the internal transcribed spacer region (ITS) (Friesen et al. 2006). *Allium* species have a high rate of endemism, particularly with respect to the Mediterranean area, which is regarded as the main *Allium* diversity center (Brullo et al. 2019). Bedair et al. (2023) reported that *A. barthianum* Asch. & Schweinf., *A. blomfieldianum* Asch. & Schweinf., *A. mareoticum* Bornm. & Gauba and *A. trifoliatum* Cirillo are Mediterranean endemic species; these species are included in this study.

In the Flora of Egypt, El Garf (2000) recognized 20 *Allium* species, and Boulos (2009) recorded 29 *Allium* taxa (21 wild, four cultivated species, and four subspecies). According to the classification of Friesen et al. (2006), those taxa occupied four subgenera and six sections: *Allium* subg. *Allium* L. (*Allium* sect. *Allium* L. and *A.* sect. *Codonoprasum* Rchb.), *A.* subg. *Amerallium* Traub. (*A.* sect. *Briseis* (Salisb.) Stearn. and *A.* sect. *Molium* G.Don ex Koch.), *A.* subg. *Cepa* Radic (*A.* sect. *Cepa* L.), and *A.* subg. *Melanocrommyum* Webb et Berth. (*A.* sect. *Melanocrommyum*). *Allium crameri* Asch. & Boiss. and *A. mareoticum* are endemic to Egypt (Abdelaal et al. 2018), while *A. barthianum* and *A. blomfieldianum* are near-endemic (Bedair et al. 2023). A restricted distribution was observed for *A. artemisietorum* Eig & Feinbrun, *A. desertorum* Forssk., and *A. papillare* Boiss. (from Egypt to Jordan), *A. erdelii* Zucc. (from Northeast Libya to Syria), *A. sinaiticum* Boiss. (from Sinai, Egypt, to Northwest Saudi Arabia), and *A. spathaceum* Steud. ex A.Rich. (from East Sudan to North Somalia) (POWO 2021). Although *A. spathaceum* was recorded in the Egyptian Flora as a rare species collected earlier from Gebel Elba, in the southeastern corner of Egypt, it was included in this study (Täckholm 1974).

The taxonomic significance of the quantitative and qualitative traits of *Allium* seeds has been studied. Some studies focused on a particular region, including those in Europe. Cesmedziev and Terzijski (1997) investigated the spermoderm structures of 18 Bulgarian species of *A.* subg. *Codonoprasum*. Eight *Allium* species, following five subgenera and five sections, were examined in Poland by Bednorz et al. (2011), revealing the presence of unusually raised anticlinal walls. Moreover, sixty-two *Allium* taxa from Türkiye were classified into four subgenera, and nine sections were examined to determine the taxonomic relevance of the epidermal cell shape; sculpturing of periclinal walls; and position, shape, and undulation type of anticlinal walls (Celep et al. 2012).

Several studies were carried out on the Asian *Allium*; Lin and Tan (2017) investigated 38 species belonging to seven subgenera and 19 sections from Xinjiang, China. Baasanmunkh et al. (2020) also described 48 species from Uzbekistan, Kyrgyzstan, and Mongolia, representing seven subgenera and 24 sections. There were differences in seed size and shape, the arrangement of epidermal cells, and the different anticlinal and periclinal wall traits between the species and sections. These differences were shown in both studies. The Iranian *Allium* was examined based on 20 species classified into four subgenera and 11 sections studied by Neshati and Fritsch (2009). Veiskarami et al. (2018) investigated 23 species from two subgenera that compose the *A. ampeloprasum* L. alliance. Khorasani et al. (2020) examined thirteen species and five sections. The authors found that the most influential traits were seed shape, periclinal wall sculpture, anticlinal wall undulations, and type of verruca.

Other publications address the testa ultrastructure of 88 taxa belonging to 15 sections in *A.* subg. *Melanocrommyum* was investigated by Fritsch et al. (2006). Yusupov et al. (2022) studied 95 worldwide species belonging to 14 subgenera and 58 sections. The latter reported that the description of the periclinal wall shape and the anticlinal wall curvature could indicate the evolutionary state of a species. A new technique called unsupervised machine learning was implemented to analyze the seed coat patterns of approximately 100 species of *Allium* that have been previously described (Ariunzaya et al. 2022). The authors classified the studied taxa according to their anticlinal wall pattern: irregularly curved, irregularly curved to nearly straight, straight, S-type, U-type, U- to Ω-type, and Ω-type. The periclinal walls were also divided into five types: granule, small verrucae, large verrucae, marginal verrucae, and verrucate verrucae. Some phylogenetic studies of *Allium* correlate the morphological characteristics of seeds with the evolutionary status of each species (Choi et al. 2012, Yusupov et al. 2022).

The present study provided a detailed seed morphological description of 22 *Allium* taxa – using stereomicroscopy and scanning electron microscopy (SEM) – to provide information on the native, endemic, and near-endemic species in Egypt and address the significance of seed traits for infrageneric classification. This work provides the first description of the seeds of 13 *Allium* taxa, including *A. artemisietorum*, *A. barthianum*, *A. blomfieldianum*, *A. crameri*, *A. desertorum*, *A. erdelii*, *A. mareoticum*, *A. papillare*, *A. roseum* subsp. *tourneuxii* Boiss., *A. sativum* L., *A. sinaiticum*, *A. spathaceum*, and *A. trifoliatum*. Additionally, this study reports for the first time a comparative investigation of dorsal seed surface traits against ventral traits, revealing conspicuous differences for most species and highlighting the most informative diagnostic seed traits for distinguishing taxa.

Material and methods

Plant material

Twenty-two *Allium* species were investigated using fresh or dried materials from their mature seeds. The voucher specimens were deposited in two herbaria: the Cairo University Herbarium (CAI), located at the Botany Department, Faculty of Science, Cairo University, Egypt; the Agricultural Research Center Herbarium (CAIM), located at the Flora and Phytotaxonomy Research Department, Horticultural Research Institute, Cairo, Egypt; and the South Valley University Herbarium, Qena, Egypt (On-line Suppl. Tab. 1). The studied taxa were identified according to Boulos (2009). The nomenclature and synonyms used were revised according to the International Plant Names Index (IPNI 2022).

Seed macro- and micromorphology

Seeds were washed with 70% ethyl alcohol to remove dust or any attached floral parts. For the macromorphological study, the seeds were examined using an Olympus stereomicroscope supported with a 1 cm ocular micrometer and photographed to measure the following seed size parameters: length, width, length/width (L/W) ratio, area, and seed shape.

The dorsal and ventral sides of the seeds were mounted on a copper stub with double-sided tape for micromorphology. The samples were then gold-coated in a fine-coat JEOL JFC-1100E (Japan) ion sputtering device for five minutes. The seeds were investigated using a JEOL JSM-IT200 SEM (Tokyo, Japan) at the Faculty of Science, Shatebi Building, Alexandria University, Alexandria, Egypt. Thirty-seven quantitative and qualitative traits were investigated. Diagnostic quantitative characteristics were evaluated using ImageJ (1.51j8). The number of epidermal cells was counted at a magnification of 700×, equivalent to a field view area of 182.9 × 137.1 µm. The terminology used comes from Barthlott et al. (1981) and Yusupov et al. (2022).

Data analysis

The quantitative data were analyzed using Minitab Ltd. version 19.1 (64-bit). Descriptive statistics were calculated for each variable on both seed surfaces. Different comparisons were conducted using one-way analysis of variance (ANOVA). The P values were considered significant at < 0.05. A post hoc analysis of twenty-two taxa was conducted for each variable using Tukey’s test for pairwise mean comparisons. The results are represented as letters, where means that do not share similar letters are significantly different. Furthermore, a post hoc analysis of the interaction between the seed dorsal and ventral surfaces was performed for each taxon via Tukey’s test for pairwise mean comparisons. A P value of a trait less than 0.05 is represented by an asterisk (*) to indicate a significant difference between the two surfaces.

A principal component analysis (PCA) was conducted based on 26 quantitative traits for the studied taxa without any predefined groups. The eigenvalues and percent variances of 21 principal components and the character loadings of the first two axes were analyzed according to the seed morphometric characteristics. In addition, a discriminant analysis was performed to indicate the most discriminant traits for separating sections of *Allium*. Multivariate analysis was performed using Past software version 4.03 (Hammer et al. 2001).

Results

The descriptive morphometric measurements of *Allium* taxa seed traits for dorsal and ventral seed surfaces are illustrated in On-line Suppl. Tab. 2. The quantitative macromorphological characteristics of the examined seeds are summarized in On-line Suppl. Tab. 3, and the micromorphological characteristics of the seed coat are exemplified in On-line Suppl. Tab. 4. The qualitative seed morphological characteristics of the studied *Allium* taxa are described in On-line Suppl. Tab. 5. The scanning electron micrographs of the investigated samples, illustrating the whole seeds and the detailed features of testa cells, are also exemplified in Figs. 1–5.

The seeds of the examined taxa were dull, shiny, or glossy black. The seed length varied from 1.54 mm (*A. blomfieldianum*) (Fig. 2: 5A, 5D) to 3.70 mm (*A. crameri*) (Fig. 2: 7A, 7D). The narrowest seeds (0.88 mm) were observed in *A. artemisietorum* (Fig. 1: 2A, 2D), and the widest seeds (2.55 mm) were observed in *A. cepa* (Fig. 2: 6A, 6D).

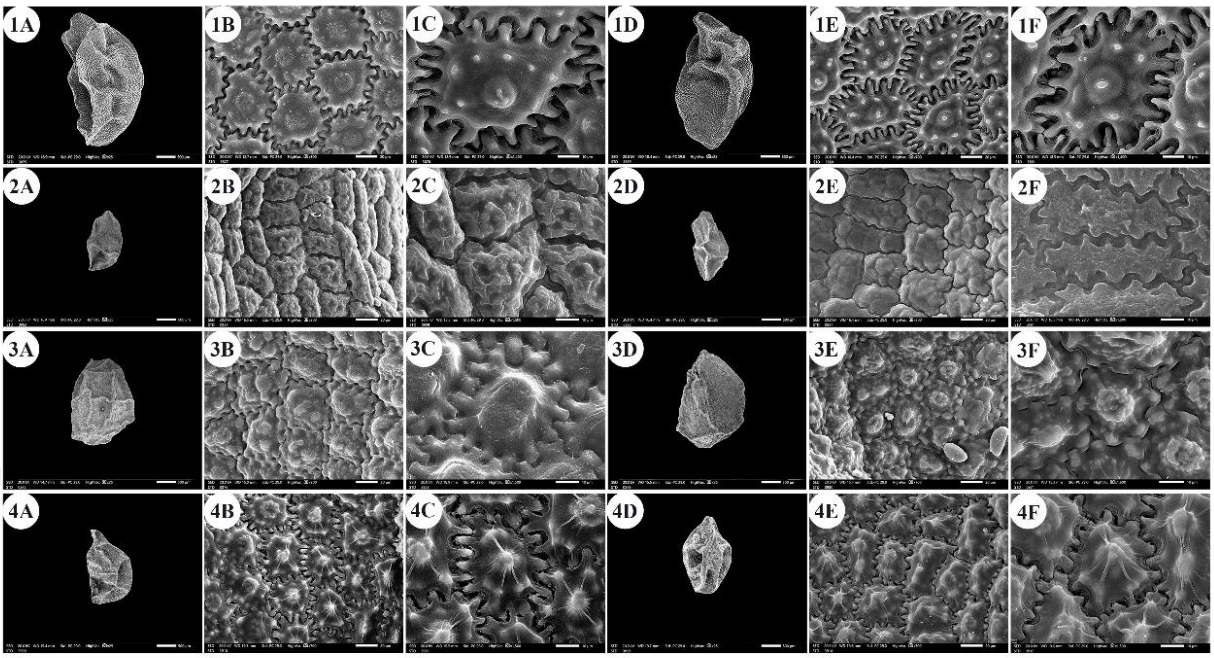

Fig. 1. A–F: scanning electron micrographs of *Allium* seeds. A–C: dorsal surface, D–F: ventral surface. 1 – *A. ampeloprasum*, 2 – *A. artemisietorum*, 3 – *A. aschersonianum*, 4 – *A. barthianum*. Scale bars: A, D = 500 μm; B, E = 20 μm; C, F = 10 μm.

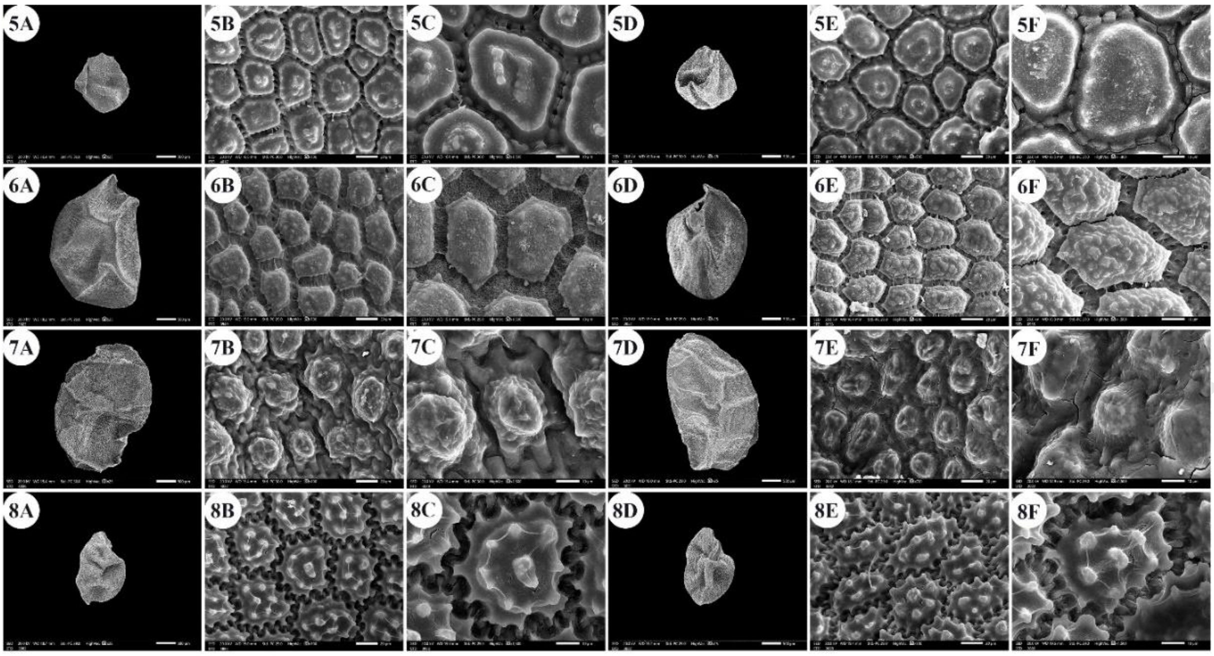

Fig. 2. A–F: scanning electron micrographs of *Allium* seeds. A–C: dorsal surface, D–F: ventral surface. 5 – *A. blomfieldianum*, 6 – *A. cepa*, 7 – *A. crameri*, 8 – *A. curtum*. Scale bars: A, D = 500 µm; B, E = 20 µm; C, F = 10 µm.

The seed length/width ratio ranged from 1.01 in *A. blomfieldianum* to 2.40 in *A. sinaiticum* (Fig. 5: 19A, 19D). The smallest seed area (1.045 mm^2) was recorded for *A. artemisietorum*, and the highest (7.148 mm^2) was recorded for *A. crameri* (On-line Suppl. Tab. 3). The seeds were widely elliptical, elliptical, widely ovate, ovate, while some taxa had mixed shapes, widely elliptical and elliptical (On-line Suppl. Tab. 5).

The number of epidermal cells per unit area ranged from 12 to 48 cells in *A. neapolitanum* Cirillo and *A. pallens* L. (Fig. 4: 13E, 14B). Notably, the epidermal cell count at the dorsal surface was greater than that at the ventral surface (On-line Suppl. Tab. 2). The minimum epidermal cell length was recorded for *A. spathaceum* (18.54 µm) (Fig. 5: 20E, 20F), and the maximum length was 99.97 µm for *A. crameri* (Fig. 2: 7E, 7F). The lowest epidermal cell width was 21.22 µm in *A. desertorum* (Fig. 3: 9E, 9F), and the greatest width was 97.18 µm in *A. neapolitanum* (Fig. 4: 13B, 13C). However, the epidermal cell length/width ratio varies within species, where the cell length is sometimes greater than the cell width and sometimes otherwise. This ratio ranges from 0.31 (as in *A. spathaceum*; Fig. 5: 20E, 20F) to 2.42 (as in *A. cepa*; Fig. 2: 6B, 6C). Its area ranged from 582.90 μm^2 in *A. pallens* (Fig. 4: 13B, 13C) to 5785.0 μm^2 in *A. crameri* (Fig. 2: 7E, 7F). The epidermal cell shape varied from orbicular to widely elliptic, elliptic, oblong, or polygonal with 4 to 8 edges. The cells may be arranged in a jigsaw-like pattern or side-by-side. The epidermal cells may be close to each other with no intercellular space, as in *A. neapolitanum* and *A. spathaceum* (Fig. 4: 13B and Fig. 5: 20E, respectively), or distant where the intercellular space length may reach up to 13.45 µm, as in *A. cepa* (Fig. 2: 6B, On-line Suppl. Tab. 4).

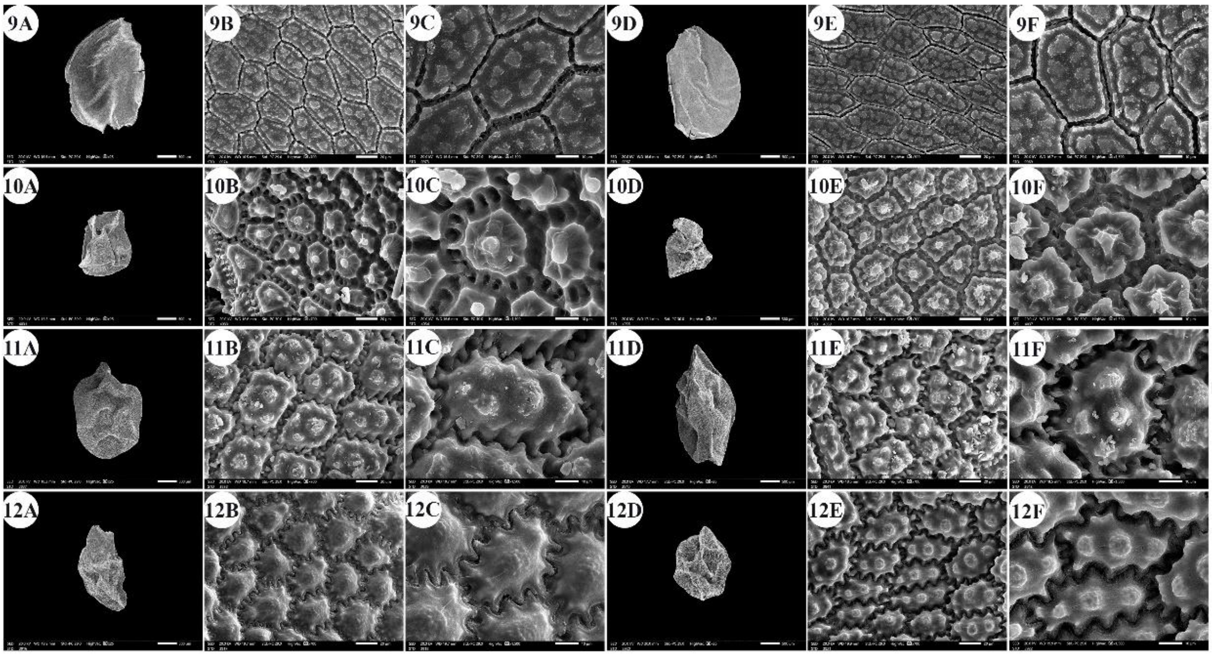

Fig. 3. A–F: scanning electron micrographs of *Allium* seeds. A–C: dorsal surface, D–F: ventral surface. 9 – *A. desertorum*, 10 – *A. erdelii*, 11 – *A. kurrat*, 12 – *A. mareoticum*. Scale bars: A, D = 500 µm; B, E = 20 µm; C, F = 10 µm.

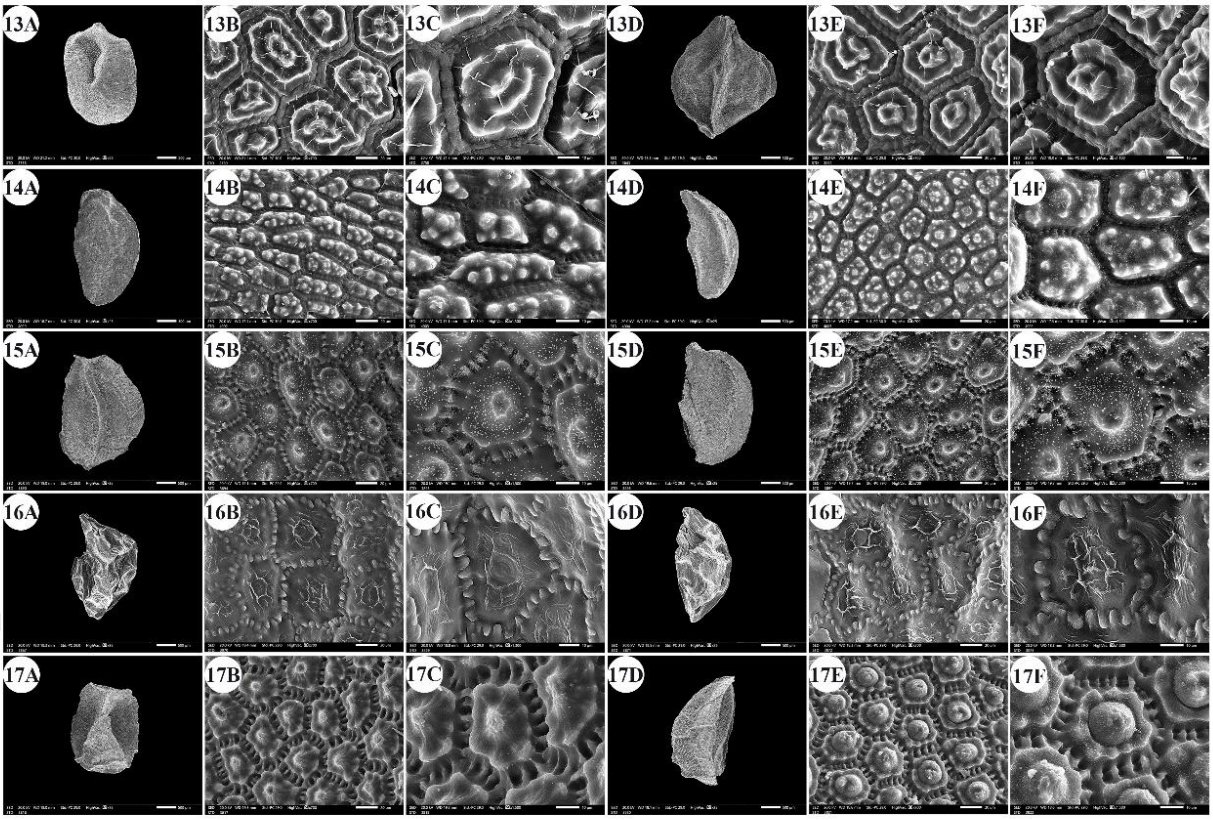

Fig. 4. A–F: scanning electron micrographs of *Allium* seeds. A–C: dorsal surface, D–F: ventral surface. 13 – *A. neapolitanum*, 14 – *A. pallens*, 15 – *A. papillare*, 16 – *A. porrum*, 17 – *A. roseum* subsp. *tourneuxii*. Scale bars: A, D = 500 µm; B, E = 20 µm; C, F = 10 µm.

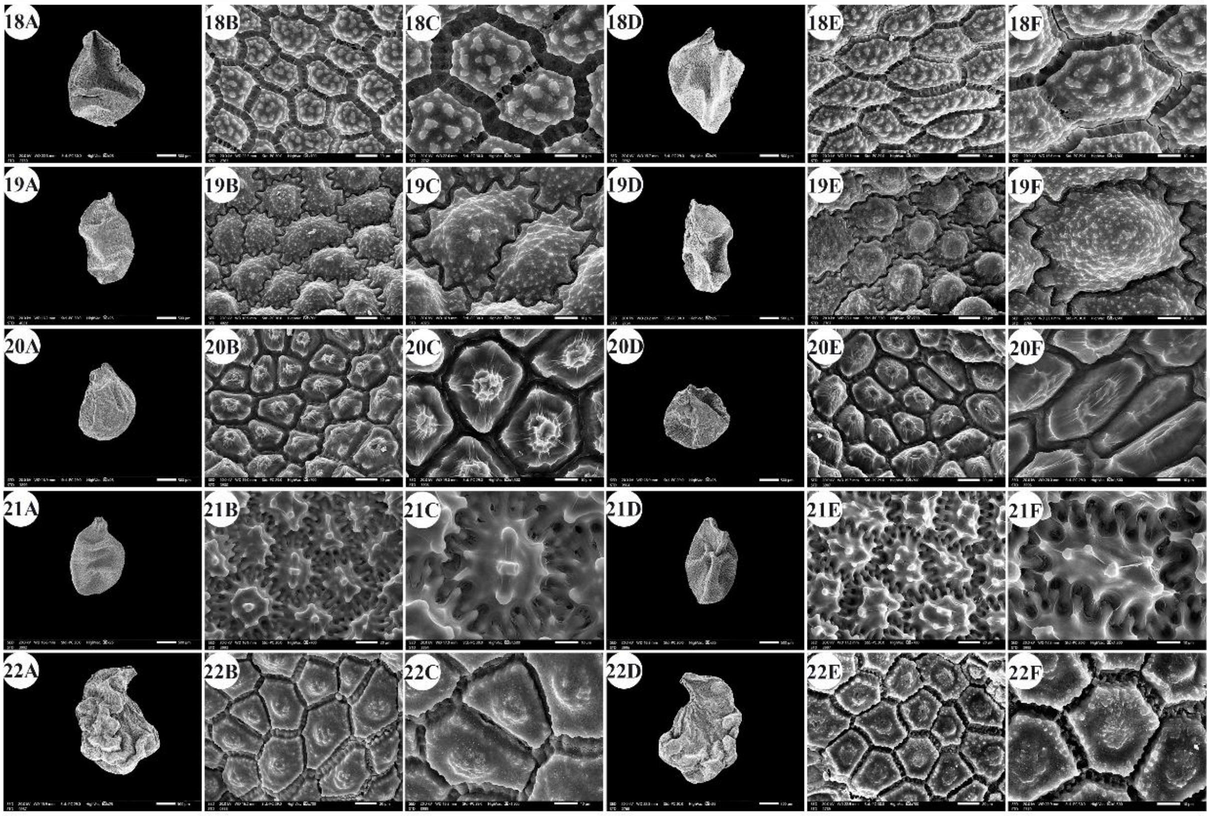

Fig. 5. A–F: scanning electron micrographs of *Allium* seeds. A–C: dorsal surface, D–F: ventral surface. 18 – *A. sativum*, 19 – *A. sinaiticum*, 20 – *A. spathaceum*, 21 – *A. sphaerocephalon*, 22 – *A. trifoliatum*. Scale bars: A, D = 500 µm; B, E = 20 µm; C, F = 10 µm.

The anticlinal wall (AW) may be straight, irregularly curved, or undulating with various forms of undulation elements, such as S-type, U-type, or Ω-type (Omega-type) (On-line Suppl. Tab. 5). The count of undulation elements per cell varied from 8 (*A. crameri*) (Fig. 2: 7B, 7C) to 33 (as in *A. pallens*; Fig. 4: 13B, 13C). The length of the undulation elements fluctuates from 1.29 µm (as in *A. artemisietorum*; Fig. 1: 2B, 2C) to 14.35 µm (as in *A. crameri*) (Fig. 2: 7B, 7C), and the width ranges from 1.99 µm (as in *A. trifoliatum*; Fig. 5: 22E, 22F) to 11.20 µm (as in *A. crameri*; Fig. 2: 7B, 7C). The L/W ratio of the undulation elements ranged from 0.40 (as in *A. spathaceum*; Fig. 5: 20B, 20C) to 2.60 (as in *A. barthianum*; Fig. 1: 4B, 4C). The distance between each of the two undulation elements varied from 0.58 µm in *A. spathaceum* (Fig. 5: 20E, 20F) to 17.58 µm in *A. crameri* (Fig. 2: 7E, 7F) (On-line Suppl. Tab. 4). The cell boundaries were channeled in most taxa or raised in *A. neapolitanum* (Fig. 4: 13C, 13F) and *A. papillare* (Fig. 4: 15C, 15F). The relief of the intercellular space or cell boundary was scabrate (*A. artemisietorum*; Fig. 1: 2C, 2F), *A. erdelii*, *A. porrum* L., *A. roseum* subsp. *tourneuxii*, *A. pallens*, *A. papillare*, *A. spathaceum*, and members of *A.* subg. *Melanocrommyum*), striate (*A. neapolitanum*; Fig. 4: 13C, 13F), reticulate with a broad mesh of connecting threads (*A. cepa*; Fig. 2: 6C, 6F, and *A. sativum*; Fig. 5: 18C, 18F), or with a narrow mesh of thin connecting threads in the remaining species. The curvature of the periclinal wall is generally convex, except for that of *A. desertorum*, which was flat (Fig. 3: 9C, 9F), and that of *A. porrum*, which was flat and concave toward the center (Fig. 4: 16C, 16F). All the studied taxa had verrucate periclinal walls, while verrucae were absent for *A. artemisietorum* (Fig. 1: 2C, 2F), *A. papillare* (Fig. 4: 15C, 15F), and *A. porrum* (Fig. 4: 16C, 16F). *Allium artemisietorum* and *A. papillare* have densely granulated periclinal walls (On-line Suppl. Tab. 5).

Data analysis

One-way ANOVA, which was utilized to test the variation between the dorsal and ventral seed surfaces, revealed a significant difference in the epidermal cell count for most taxa except *A.* subg. *Cepa* (*A. cepa*) and *A.* subg. *Melanocrommyum* (*A. aschersonianum* Barbey and *A. crameri*) showed a non-significant difference between the surfaces. The distance between two undulation elements showed non-significant variation for both surfaces of the studied taxa, except for *A. artemisietorum* and *A. roseum* subsp. *tourneuxii*. The highest number of traits showing significant differences between the two surfaces was recorded in *A. erdelii*; these traits included epidermal cell count per unit area, epidermal cell length, width, the L/W ratio, undulation element width, and the L/W ratio. In contrast, *A. cepa* demonstrated insignificant variation between the two surfaces except in the epidermal cell area (On-line Suppl. Tab. 4).

One-way ANOVA was used to assess the significant differences in the variation among taxa. For *A.* sect. *Allium*, the studied traits were significant for each pair of taxa; however, the epidermal cell L/W ratio (dorsal surface) was insignificant for all taxa. The two species of *A.* sect. *Codonoprasum* are very different in terms of the number of epidermal cells per unit area, the length of epidermal cells (dorsal surface), the number of undulation elements per cell, the width of undulation elements, and the L/W ratio of undulation elements. There were also non-significant differences in the following traits among the members of *A.* sect. *Molium*: epidermal cell length, epidermal cell width (ventral surface), epidermal cell L/W ratio, epidermal cell area (ventral surface), undulation element length, and distance between two undulation elements (ventral surface). The other traits exhibited significant variation between each pair of species. The two species comprising *A.* sect. *Melanocrommyum* were significantly different in the following traits: seed length and area, undulation element length (dorsal surface), undulation element width, undulation element L/W ratio (ventral surface), and the distance between two undulation elements (dorsal surface) (On-line Suppl. Tab. 4).

PCA explained 99.96% of the total variation in the first two components (Fig. 6, On-line Suppl. Tab. 6).

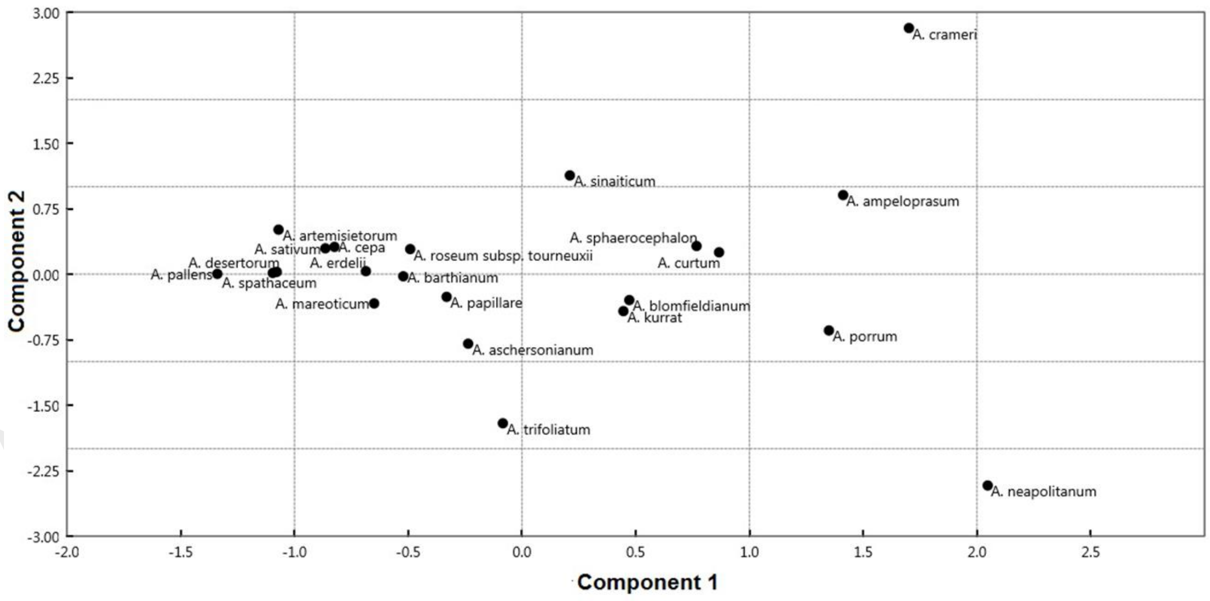

Fig. 6. Scatterplot of the first two axes from principal component analysis (PCA) of the 22 *Allium* taxa based on analyzed seed morphological traits.

The first component exhibited 87.90% of the total variation. This component separates some species of *A.* sect. *Allium* (*A. ampeloprasum*, *A. curtum* Boiss. & Gaill., *A. kurrat* Schweinf. ex

K.Krause, *A. porrum*, *A. sinaiticum*, and *A. sphaerocephalon* L.); *A. crameri* of *A.* sect. *Melanocrommym*; and *A.* sect. *Molium* (*A. blomfieldianum* and *A. neapolitanum*) in the right side from the other taxa of *A.* sect. *Allium* (*A. artemisietorum*, *A. barthianum*, *A. mareoticum*, and *A. sativum*); *A.* sect. *Briseis* (*A. spathaceum*); *A.* sect. *Cepa* (*A. cepa*); *A.* sect. *Codonoprasum* (*A. desertorum* and *A. pallens*); *A. aschersonianum* of *A.* sect. *Melanocrommym*; and *A. erdelii*, *A. papillare*, *A. roseum* subsp. *tourneuxii*; and *A. trifoliatum* of *A.* sect. *Molium*. Species on the right side were characterized by larger epidermal cell area ranging from 2013.37 to 3821.03 mm^2, whereas the left side taxa have smaller values ranging from 880.10 to 1557.04 mm^2. The contribution of the individual measured traits to the first and second components are illustrated in On-line Suppl. Tab. 7. The discriminant analysis results showed that seven sections of *Allium* were successfully identified. Twenty seed traits represent the most important variables in discriminating the studied taxa (Fig. 7A and 7B). These characteristics are used to perform an artificial key for 22 *Allium* taxa.

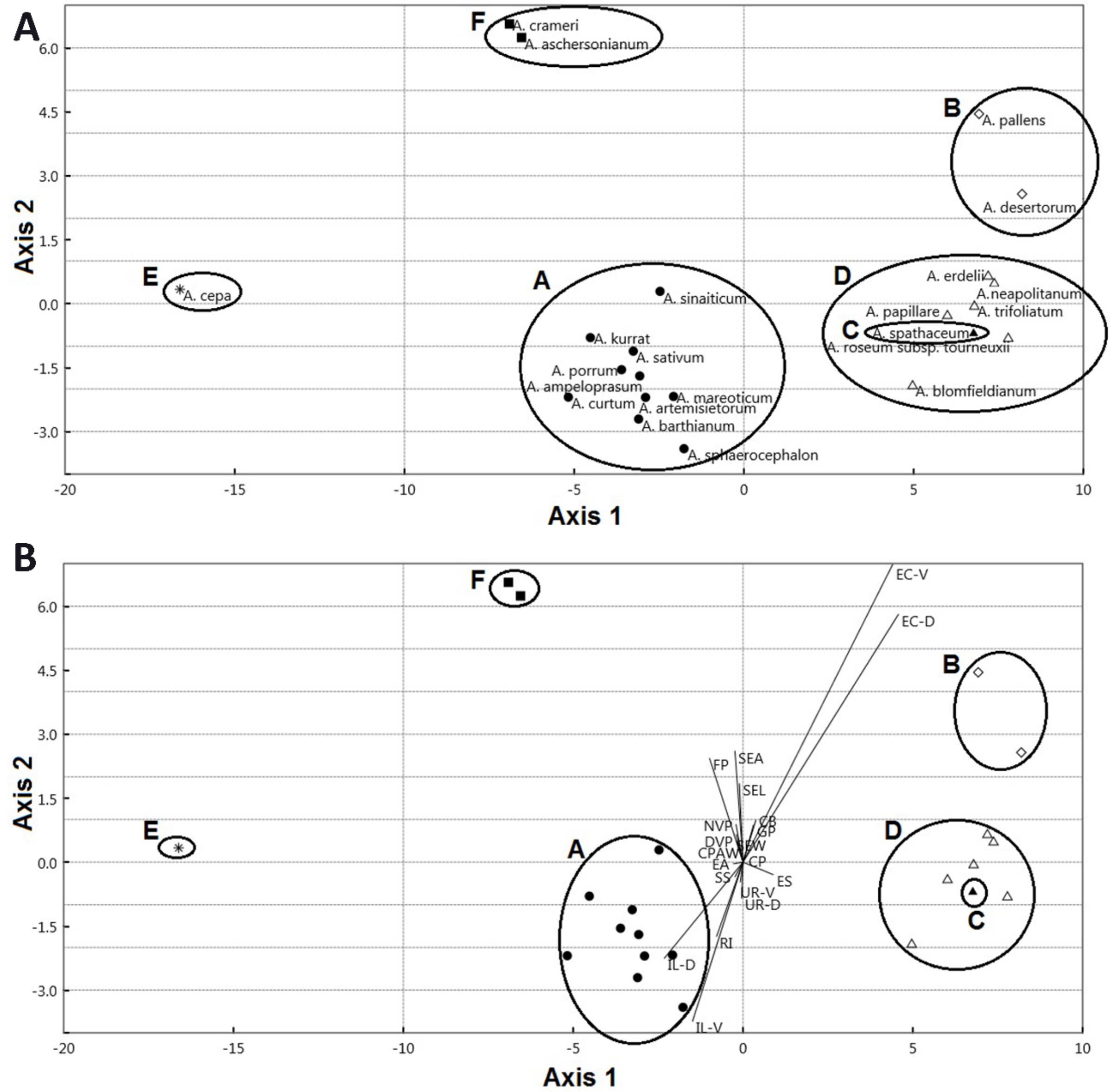

Fig. 7. Scatterplot (A) and biplot (B) of the first two axes from Discriminant Analysis for the sectional classification of *Allium*. A – *A.* sect. *Allium*, B – *A.* sect. *Codonoprasum*, C – *A.* sect.

Briseis, D – *A.* sect. *Molium*, E – *A.* sect. *Cepa*, F – *A.* sect. *Melanocrommyum*. Abbreviations: SEL – seed length, SEW – seed width, SEA – seed area, EC-D – epidermal cell count/unit area (dorsal), EC-V – epidermal cell count/unit area (ventral), IL-D – intercellular space length (dorsal), IL-V – intercellular space length (ventral), UR-D – undulation element L/W ratio (dorsal), UR-V – undulation element L/W ratio (ventral), SS – seed shape, ES – epidermal cell shape, EA – epidermal cell arrangement, CPAW – curvature pattern of the anticlinal wall, CB – cell boundary, RI – relief of intercellular space (cell boundary), CP – curvature of the periclinal wall (PW), FP – fine relief of the PW, DVP – diameter of verrucae on PW, NVP – number of verruca on PW, GP – P/A of granules on PW.

Artificial key of *Allium* taxa based on the most significant seed quantitative traits and qualitative macro- and micromorphological traits

1.a. The epidermal cell arrangement is a jigsaw-like pattern………………………………… **2**
b. The epidermal cell arrangement is a side-by-side pattern ……………..……………..…… **12**
2.a. The undulation pattern of the anticlinal wall is Ω-type ………………………………….. **3**
b. The undulation pattern of the anticlinal wall is otherwise ……...…………………...….. **5**
3.a. The seed length is 3.4–3.7 mm, and the seed area is 6.08–7.14 mm^2……..….. ***A. crameri***
b. The seed length is 1.95–2.76 mm, and the seed area is 1.81–4.81 mm^2 ……….....…... **4**
4.a. The intercellular space length is 0.23–0.93 μm, and the periclinal wall is sparsely granulated …………………………………………….....……….… ***A. aschersonianum***
b. The intercellular space length is 2.04–5.99 μm, and the periclinal wall has no granules……………………………………………………………………….….… ***A. curtum***
5.a. The undulation pattern of the anticlinal wall is S-type undulation …... ***A. artemisietorum***
b. The undulation pattern of the anticlinal wall is U-type undulation ………………….….. **6**
6.a. Polygonal epidermal cells, and the curvature of the periclinal wall is flat and centrally concave without verrucae ………………………..………………..……….... ***A. porrum***
b. Orbicular, widely elliptic, or elliptic epidermal cells, and the curvature of the periclinal wall is convex with verrucae …………………………………......……..…..………………**7**
7.a. Ovate seed shape, the seed length is 3.4–3.58 mm, the seed width is 1.99–2.3 mm, and the seed area is 4.84–5.63 mm^2 .... ***A. ampeloprasum***
b. Widely elliptic or elliptic seed shape: the seed length is 1.7–3.0 mm, the seed width is 0.88–1.83 mm, and the seed area is 1.10–3.58 mm^2 ………………………………………… **8**
8.a. The seed length is 2.49–3.0 mm, the seed width is 1.55–1.83 mm, and the seed area is 3.16–3.58 mm^2 ……………………………….…………………………………... ***A. kurrat***
b. The seed length is 1.76–2.10 mm, the seed width is 0.88–1.44 mm, and the seed area is 1.10–2.32 mm^2……………………………………………………………………..….... **9**
9.a. The epidermal cell count per unit area is 30–31 cells…………..……..... ***A. mareoticum***
b. The epidermal cell count per unit area is 17–27 cells ……………………...…...…..…… **10**
10.a. The number of periclinal wall verrucae is ≤ 15 …........................... ***A. sphaerocephalon***
b. The number of periclinal wall verrucae is > 15 ……..…………………..…..……..… **11**
11.a. The intercellular space length is 3.4–8.92 μm, and the undulation element L/W ratio is 1.1–2.60 ……………………………………..………………………... ***A. barthianum***
b. The intercellular space length is 1.24–2.05 μm, and the undulation element L/W ratio is 0.8–0.99 ……………………………………..……………………………..... ***A. sinaiticum***
12.a. The anticlinal wall is straight to irregularly curved ……….……….…….…..…… **13**
b. The anticlinal wall is undulated …………………………………………..………… **15**

13.a. The relief of the intercellular space is a narrow mesh of thin connecting threads, the epidermal cell count per unit area is 33–35 cells, the intercellular space length is 1.75–2.78 µm, and the periclinal wall is non-granulated …………………...………………… ***A. desertorum***

b. The relief of the intercellular space is reticulate with a broad mesh of connecting threads, the epidermal cell count per unit area is 21–28 cells, the intercellular space length is 5.94–13.4 µm, and the periclinal wall is granulated ………………….……………..……... **14**

14.a. The seed area is 4.2–6.09 mm^2……………………………………………….... ***A. cepa***

b. The seed area is 3.2–3.3 mm^2………...…...………………………….………… ***A. sativum***

15.a. The undulation pattern of the anticlinal wall is U-type …………….…...………… **16**

b. The undulation pattern of the anticlinal wall is S-type …………...…...………...…… **18**

16.a. Raised cell boundary, and the periclinal wall is without verrucae ...………. ***A. papillare***

b. Channeled cell boundary, and verrucate periclinal wall ……………………………… **17**

17.a. The seed length is 1.56–1.64 mm, the seed area is 1.25–1.75 mm^2, the epidermal cell count per unit area is 32–35 cells, and the periclinal wall has one large central dome ………………………………………………………………………………….. ***A. erdelii***

b. The seed length is 2.24–2.45 mm, the seed area is 2.62–3.37 mm^2, the epidermal cell count per unit area is 23–24 cells, and the periclinal wall has one small central dome .... ***A. roseum* subsp. *tourneuxii***

18 a. The epidermal cells are close to each other (intercellular space is absent) …………..... **19**

b. The epidermal cells are distant from each other (intercellular space is present) …....... **20**

19.a. Raised striate relief of cell boundary, the seed length is 2.61–3.16 mm, seed width is 1.77–2.54 mm, seed area is 3.84–5.36 mm^2, and the epidermal cell count per unit area is 12–14 cells ……………..…. ***A. neapolitanum***

b. Channeled scabrate relief of cell boundary, the seed length is 1.84–1.99 mm, seed width is 1.42–1.48 mm, seed area is 2.08–2.15 mm^2, and the epidermal cell count per unit area is 33–34 cells ....…… ***A. spathaceum***

20.a. The seed length is 1.54–1.77 mm, and the seed area is 1.48–2.03 mm^2………………………………………………………………….. ***A. blomfieldianum***

b. The seed length is 2.56–3.16 mm, and the seed area is 2.72–4.14 mm^2……………... **21**

21.a. Ovate seed shape, the epidermal cell count per unit area is 43–44 cells, the undulation element L/W ratio is 0.72–0.95, and the periclinal wall has many small domes ……………………………………………………………………………… ***A. pallens***

b. Elliptic seed shape, the epidermal cell count per unit area is 27–28 cells, the undulation element L/W ratio is 1.23–1.47, and the periclinal wall has one small central dome ………………..…………...…… ***A. trifoliatum***

Discussion

A high degree of seed morphological diversity has been observed in the genus *Allium*, as scanning electron microscopy (SEM) can clearly illustrate the details of the seed testa (Neshati and Fritsch 2009, Bednorz et al. 2011, Celep et al. 2012, Veiskarami et al. 2018, Baasanmunkh et al. 2020, Khorasani et al. 2020, Yusupov et al. 2022). Yusupov et al. (2022) noted that Kruse (1988) reported the inter- and intraspecific variation of *Allium*, indicating that some seed testa traits are section- and species specific. Our results follow the latter seed morphological studies, indicating the most informative diagnostic traits for distinguishing *Allium* taxa at the species level. Discriminant analysis is a very informative method for evaluating the utility and importance of the studied morphological traits by determining which traits were most useful for maximizing differentiation between the studied groups (Temunović et al. 2024). These traits are summarized as seed length, width, area, and shape, epidermal cell count/unit area, intercellular space length, undulation element L/W ratio, epidermal cell shape and arrangement, curvature pattern of the anticlinal wall, cell boundary, relief of intercellular space, curvature and fine relief of the periclinal wall, diameter and number of verrucae on PW, and the presence/absence of granules on the periclinal wall.

Fritsch et al. (2006) recognized that S-like, U-like, and Ω-like are the most common anticlinal wall undulation modes and, the present study revealed the same types of undulations. A limited amount of variation in the different parts of a single seed surface was observed also by Fritsch et al. (2006); this variation was restricted to the presence or absence of granules on the periclinal wall of epidermal cells and their size. This study reported for the first time a detailed comparative investigation of the quantitative traits of dorsal and ventral seed surfaces. The variation between the dorsal and ventral seed surfaces exhibited a conspicuous difference for 19 out of 22 species in terms of epidermal cell count/unit area. Additionally, there was significant variation in undulation element width (seven species); the epidermal cell L/W ratio; the area; the count of undulation elements per cell (six species); undulation element length and the undulation element L/W ratio (five species); epidermal cell length, width, and intercellular space length (four species); and the distance between two undulation elements (two species).

Fritsch (2001) described the seed sizes of the different subgenera but reported numerous exceptions: *A.* subg. *Allium* is roughly light-grained; *A.* subg. *Melanocrommyum* is heavy-grained, whereas *A.* subg. *Amerallium* ranges from small to large-grained. In the present study, the seed size of *A.* subg. *Allium* is 1.61–3.59 × 0.89–2.30 mm, *A.* subg. *Amerallium* is 1.54–3.47 × 1.21–2.55 mm, *A.* subg. *Cepa* is 2.54–3.26 × 1.98–2.55 mm, and *A.* subg. *Melanocrommyum* is 1.95–3.70 × 1.34–2.40 mm.

Our observations revealed that the epidermal cell shape was not different in *A.* subg. *Amerallium* to that in other subgenera. This study agrees with the findings of Yusupov et al. (2022): the seeds are broad to narrowly ovoid, and the anticlinal wall undulation type is mostly straight to arched. Species of *A.* sect. *Molium*, on the other hand, are arched to the S-type. Yusupov et al. (2022) mentioned that Kruse (1988) described *A.* sect. *Molium* as having wide, depressed channel-like anticlinal walls and prominent verrucose structures on their periclinal walls. However, the present study revealed that two out of five species had raised walls: *A. neapolitanum* and *A. papillare*. Celep et al. (2012) measured the seed size of *A.* subg. *Amerallium* to be in the range of 2.5–3.90 × 1.0–1.86 mm, and the seed L/W is 2.10–2.64. Our results differ slightly for the seed minimum length, which is 1.54–3.47 × 1.21–2.54 mm, 1.01–1.99. The smallest seed length in the subgenus was detected for *A. blomfieldianum* (1.54–1.77 × 1.21–1.59 mm), and the widest seed was *A. neapolitanum* (2.61–3.16 × 1.77–2.54 mm). They also reported that Meikle (1985) performed similar measurements for *A. neapolitanum*. The latter researchers also reported that *A.* sect. *Molium* shares a polyhedral cell with a striate or rugulate intercellular region covered by many small verrucae coalescing to a marginal ledge and with mostly one verruca in the center of the periclinal wall. This finding is compatible with our description, as the relief of the cell boundary was striate in *A. neapolitanum*, scabrate in *A. erdelii* and *A. papillare*, or had a narrow mesh of thin connecting threads in *A. blomfieldianum* and *A. trifoliatum*.

According to Fritsch et al. (2006), the epidermal cells of *A.* subg. *Melanocrommyum* demonstrated less variation than the other subgenera. The latter authors reported similar results for members of *A.* sect. *Melanocrommyum* because they had anticlinal walls that were Ω-like undulations and convex periclinal walls with verrucate sculptures. Some species have agranulous periclinal walls, while others, such as *A. aschersonianum*, do not have any granules. In addition, Celep et al. (2012) revealed that periclinal walls contain several or more verrucae.

The multivariate analyses revealed that members of *A.* subg. *Allium* have a wide range of variation characterizing the subgenus. This finding is congruent with the finding of Fritsch (2001) that *A.* subg. *Allium* is the most diverse and rich subgenus of the genus *Allium*. Minor dissimilarities in epidermal cell arrangement were observed between the members. Although the seed shape and the anticlinal and periclinal walls of the members of *A.* sect. *Allium* were variously undulated, these results are consistent with those of Neshati and Fritsch (2009), Veiskarami et al. (2018), and Baasanmunkh et al. (2020). Bednorz et al. (2011) revealed the presence of unusually raised anticlinal walls in some species of *A.* sect. *Allium*. In contrast, a channeled pattern was observed for the investigated members of *A.* sect. *Allium*.

Allium ampeloprasum is a polymorphic species complex sometimes treated as a wild leek without considering any subspecies, and sometimes as a cultivated leek with subspecies or varieties (Dey and Khaled 2013, Guenaoui et al. 2013). In the present study, *A. ampleoprasum* was treated as a wild accession, while *A. kurrat* and *A. porrum* were recorded as cultivated culinary species; this follows Boulos's (2009) work on the Egyptian flora. *Allium kurrat* and *A. porrum* have not been observed naturalizing in other habitats far from their cultivation fields (Mifsud and Mifsud 2018). *Allium ampeloprasum*, *A. kurrat*, and *A. porrum* exhibited significant differences between pairs of species in terms of seed length, L/W ratio, area, epidermal cell count per unit area, intercellular space length (dorsal surface), undulation element length and width, the L/W ratio, and the distance between two undulation elements (dorsal surface). Moreover, there were non-significant differences in the following traits: seed width, epidermal cell size parameters, intercellular space length (ventral surface), count of undulation elements per cell, and distance between two undulation elements (ventral surface). The epidermal cells of the three species exhibit a jigsaw-like arrangement, and the anticlinal walls exhibit a U-type undulation mode with channeled cell boundaries. *Allium ampeloprasum* and *A. kurrat* share many characteristics, but the latter species has more verrucae (>15) on the periclinal walls. *Allium porrum* was distinguished from the other two species by its variably polygonal epidermal cells with 5 to 7 edges; the periclinal wall is peripherally flat, centrally concave, and wrinkled but lacking verrucae. The description of *A. porrum* is well matched with that of Lin and Tan (2017).

Conclusions

The present study carried out a detailed seed macro- and micromorphological investigation of 22 *Allium* taxa, including 11 species that are described for the first time; six of them are endemic species: *A. barthianum*, *A. blomfieldianum*, *A. mareoticum*, *A. trifoliatum* (Mediterranean endemic species), *A. crameri* and *A. mareoticum* (endemic to Egypt). Our results highlighted the most informative diagnostic traits for distinguishing *Allium* taxa. These traits are summarized as seed length, width, area, and shape, epidermal cell count/unit area, intercellular space length, undulation element L/W ratio, epidermal cell shape and arrangement, curvature pattern of the anticlinal wall, cell boundary, relief of intercellular space, curvature and fine relief of the periclinal wall, diameter and number of verrucae on PW, and the presence/absence of granules on the periclinal wall. The count of undulation elements per cell, the undulation element length and width, the L/W ratio, and the distance between two adjacent undulation elements were measured for the first time in this study. This study reported for the first time a detailed comparative investigation of the quantitative traits of dorsal and ventral seed surfaces. Dorsal and ventral seed surface variations exhibited conspicuous differences in most species. Multivariate analysis revealed that members of *A.* subg. *Allium* have a wide range of variation characterizing the subgenus. *Allium* subg. *Allium* is the most diverse and rich subgenus of the genus. *Allium ampleoprasum* is treated as a wild accession, while *A. kurrat* and *A. porrum* are recorded as cultivated culinary species in the Egyptian flora because they have not been observed naturalizing in other habitats far from their cultivation fields. *Allium ampeloprasum*, *A. kurrat*, and *A. porrum* exhibited significant differences between pairs of species; as a result, they are treated herein as distinct species. Additional regional studies should be conducted on the seeds of native, endemic, and near-endemic *Allium* taxa for the better understanding of the variation within the genus. Finally, *Allium* merits being subjected to integrated investigations through different approaches to resolve the taxonomic problems of the genus.

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ON-LINE SUPPLEMENTARY MATERIAL

Seed Morphological Diversity of Egyptian *Allium* L. (Amaryllidaceae) and its Taxonomic Significance

On-line Suppl. Tab. 1. List of *Allium* taxa examined in this study with voucher information.

No.	Studied taxa	Subgenus/ Section	Collector	Date of collection	Locality	Herbarium
1	*Allium ampeloprasum* L.	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	G. Maire s.n.	20/05/1907	M: Kinghi Mariut, Egypt.	CAI
			J. Hobbs 75	14/07/1989	S: Sinai, Wadi Tinya, 1750 a.s.l., Egypt.	
2	*Allium artemisietorum* Eig & Feinbrun	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	S. Eid s.n.	04/1964	S: N. Sinai, Gebel El Halal, Egypt.	CAI
3	*Allium aschersonianum* Barbey	*Allium* subg. *Melanocrommyum* Webb et Berth./ *Allium* sect. *Melanocrommyum* Webb et Berth.	El Garf s.n.	15/03/2021	M: East Mersa Matruh, Wadi Hashim, Egypt.	CAI
			El Garf s.n.	22/03/2022	M: West Mersa Matruh, Barley fields, Wadi Hashim, Egypt.	
4	*Allium barthianum* Asch. & Schweinf.	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	V. Täckholm et al s.n.	22/03/1975	M: Mersa Matruh area, Egypt.	CAI
5	*Allium blomfieldianum* Asch. & Schweinf.	*Allium* subg. *Amerallium* Traub./ *Allium* sect. *Molium* G.Don ex Koch.	V. Täckholm s.n.	22/05/1958	M: 18 km West of Mersa Matrouh to the right of Sidi Barrani Road, El Sidra, Egypt.	CAI
			El Garf s.n.	24/03/2022	M: Mersa Matruh, Wadi Halazeen, Egypt.	
6	*Allium cepa* L.	*Allium* subg. *Cepa* Radi/ *Allium* sect. *Cepa* (Mill.) Prokh.	N. El Hadidi	04/1954	N: Giza, Faculty of Agriculture, Egypt.	CAI
			R. Hamdy	01/2021	N: Fayum, Egypt.	
7	*Allium crameri* Asch. & Boiss.	*Allium* subg. *Melanocrommyum* Webb et Berth./ *Allium* sect. *Melanocrommyum* Webb et Berth.	V. Holmén	14/05/1965	N: Wadi Degla, Maadi near Great petrified forest, Egypt.	CAI
8	*Allium curtum* Boiss. & Gaill.	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	L. Boulos s.n.	27/05/1958	M: Mariut, near Burg el Arab, Abu Sir, Egypt.	CAI
			F. Hussein s.n.	1958	M: Mariut, Abu Sir, near Burg el Arab, Egypt.	
9	*Allium desertorum* Forssk.	*Allium* subg. *Allium* L./ *Allium* sect. *Codonoprasum* Rchb.	Imam s.n.	04/04/1957	De: Suez desert road, Egypt.	CAI
			J. Shabetai 106.255	05/03/1945	De: Suez desert road, Gebel Yahmum El Asmar, Egypt.	
10	*Allium erdelii* Zucc.	*Allium* subg. *Amerallium* Traub./ *Allium* sect. *Molium* G.Don ex Koch.	M. Hassib s.n.	20/03/1930	M: Mariut, Egypt.	CAI

No.	Studied taxa	Subgenus/ Section	Collector	Date of collection	Locality	Herbarium
11	*Allium kurrat* Schweinf. ex K.Krause	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	El-Garf s.n.	04/1995	M:Cultivated field, Burg El Arab, Egypt.	CAI
			N. El Hadidi s.n.	04/1953	N: Giza, Faculty of Agriculture farm, Egypt.	
12	*Allium mareoticum* Bornm. & Gauba	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	M. Drar s.n.	01/04/1940	M: Northwest Coast, El Hammam, El Omayid, in Sand, Egypt.	CAIM
13	*Allium neapolitanum* Cirillo	*Allium* subg. *Amerallium* Traub./ *Allium* sect. *Molium* G.Don ex Koch.	Salah Eid s.n.	Spring, 1980	M: El-Sallum, Egypt.	CAI
			L. Boulos s.n.	11/03/1968	Wadi Maboul, Gebl Akhdar, Libya.	
14	*Allium pallens* L.	*Allium* subg. *Allium* L./ *Allium* sect. *Codonoprasum* Rchb.	V. Täckholm s.n.	30/05/1962	M: Mariut, Abu Sir, in sandy dunes, Egypt.	CAI
15	*Allium papillare* Boiss.	*Allium* subg. *Amerallium* Traub./ *Allium* sect. *Molium* G.Don ex Koch.	G. Täckholm s.n.	22/03/1928	S: Sinai, Rafah, near the Station, Egypt.	CAI
16	*Allium porrum* L.	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	N. El Hadidi s.n.	04/1953	N: Giza, Faculty of Agriculture farm, Egypt.	CAI
17	*Allium roseum* subsp. *tourneuxii* Boiss.	*Allium* subg. *Amerallium* Traub./ *Allium* sect. *Molium* G.Don ex Koch.	V. Täckholm s.n.	22/05/1958	M: 18 km West of Mersa Matrouh to the right of Sidi Barrani Road, Elsidra, Egypt.	CAI
			Merxmüller et al. s.n.	03/08/1978	M: Burg El-Arab, El-Omaid, Egypt.	
			Adel El-Gazzar et al. s.n.	24/03/1977	M: Burg El Arab, Egypt.	
			A.K. Osman s.n.	15/03/2022	M: El-Sallum, Egypt.	South Valley University Herbarium, Qena
18	*Allium sativum* L.	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	J.D.C. Pfund	6/1875	Kordofan "Bara", Sudan.	CAI
19	*Allium sinaiticum* Boiss.	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	S. Eid s.n.	04/1965	Wadi el Hommur at El-Ramla Plain, near Abu Zenema, Egypt.	CAIM
20	*Allium spathaceum* Steud. ex A.Rich.	*Allium* subg. *Amerallium* Traub./ *Allium* sect. *Briseis* (Salisb.) Stearn.	M. Drar	06/03/1938	Erkwit, Gebel Sila, Sudan.	CAI
21	*Allium sphaerocephalon* L.	*Allium* subg. *Allium* L./ *Allium* sect. *Allium* L.	V. Täckholm, L. Boulos, Ibrahim, Mahdi s.n.	01/06/1964	Along the Road of Burg El-Arab to El Alamein, Egypt.	CAI
22	*Allium trifoliatum* Cirillo	*Allium* subg. *Amerallium* Traub./ *Allium* sect. *Molium* G.Don ex Koch.	Maire s.n.	15/03/1908	M: El-Amriya, Egypt.	CAI

On-line Suppl. Tab. 2. Descriptive quantitative data of *Allium* taxa seed morphometry.

	Variable	Mean ± SD	SE Mean	Minimum	Q1	Median	Q3	Maximum	IQR
	Seed length (mm)	2.5358 ± 0.5938	0.069	1.54	2.0097	2.5355	3.0135	3.7	1.0038
	Seed width (mm)	1.6843 ± 0.4275	0.0497	0.89	1.3345	1.6355	2.0457	2.55	0.7112
	Seed L/W ratio	1.5342 ± 0.2577	0.03	1.017	1.343	1.5062	1.6763	2.41	0.3333
	Seed area (mm^2)	3.257 ± 1.493	0.172	1.045	1.872	3.169	4.4	7.15	2.528
Dorsal surface	Epidermal cell count/unit area	26.667±7.715	0.95	14	20	27	31	48	11
	Epidermal cell length (µm)	47.53±14.56	1.69	19.2	37.43	47.72	55.07	83.88	17.64
	Epidermal cell width (µm)	46.63±15.4	1.79	23.23	35.68	43.9	54.23	97.18	18.55
	Epidermal cell L/W ratio	1.0423±0.3735	0.0434	0.4471	0.7601	0.9988	1.2669	2.4213	0.5067
	Epidermal cell area ($µm^2$)	1663.8±841	98.4	582.9	993.5	1418.1	2115.6	4753.4	1122
	Intercellular space length (µm)	4.105±3.352	0.392	0	1.771	3.06	6.022	13.448	4.252
	Count of undulation elements/cell (if present)	18.397±6.516	0.856	8	13.75	16.5	23.25	33	9.5
	Undulation element length (µm) (if present)	6.092±3.107	0.408	1.296	3.898	5.425	8.207	14.351	4.31
	Undulation element width (µm) (if present)	5.13±1.994	0.262	2.115	3.695	4.785	6.195	11.197	2.501
	Undulation element L/W ratio (if present)	1.2091±0.50	0.0656	0.4005	0.8596	1.224	1.4916	2.6003	0.632
	Distance between two undulation elements (µm) (if present)	5.141±2.832	0.372	0.991	2.444	4.894	7.295	11.648	4.851
Ventral surface	Epidermal cell count/unit area	24.106±7.052	0.868	12	20	23	28	43	8
	Epidermal cell length (µm)	47.89±14.53	1.74	18.55	36.3	44.75	56.52	99.98	20.22
	Epidermal cell width (µm)	50.53±15.7	1.88	21.22	38.95	47.01	64.19	90.38	25.24
	Epidermal cell L/W ratio	0.9652±0.339	0.0405	0.314	0.7448	0.8984	1.2079	1.8507	0.463
	Epidermal cell area ($µm^2$)	1794±889	106	856	1131	1561	2203	5785	1071
	Intercellular space length (µm)	3.477±2.686	0.321	0	1.532	2.859	5.047	11.378	3.516
	Count of undulation elements/cell (if present)	17.552±5.685	0.747	10	13	16.5	21.25	32	8.25
	Undulation element length (µm) (if present)	5.887±2.781	0.365	2.017	3.384	5.099	7.975	12.701	4.591
	Undulation element width (µm) (if present)	5.278±1.721	0.226	1.993	4.169	5.091	6.626	9.095	2.457
	Undulation element L/W ratio (if present)	1.1415±0.4547	0.0597	0.519	0.7479	1.1497	1.3983	2.5881	0.6504
	Distance between two undulation elements (µm) (if present)	5.738±3.155	0.414	0.586	3.052	5.916	7.872	17.583	4.82

On-line Suppl. Tab. 3. Quantitative seed macromorphological traits of the studied *Allium* taxa. Grouping information was obtained using Tukey pairwise comparisons at 95% confidence.

No	Studied taxa	Seed length (mm)		Seed width (mm)		Seed L/W ratio		Seed area (mm^2)	
		Min−Max	**Mean±SD**	**Min−Max**	**Mean±SD**	**Min−Max**	**Mean±SD**	**Min−Max**	**Mean±SD**
1	*A. ampeloprasum* L.	3.40−3.58	3.50±0.08^{AB}	1.99−2.30	2.14±0.12^{ABC}	1.55−1.73	1.63±0.07^{ABC}	4.84−5.63	5.10±0.36^{AB}
2	*A. artemisietorum* Eig & Feinbrun	1.61−2.00	1.80±0.19^{JKL}	0.89−0.91	0.90±0.01^{J}	1.75−2.24	1.98±0.24^{A}	1.04−1.13	1.07±0.04^{I}
3	*A. aschersonianum* Barbey	1.95−2.76	2.37±0.34^{EFGHI}	1.33−2.40	1.77±0.38^{BCDEFG}	1.15−1.46	1.35±0.11^{BCDE}	1.86−4.87	3.41±1.12^{CD}
4	*A. barthianum* Asch. & Schweinf.	1.76−2.10	1.94±0.13^{IJKL}	1.03−1.27	1.17±0.11^{IJ}	1.57−1.73	1.66±0.06^{ABC}	1.22−1.87	1.61±0.27^{I}
5	*A. blomfieldianum* Asch. &	1.54−1.77	1.64±0.11^{KL}	1.21−1.59	1.45±0.21^{EFGHI}	1.01−1.27	1.14±0.12^{E}	1.48−2.03	1.78±0.28^{GHI}
6	*A. cepa* L. (Giza 20)	2.54−3.26	2.91±0.27^{C}	1.97−2.55	2.25±0.21^{A}	1.07−1.43	1.30±0.12^{DE}	4.20−6.09	4.98±0.72^{AB}
7	*A. crameri* Asch. & Boiss.	3.41−3.70	3.59±0.15^{A}	2.2−2.38	2.26±0.10^{AB}	1.43−1.67	1.59±0.13^{ABCD}	6.08−7.14	6.50±0.56^{A}
8	*A. curtum* Boiss. & Gaill.	1.97−2.02	2.00±0.02^{IJKL}	1.28−1.32	1.29±0.02^{HI}	1.52−1.58	1.54±0.03^{ABCD}	1.81−1.86	1.83±0.02^{FGHI}
9	*A. desertorum* Forssk.	2.68−3.17	2.94±0.24^{ABCD}	1.81−2.13	2.00±0.16^{ABCDE}	1.44−1.48	1.47±0.02^{ABCDE}	4.14−5.02	4.62±0.44^{ABC}
10	*A. erdelii* Zucc.	1.56−1.64	1.60±0.04^{L}	1.20−1.29	1.24±0.04^{HIJ}	1.27−1.31	1.29±0.01^{A}	1.25−1.75	1.57±0.27^{I}
11	*A. kurrat* Schweinf. ex K.Krause	2.49−3.0	2.68±0.32^{CDEFGH}	1.55−1.83	1.70±0.14^{ABCDEFGH}	1.35−1.96	1.58±0.32^{CDE}	3.16−3.58	3.33±0.22^{CDE}
12	*A. mareoticum* Bornm. & Gauba	1.90−2.39	2.12±0.24^{HIJKL}	1.20−1.44	1.33±0.12^{GHI}	1.31−1.98	1.60±0.33^{ABCD}	1.67−2.05	1.88±0.19^{EFGHI}
13	*A. neapolitanum* Cirillo	2.61−3.16	2.84±0.28^{CDEF}	1.77−2.54	2.11±0.39^{ABC}	1.24−1.47	1.35±0.11^{ABCD}	3.84−5.36	4.52±0.76^{ABC}
14	*A. pallens* L.	2.56−3.00	2.80±0.22^{CDEF}	1.47−1.70	1.58±0.11^{CDEFGHI}	1.63−1.93	1.77±0.15^{BCDE}	2.72−3.85	3.15±0.60^{CDEFG}
15	*A. papillare* Boiss.	3.07−3.47	3.25±0.20^{ABC}	1.74−2.04	1.89±0.14^{ABCDEF}	1.50−1.99	1.72±0.24^{AB}	4.55−4.90	4.68±0.19^{ABC}
16	*A. porrum* L.	2.73−2.96	2.87±0.12^{BCDE}	1.45−1.79	1.63±0.17^{BCDEFGH}	1.64−2.03	1.78±0.22^{ABC}	3.00−3.69	3.24±0.38^{CDEF}
17	*A. roseum* subsp. *tourneuxii* Boiss.	2.24−2.45	2.33±0.10^{DEFGHIJ}	1.46−1.74	1.58±0.14^{CDEFGHI}	1.28−1.67	1.48±0.19^{AB}	2.62−3.37	3±0.37^{CDEFGH}
18	*A. sativum* L.	2.73−2.76	2.74±0.01^{CDEFG}	2−2.1	2.03±0.05^{ABCD}	1.31−1.37	1.35±0.03^{ABCDE}	3.2−3.3	3.26±0.05^{CDEF}
19	*A. sinaiticum* Boiss.	2.13−2.38	2.22±0.13^{FGHIJ}	0.88−1.34	1.14±0.23^{IJ}	1.77−2.40	1.99±0.36^{BCDE}	1.10−2.32	1.71±0.60^{HI}
20	*A. spathaceum* Steud. ex A.Rich.	1.84−1.99	1.91±0.07^{IJKL}	1.42−1.48	1.45±0.03^{DEFGHI}	1.23−1.39	1.31±0.07^{BCDE}	2.08−2.15	2.11±0.03^{DEFGHI}
21	*A. sphaerocephalon* L.	2.10−2.25	2.16±0.07^{GHIJK}	1.33−1.39	1.36±0.03^{FGHI}	1.50−1.69	1.59±0.09^{ABCD}	2.03−2.17	2.10±0.07^{DEFGHI}
22	*A. trifoliatum* Cirillo	3.10−3.16	3.13±0.03^{ABC}	2−2.09	2.05±0.04^{ABC}	1.51−1.55	1.52±0.02^{ABCD}	4.12−4.14	4.13±0.01^{BC}

Means that do not share a letter are significantly different.

On-line Suppl. Tab. 4. Quantitative seed micromorphological traits of the studied *Allium* taxa. Grouping information was obtained using Tukey pairwise comparisons at 95% confidence.

No	Studied taxa	Epidermal cell count/unit area				Epidermal cell length (µm)				Epidermal cell width (µm)			
		Dorsal		Ventral		Dorsal		Ventral		Dorsal		Ventral	
		Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD
1	*A. ampeloprasum* L.	17−17	17±0^{MN*}	14−14	14±0^{M*}	41.58−58.83	50.53±8.63^{ABC}	57.49−65.96	62.76±4.59^{ABC}	80.13−84.03	81.94±1.96^{A}	69.98−82.56	77.08±6.44^{AB}
2	*A. artemisietorum* Eig & Feinbrun	37−37	37±0^{B*}	28−28	28±0^{DE*}	23.70−30.79	26.93±3.58^{DE}	27.34−36.36	31.77±4.51^{DE}	34.24−37.88	36.51±1.98^{CDEF}	39.52−64.48	50.40±12.7^{ABCDEF}
3	*A. aschersonianum* Barbey	21−22	21.6±0.57^{J}	20−21	20.6±0.57^{IJ}	41.99−54.43	46.57±5.42^{ABC}	33.04−61.67	45.81±12.8^{ABCDE}	46.21−58.87	52.10±5.49^{ABCDE*}	38.42−47.69	42.46±3.85^{CDEFG*}
4	*A. barthianum* Asch. & Schweinf.	27−27	27±0^{G*}	26−26	26±0^{EF*}	44.21−52.82	48.58±4.30^{ABC}	42.70−61.44	49.96±10.0^{ABCDE}	38.28−47.92	43.43±4.84^{BCDEF}	38.08−52.81	43.49±8.10^{CDEFG}
5	*A. blomfieldianum* Asch. & Schweinf.	27−27	27±0^{G*}	22−22	22±0^{HI*}	43.71−67.59	54.20±12.2^{AB}	42.87−56.17	51.43±7.42^{ABCD}	44.73−55.08	51.33±5.72^{ABCDE}	39.56−66.20	53.28±13.3^{ABCDEF}
6	*A. cepa* L. (Giza 20)	26−28	27±1^{G}	21−26	23.6±2.51^{GH}	32.27−56.23	42.69±8.48^{BCD}	39.19−56.11	49.85±7.64^{ABCD}	23.22−35.83	29.50±5.26^{F}	26.61−39.12	33.97±4.22^{FG}
7	*A. crameri* Asch. & Boiss.	20−22	21±1^{JK}	20−20	20±0^{JK}	48.61−80.98	62.11±16.8^{AB}	42.63−99.97	76.34±29.9^{A}	57.3−65.59	61.84±4.20^{ABC}	34.85−82.09	61.20±24.0^{ABCDE}
8	*A. curtum* Boiss. & Gaill.	20−20	20±0^{KL*}	19−19	19±0^{K*}	54.25−68.45	62.36±7.30^{AB}	45.60−56.19	52.08±5.68^{ABCD}	50.39−70.41	57.43±11.2^{ABCD}	72.58−90.38	79.54±9.51^{A}
9	*A. desertorum* Forssk.	35−35	35±0^{C*}	33−33	33±0^{B*}	31.71−54.67	42.77±11.4^{BCD}	33.75−59.44	47.95±13.0^{ABCDE}	23.67−27.01	25.22±1.68^{F}	21.22−32.73	26.14±5.93^{G}
10	*A. erdelii* Zucc.	35−35	35±0^{C*}	32−32	32±0^{BC*}	40.46−50.56	45.17±5.08^{ABCD*}	33.46−37.90	35.82±2.22^{BCDE*}	31.98−42.18	36.15±5.34^{DEF*}	42.65−44.32	43.51±0.83^{CDEFG*}
11	*A. kurrat* Schweinf. ex K.Krause	19−19	19±0^{LM*}	20−20	20±0^{JK*}	44.16−65.73	53.43±11.1^{ABC}	46.82−58.48	52.67±5.83^{ABCD}	47.86−59.44	52.85±5.95^{ABCDE}	46.90−60.28	52.76±6.83^{ABCDEF}
12	*A. mareoticum* Bornm. & Gauba	31−31	31±0^{E*}	30−30	30±0^{CD*}	47.15−52.64	49.35±2.89^{ABC*}	28.08−43.98	35.44±8.01^{CDE*}	37.79−42.76	40.07±2.51^{CDEF*}	51.12−67.82	58.55±8.50^{ABCDE*}
13	*A. neapolitanum* Cirillo	14−14	14±0^{N*}	12−12	12±0^{N*}	66.30−83.87	73.95±9.00^{A*}	37.86−57.90	46.65±10.2^{ABCDE*}	45.46−97.18	72.75±25.9^{AB}	52.77−70.55	63.03±9.20^{ABCD}
14	*A. pallens* L.	48−48	48±0^{A*}	43−43	43±0^{A*}	19.19−24.82	21.72±2.85^{E*}	32.22−37.79	35.18±2.79^{CDE*}	35.17−43.71	40.60±4.72^{BCDEF}	33.00−38.26	34.99±2.85^{EFG}
15	*A. papillare* Boiss.	27−27	27±0^{G*}	23−23	23±0^{H*}	50.09−64.62	56.09±7.58^{AB}	33.64−50.47	41.33±8.50^{ABCDE}	34.03−40.60	38.15±3.59^{CDEF}	37.73−47.11	42.02±4.74^{CDEFG}
16	*A. porrum* L.	20−20	20±0^{KL*}	17−17	17±0^{L*}	64.51−73.55	67.82±4.98^{AB}	63.06−68.71	65.26±3.02^{AB}	54.38−65.75	58.67±6.17^{ABCD}	52.31−70.62	59.19±9.96^{ABCDE}
17	*A. roseum* subsp. *tourneuxii* Boiss.	24−24	24±0^{I*}	23−23	23±0^{H*}	37.33−42.64	39.98±2.65^{BCD}	41.87−43.53	42.91±0.90^{ABCDE}	34.62−44.64	40.69±5.33^{BCDEF}	42.72−46.61	44.10±2.17^{BCDEFG}
18	*A. sativum* L.	28−28	28±0^{F*}	25−25	25±0^{FG*}	22.73−39.38	33.12±6.22^{CDE}	28.98−33.18	30.56±2.28^{DE}	27.20−51.89	39.20±8.36^{DEF*}	56.05−65.81	61.98±5.20^{ABCD*}
19	*A. sinaiticum* Boiss.	26−26	26±0^{H*}	22−22	22±0^{HI*}	37.45−54.01	47.31±8.72^{ABCD}	54.17−72.98	65.60±10.0^{AB}	37.50−73.66	53.25±18.5^{ABCDE}	39.43−62.66	50.21±11.7^{ABCDEF}
20	*A. spathaceum* Steud. ex A.Rich.	34−34	34±0^{D*}	33−33	33±0^{B*}	27.75−40.62	31.81±6.01^{CDE}	18.54−35.46	28.21±8.71^{E}	25.48−42.83	34.76±7.99^{EF}	32.60−59.05	45.93±13.2^{BCDEFG}
21	*A. sphaerocephalon* L.	20−20	20±0^{KL*}	17−17	17±0^{L*}	54.65−58.45	55.93±2.18^{AB}	54.19−68.19	60.66±7.05^{ABC}	49.44−71.21	57.80±11.7^{ABCD}	57.16−75.37	68.98±10.2^{ABC}
22	*A. trifoliatum* Cirillo	28−28	28±0^{F*}	27−27	27±0^{E*}	34.92−76.19	57.85±21.0^{AB}	43.36−45.30	44.07±1.06^{ABCDE}	42.15−57.19	48.28±7.89^{ABCDE}	30.83−43.61	37.94±6.51^{DEFG}

Means that do not share a letter are significantly different.

Asterisks (*) indicate a significant difference between the seed's dorsal and ventral surfaces.

On-line Suppl. Tab. 4. Continued

No	Studied taxa	Epidermal cell L/W ratio				Epidermal cell area (µm^2)				Intercellular space length (µm)			
		Dorsal		Ventral		Dorsal		Ventral		Dorsal		Ventral	
		Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD
1	*A. ampeloprasum* L.	0.51−0.70	0.61±0.09^{BC*}	0.79−0.82	0.81±0.01^{ABCD*}	2292.36−2978.83	2574.16±359.34^{ABC}	2652.27−3459.98	3071.51±404.73^{A}	5.61−7.28	6.31±0.86^{BCD}	4.75−6.00	5.31±0.63^{ABCD}
2	*A. artemisietorum* Eig & Feinbrun	0.63−0.89	0.74±0.13^{ABC}	0.42−0.80	0.66±0.20^{BCD}	715.773−853.892	766.861±75.750^{HI*}	999.605−1339.14	1213.60±186.25^{BCDE*}	2.68−3.85	3.25±0.58^{DEFG}	2.01−3.20	2.76±0.64^{CDEF}
3	*A. aschersonianum* Barbey	0.76−1.10	0.90±0.14^{ABC}	0.79−1.60	1.09±0.35^{ABCD}	1364.09−2042.23	1748.84±281.83^{CDEF}	1042.20−1844.65	1426.81±404.46^{ABCDE}	0.46−3.06	2.08±1.15^{FG*}	0.23−0.93	0.44±0.33^{F*}
4	*A. barthianum* Asch. & Schweinf.	1.00−1.27	1.12±0.13^{ABC}	0.86−1.55	1.17±0.34^{ABC}	1146.03−1619.37	1327.97±254.94^{DEFGH}	1057.37−1679.20	1446.65±339.24^{ABCDE}	7.14−8.92	8.04±0.88^{ABC}	3.42−8.29	5.58±2.47^{ABC}
5	*A. blomfieldianum* Asch. & Schweinf.	0.94−1.22	1.05±0.15^{ABC}	0.79−1.41	1.01±0.35^{ABCD}	1501.31−2852.58	2164.09±676.00^{BCDE}	1765.26−2626.42	2067.81±484.32^{ABCD}	0.76−2.06	1.26±0.69^{FG*}	2.38−2.93	2.59±0.29^{CDEF*}
6	*A. cepa* L. (Giza 20)	1.07−2.42	1.50±0.51^{A}	1.21−1.60	1.46±0.14^{A}	893.825−1108.49	1007.69±77.295^{GHI*}	918.541−1652.13	1329.95±285.95^{BCDE*}	6.45−13.45	9.59±2.58^{AB}	5.94−11.3	8.44±2.30^{A}
7	*A. crameri* Asch. & Boiss.	0.74−1.29	1.00±0.27^{ABC}	1.21−1.29	1.24±0.04^{ABC}	1900.39−2924.80	2298.81±548.81^{ABCD}	978.15−5785.03	3821.03±2521.0^{AB}	2.00−4.95	3.38±1.48^{DEFG}	0.76−2.50	1.56±0.87^{EF}
8	*A. curtum* Boiss. & Gaill.	0.77−1.35	1.12±0.31^{ABC*}	0.60−0.75	0.65±0.08^{BCD*}	2321.16−2328.42	2325.30±3.7362^{ABC}	2113.55−2915.24	2500.94±401.52^{AB}	3.74−5.99	5.02±1.16^{CDEF}	2.04−4.28	2.90±1.20^{CDEF}
9	*A. desertorum* Forssk.	0.45−0.85	0.62±0.20^{BC}	0.35−0.96	0.60±0.32^{CD}	706.027−1122.86	887.037±213.75^{HI}	1001.32−1126.04	1070.02±63.315^{CDE}	2.17−2.56	2.41±0.21^{EFG}	1.75−2.78	2.16±0.54^{CDEF}
10	*A. erdelii* Zucc.	1.05−1.47	1.26±0.20^{ABC*}	0.76−0.88	0.82±0.06^{ABCD*}	930.399−1428.32	1186.32±249.25^{FGHI}	1174.90−1455.78	1348.11±151.46^{ABCDE}	1.91−5.53	3.65±1.81^{DEFG}	2.12−4.31	3.49±1.19^{CDEF}
11	*A. kurrat* Schweinf. ex K.Krause	0.92−1.10	1.00±0.09^{ABC}	0.77−1.24	1.01±0.23^{ABCD}	1709.61−2759.91	2177.03±534.0^{BCDE}	1996.53−2045.97	2013.37±28.2^{ABCD}	2.07−4.89	3.37±1.42^{DEFG}	3.21−7.24	5.09±2.03^{BCDE}
12	*A. mareoticum* Bornm. & Gauba	1.12−1.32	1.23±0.09^{ABC*}	0.49−0.67	0.60±0.09^{CD*}	1157.11−1567.37	1310.40±223.91^{DEFGH}	1025.55−1630.47	1267.88±319.88^{BCDE}	1.30−2.49	1.83±0.60^{FG}	0.94−1.79	1.43±0.44^{EF}
13	*A. neapolitanum* Cirillo	0.68−1.84	1.15±0.60^{ABC}	0.62−0.88	0.74±0.12^{BCD}	3062.23−4753.42	3930.24±846.48^{A}	1800.90−3298.44	2570.01±749.59^{AB}	0−0	0±0^{G}	0−0	0±0^{F}
14	*A. pallens* L.	0.44−0.60	0.53±0.08^{C*}	0.84−1.14	1.01±0.15^{ABCD*}	582.905−769.823	691.625±97.125^{I*}	856.108−903.21	880.095±23.563^{E*}	1.56−1.99	1.70±0.24^{FG}	1.31−2.39	1.83±0.54^{DEF}
15	*A. papillare* Boiss.	1.23−1.62	1.47±0.21^{AB}	0.71−1.22	0.99±0.26^{ABCD}	1375.89−1698.98	1535.98±161.56^{CDEFG}	1327.67−1857.98	1513.82±298.37^{ABCDE}	3.18−4.62	4.02±0.74^{DEF}	4.16−5.12	4.73±0.50^{BCDE}
16	*A. porrum* L.	0.99−1.35	1.16±0.17^{ABC}	0.97−1.20	1.11±0.12^{ABCD}	2621.64−3294.19	2930.50±339.61^{AB}	2315.49−2889.17	2585.38±288.33^{AB}	0.53−2.02	1.46±0.81^{FG}	1.42−2.13	1.84±0.37^{DEF}
17	*A. roseum* subsp. *tourneuxii* Boiss.	0.83−1.23	1.00±0.20^{ABC}	0.93−1.00	0.97±0.03^{ABCD}	1153.17−1343.74	1270.43±102.0^{EFGH*}	1505.43−1631.02	1557.03±65.7^{ABCDE*}	4.37−7.17	5.76±1.40^{CDE}	4.10−5.10	4.72±0.54^{BCDE}
18	*A. sativum* L.	0.51−1.44	0.89±0.33^{ABC*}	0.44−0.52	0.49±0.04^{D*}	801.207−1244.47	981.082±162.41^{GHI*}	1133.28−1437.73	1297.15±153.55^{ABCDE*}	8.97−12.2	10.2±1.19^{A*}	6.56−9.18	8.03±1.33^{AB*}
19	*A. sinaiticum* Boiss.	0.50−1.44	0.99±0.46^{ABC}	0.86−1.85	1.38±0.49^{AB}	1309.12−2045.07	1590.76±397.20^{CDEFG}	2013.68−2667.49	2291.02±337.98^{ABC}	1.28−1.63	1.41±0.18^{FG}	1.24−2.05	1.53±0.44^{EF}
20	*A. spathaceum* Steud. ex A.Rich.	0.65−1.59	0.98±0.42^{ABC}	0.31−1.09	0.69±0.38^{BCD}	701.156−978.432	876.344±152.40^{HI}	874.347−1298.99	1054.29±219.60^{DE}	0−0	0±0^{G}	0.67−1.17	0.92±0.24^{F}
21	*A. sphaerocephalon* L.	0.76−1.18	0.99±0.21^{ABC}	0.72−1.19	0.90±0.25^{ABCD}	1826.50−2959.16	2230.23±632.48^{BCDE}	2235.94−2662.92	2451.81±213.53^{AB}	1.16−3.25	2.10±1.05^{EFG*}	3.56−5.93	5.11±1.34^{BCDE*}
22	*A. trifoliatum* Cirillo	0.61−1.80	1.26±0.60^{ABC}	0.99−1.41	1.18±0.21^{ABC}	1769.19−2448.59	2103.50±339.82^{BCDE*}	1013.03−1530.22	1274.44±258.63^{BCDE*}	2.09−2.55	2.35±0.23^{EFG}	2.29−3.35	2.91±0.55^{CDEF}

Means that do not share a letter are significantly different.

Asterisks (*) indicate a significant difference between the seed's dorsal and ventral surfaces.

On-line Suppl. Tab. 4. Continued

No	Studied taxa	Count of undulation elements/cell				Undulation element length (µm)				Undulation element width (µm)			
		Dorsal		Ventral		Dorsal		Ventral		Dorsal		Ventral	
		Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD
1	*A. ampeloprasum* L.	16−18	17±1DE	17−19	18±1^{DEFG}	8.51−9.40	8.90±0.45^{BC*}	11.3−12.7	12.1±0.73^{A*}	4.06−4.42	4.24±0.18^{EFGH*}	4.78−5.21	5.00±0.21^{CDEFG*}
2	*A. artemisietorum* Eig & Feinbrun	12−14	13±1^{FG}	12−12	12±0^{JKL}	1.29−2.91	2.24±0.84^{KLM}	2.91−5.03	4.31±1.21^{EFGH}	2.11−4.53	3.60±1.30^{FGH*}	5.07−6.71	6.09±0.88^{BCDE*}
3	*A. aschersonianum* Barbey	11−13	12±0^{GH}	10−12	11±0^{L}	4.20−8.59	6.67±1.82^{CDEFG}	4.28−8.31	5.81±1.74^{CDEFG}	6.34−7.75	6.96±0.61^{B}	6.62−8.26	7.62±0.73^{AB}
4	*A. barthianum* Asch. & Schweinf.	13−14	13±0^{EFG}	12−17	14±2^{GHIJKL}	7.84−9.27	8.58±0.71^{BCD}	5.18−8.69	7.42±1.94^{BCD}	3.56−3.83	3.66±0.14^{FGH}	3.54−7.87	5.38±2.23^{CDEF}
5	*A. blomfieldianum* Asch. & Schweinf.	24−27	26±1^{BC*}	14−16	15±1^{GHIJKL*}	3.02−3.06	3.04±0.01^{IJKL}	2.94−4.57	3.65±0.83^{GH}	4.72−6.07	5.21±0.74^{BCDEF}	4.72−8.67	6.46±2.01^{ABCD}
6	*A. cepa* L. (Giza 20)	0−0	0±0^{I}	0−0	0±0^{M}	0−0	0±0^{M}	0−0	0±0^{J}	0−0	0±0^{I}	0−0	0±0^{J}
7	*A. crameri* Asch. & Boiss.	8−9	8.±0^{H*}	10−12	11±1^{KL*}	12.7−14.35	13.4±0.82^{A*}	4.62−6.45	5.59±0.91^{CDEFG*}	10.5−11.1	10.8±0.34^{A*}	3.82−5.30	4.56±0.74^{CDEFG*}
8	*A. curtum* Boiss. & Gaill.	13−14	13±0^{EFG*}	16−17	16±0^{FGHI*}	7.63−8.10	7.84±0.24^{BCDE}	6.84−9.63	8.59±1.52^{BC}	4.22−5.75	5.03±0.77^{CDEF}	5.78−6.89	6.43±0.58^{ABCD}
9	*A. desertorum* Forssk.	0−0	0±0^{I}	0−0	0±0^{M}	0−0	0±0^{M}	0−0	0±0^{IJ}	0−0	0±0^{I}	0−0	0±0^{IJ}
10	*A. erdelii* Zucc.	18−21	19±1^{D}	16−18	16±1^{FGHI}	3.48−4.74	4.05±0.63^{HIJKL}	2.95−3.43	3.19±0.23^{GH}	2.63−3.72	3.05±0.58^{GH*}	4.04−4.76	4.32±0.38^{DEFGH*}
11	*A. kurrat* Schweinf. ex K.Krause	16−20	18±2.30^{D}	15−17	16±1^{FGHIJ}	5.28−5.76	5.48±0.25^{EFGHI*}	6.93−7.67	7.28±0.37^{BCDE*}	4.73−4.84	4.79±0.05^{CDEFG}	4.52−5.26	4.96±0.39^{CDEFG}
12	*A. mareoticum* Bornm. & Gauba	13−14	13±0^{EFG}	13−13	13±0^{HIJKL}	6.33−7.85	7.27±0.82^{BCDEF}	5.66−8.75	6.80±1.69^{CDEF}	5.16−6.00	5.69±0.45^{BCDE}	4.07−6.00	5.07±0.96^{CDEFG}
13	*A. neapolitanum* Cirillo	27−33	30±3^{AB}	23−29	26±3^{ABC}	3.82−4.14	4.01±0.16^{HIJKL}	3.54−4.30	3.98±0.39^{FGH}	5.21−6.79	5.98±0.79^{BCDE*}	4.74−4.81	4.77±0.03^{CDEFG*}
14	*A. pallens* L.	32−33	32±0^{A*}	23−29	27±3^{AB*}	1.91−2.67	2.32±0.38^{JKLM}	2.01−2.80	2.41±0.39^{HIJ}	2.43−3.03	2.68±0.30^{H}	2.79−3.30	3.01±0.26^{GH}
15	*A. papillare* Boiss.	23−25	24±1^{C}	20−26	22±3^{BCD}	3.92−5.99	4.81±1.06^{FGHIJK}	4.05−5.10	4.64±0.53^{DEFGH}	2.82−4.58	3.54±0.92^{FGH}	3.42−4.35	3.97±0.48^{EFGH}
16	*A. porrum* L.	14−16	15±1^{DEFG*}	17−18	17±0^{EFGH*}	6.89−11.8	9.74±2.56^{B}	6.83−9.33	8.07±1.24^{BC}	6.68−7.69	7.02±0.57^{B}	5.38−6.82	6.15±0.72^{ABCDE}
17	*A. roseum* subsp. *tourneuxii* Boiss.	17−21	18±2.08^{D*}	22−22	22±0^{CDE*}	4.30−4.61	4.44±0.16^{GHIJKL}	3.09−4.73	4.13±0.90^{FGH}	2.42−4.19	3.46±0.92^{FGH}	2.69−4.19	3.37±0.76^{FGH}
18	*A. sativum* L.	0−0	0±0^{I}	0−0	0±0^{M}	0−0	0±0^{M}	0−0	0±0^{J}	0−0	0±0^{I}	0−0	0±0^{J}
19	*A. sinaiticum* Boiss.	13−15	13±1^{EFG}	11−13	12±1^{IJKL}	5.10−7.55	6.10±1.28^{DEFGH}	6.44−7.95	7.40±0.83^{BCDE}	5.29−7.59	6.19±1.22^{BCD*}	8.03−9.09	8.47±0.55^{A*}
20	*A. spathaceum* Steud. ex A.Rich.	17−23	19±3^{D}	20−21	20±0^{DEF}	1.40−2.07	1.83±0.37^{LM*}	2.88−3.24	3.12±0.20^{GH*}	3.50−4.99	4.42±0.80^{DEFGH}	4.43−5.25	4.97±0.46^{CDEFG}
21	*A. sphaerocephalon* L.	15−18	16±1^{DEF}	14−17	15±1F^{GHIJK}	8.52−10.4	9.74±1.06^{B}	8.10−12.2	10.3±2.07^{AB}	6.14−7.42	6.64±0.68^{BC}	6.25−6.97	6.71±0.40^{ABC}
22	*A. trifoliatum* Cirillo	26−27	26±0^{BC}	26−32	29±3^{A}	4.46−5.45	4.99±0.49^{FGHIJ*}	2.74−3.10	2.92±0.18^{GHI*}	3.44−4.16	3.73±0.37^{FGH*}	1.99−2.16	2.09±0.09^{HI*}

Means that do not share a letter are significantly different.

Asterisks (*) indicate a significant difference between the seed's dorsal and ventral surfaces.

On-line Suppl. Tab. 4. Continued

No	Studied taxa	Undulation element L/W ratio				Distance between two undulation elements (µm)			
		Dorsal		Ventral		Dorsal		Ventral	
		Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD	Min−Max	Mean±SD
1	*A. ampeloprasum* L.	2.00−2.16	2.10±0.08^{A}	2.16−2.58	2.42±0.22^{A}	8.49−10.0	9.15±0.78^{AB}	8.46−10.0	9.11±0.79^{AB}
2	*A. artemisietorum* Eig & Feinbrun	0.60−0.64	0.61±0.01^{FG}	0.57−0.76	0.69±0.10^{E}	2.44−5.14	3.38±1.52^{EFGH*}	5.98−8.92	7.31±1.48^{ABCD*}
3	*A. aschersonianum* Barbey	0.66−1.29	0.95±0.26^{CDEF}	0.51−1.10	0.77±0.25^{DE}	4.98−8.24	6.71±1.41^{BCD}	6.22−8.76	7.25±1.15^{ABCD}
4	*A. barthianum* Asch. & Schweinf.	2.18−2.60	2.34±0.22^{A*}	1.10−1.77	1.44±0.33^{B*}	7.29−8.12	7.57±0.48^{BC}	5.38−7.40	6.06±1.15^{ABCDEF}
5	*A. blomfieldianum* Asch. & Schweinf.	0.49−0.64	0.59±0.08^{FG}	0.52−0.62	0.57±0.04^{E}	2.05−2.43	2.18±0.21^{FGHI}	1.97−9.54	5.56±3.80^{BCDEF}
6	*A. cepa* L. (Giza 20)	0−0	0±0^{H}	0−0	0±0^{F}	0−0	0±0^{I}	0−0	0±0^{G}
7	*A. crameri* Asch. & Boiss.	1.13−1.31	1.23±0.08^{BCD}	1.21−1.24	1.22±0.02^{BC}	10.2−11.6	10.7±0.77^{A}	5.34−17.58	11.0±6.16^{A}
8	*A. curtum* Boiss. & Gaill.	1.32−1.84	1.58±0.26^{B}	1.18−1.40	1.32±0.12^{B}	7.58−9.35	8.43±0.88^{AB}	7.84−8.47	8.09±0.33^{ABC}
9	*A. desertorum* Forssk.	0−0	0±0^{H}	0−0	0±0^{F}	0−0	0±0^{I}	0−0	0±0^{G}
10	*A. erdelii* Zucc.	1.27−1.40	1.33±0.06^{BCD*}	0.72−0.76	0.73±0.02^{E*}	3.50−6.54	4.97±1.52^{CDEFG}	2.64−5.84	3.88±1.71^{BCDEFG}
11	*A. kurrat* Schweinf. ex K.Krause	1.10−1.21	1.14±0.06^{BCDE*}	1.31−1.60	1.47±0.14^{B*}	3.22−6.76	4.89±1.78^{CDEFG}	5.99−8.66	7.07±1.41^{ABCD}
12	*A. mareoticum* Bornm. & Gauba	1.22−1.32	1.27±0.05^{BCD}	1.16−1.45	1.33±0.15^{B}	4.83−6.09	5.26±0.71^{CDEF}	5.70−9.86	7.77±2.08^{ABCD}
13	*A. neapolitanum* Cirillo	0.61−0.78	0.67±0.09^{EFG}	0.74−0.89	0.83±0.08^{CDE}	1.45−1.69	1.57±0.12^{HI}	1.03−2.01	1.46±0.50^{EFG}
14	*A. pallens* L.	0.78−0.91	0.86±0.06^{DEFG}	0.72−0.95	0.80±0.12^{CDE}	0.99−1.68	1.29±0.35^{HI}	1.44−2.06	1.77±0.31^{EFG}
15	*A. papillare* Boiss.	1.22−1.60	1.37±0.19^{BC}	1.15−1.18	1.17±0.01^{BCD}	3.00−4.61	4.04±0.90^{DEFGH}	2.72−4.17	3.50±0.73^{CDEFG}
16	*A. porrum* L.	1.02−1.57	1.37±0.30^{BC}	1.09−1.49	1.31±0.20^{B}	5.94−7.29	6.80±0.74^{BCD}	6.35−6.65	6.47±0.15^{ABCDE}
17	*A. roseum* subsp. *tourneuxii* Boiss.	1.05−1.77	1.35±0.37^{BCD}	1.12−1.41	1.22±0.15^{BC}	4.53−4.97	4.80±0.24^{CDEFG*}	3.16−4.07	3.63±0.45^{CDEFG*}
18	*A. sativum* L.	0−0	0±0^{H}	0−0	0±0^{F}	0−0	0±0^{I}	0−0	0±0^{G}
19	*A. sinaiticum* Boiss.	0.96−0.99	0.98±0.01^{CDEF*}	0.80−0.95	0.87±0.07^{CDE*}	4.59−9.79	6.49±2.86^{BCDE}	5.83−8.58	7.34±1.39^{ABCD}
20	*A. spathaceum* Steud. ex A.Rich.	0.40−0.43	0.41±0.01^{GH*}	0.61−0.65	0.62±0.01^{E*}	1.27−3.69	2.13±1.35^{GHI}	0.58−1.47	1.15±0.49^{FG}
21	*A. sphaerocephalon* L.	1.14−1.66	1.48±0.29^{B}	1.29−1.76	1.53±0.23^{B}	4.42−5.71	5.14±0.65^{CDEFG}	5.84−8.80	7.37±1.48^{ABCD}
22	*A. trifoliatum* Cirillo	1.23−1.47	1.34±0.12^{BCD}	1.37−1.43	1.39±0.02^{B}	1.12−1.99	1.53±0.44^{HI}	1.87−3.29	2.63±0.71^{DEFG}

Means that do not share a letter are significantly different.

Asterisks (*) indicate a significant difference between the seed's dorsal and ventral surfaces.

On-line Suppl. Tab. 5. Qualitative seed morphological characteristics of the studied *Allium* taxa.

No	Studied taxa	Seed shape	Epidermal cell shape	Epidermal cell arrangement	Curvature pattern of the anticlinal wall	Cell boundary	Relief of intercellular space (cell boundary)	Curvature of the periclinal wall (PW)	Fine relief of the PW	Diameter of verrucae on PW	Number of verruca on PW	P/A of granules on PW
1	*A. ampeloprasum* L.	Ovate	Mostly orbicular (some widely elliptic & elliptic)	Jigsaw-like	U-type undulation	Channeled	Narrow mesh of thin connecting threads	convex	Many small domes with dispersed verrucae	Medium	≤15	Absent
2	*A. artemisietorum* Eig & Feinbrun	Elliptic	Oblong	Jigsaw-like	S-type undulation	Channeled	Scabrate	Convex	Many small domes without verrucae	Absent	0	Densely granulated
3	*A. aschersonianum* Barbey	Widely ovate	Mostly orbicular (some widely elliptic & elliptic)	Jigsaw-like	Ω-type undulation	Channeled	Scabrate	Convex	Many small domes with dispersed verrucae	Small	>15	Sparsely granulated
4	*A. barthianum* Asch. & Schweinf.	Elliptic	Mostly widely elliptic & elliptic (some orbicular)	Jigsaw-like	U-type undulation	Channeled	Narrow mesh of thin connecting threads	Convex	One small central dome or many domes with dispersed verrucae	Small to large	>15	Absent
5	*A. blomfieldianum* Asch. & Schweinf.	Widely ovate	Variably polygonal (4-7)	Side-by-side	S-type undulation	Channeled	Narrow mesh of thin connecting threads	Convex	One small central dome with central and marginal verrucae	Small to medium	>15	Moderately granulated
6	*A. cepa* L. (Giza 20)	Widely elliptic	Variably polygonal (5-7)	Side-by-side	Straight to Irregularly curved	Channeled	Reticulate tissue with a broad mesh of connecting threads	convex	Dispersed verrucae without domes	Small to medium	>15	Absent
7	*A. crameri* Asch. & Boiss.	Widely elliptic & elliptic	Mostly widely elliptic & elliptic (some orbicular)	Jigsaw-like	Ω-type undulation	Channeled	Scabrate	Convex	Many small domes with dispersed verrucae	Medium	>15	Absent
8	*A. curtum* Boiss. & Gaill.	Elliptic	Mostly widely elliptic & elliptic (some orbicular)	Jigsaw-like	Ω-type undulation	Channeled	Narrow mesh of thin connecting threads	Convex	Many small domes with dispersed verrucae	Small to large	≤15	Absent
9	*A. desertorum* Forssk.	Widely elliptic	Variably polygonal (4-8)	Side-by-side	Straight to Irregularly curved	Channeled	Narrow mesh of thin connecting threads	Convex	Dispersed verrucae without domes	Small to large	>15	Sparsely granulated
10	*A. erdelii* Zucc.	Widely elliptic	Variably polygonal (5-7)	Side-by-side	U-type undulation	Channeled	Scabrate	Convex	One small central dome with central and marginal verrucae	Small to large	≤15	Sparsely granulated
11	*A. kurrat* Schweinf. ex K.Krause	Widely elliptic & elliptic	Mostly orbicular (some widely elliptic & elliptic)	Jigsaw-like	U-type undulation	Channeled	Narrow mesh of thin connecting threads	Convex	Many small domes with dispersed verrucae	Medium	>15	Absent
12	*A. mareoticum* Bornm. & Gauba	Widely elliptic & elliptic	Mostly widely elliptic & elliptic (some orbicular)	Jigsaw-like	U-type undulation	Channeled	Narrow mesh of thin connecting threads	Convex	One small central dome or many domes with dispersed verrucae	Small to medium	>15	Absent

No	Studied taxa	Seed shape	Epidermal cell shape	Epidermal cell arrangement	Curvature pattern of the anticlinal wall	Cell boundary	Relief of intercellular space (cell boundary)	Curvature of the periclinal wall (PW)	Fine relief of the PW	Diameter of verrucae on PW	Number of verruca on PW	P/A of granules on PW
13	*A. neapolitanum* Cirillo	Widely elliptic	Variably polygonal (4-6)	Side-by-side	S-type undulation	Raised	Striate	Convex	One large central dome with central and marginal verrucae	Medium	≤15	Sparsely granulated
14	*A. pallens* L.	Elliptic	Variably polygonal (4-6)	Side-by-side	S-type undulation	Channeled	Scabrate	Convex	Many small domes with dispersed verrucae	Small to medium	>15	Moderately granulated
15	*A. papillare* Boiss.	Elliptic	Variably polygonal (5-6)	Side-by-side	U-type undulation	Raised	Scabrate	Convex	One small central dome without verrucae	Absent	0	Densely granulated
16	*A. porrum* L.	Elliptic	Variably polygonal (5-7)	Jigsaw-like	U-type undulation	Channeled	Scabrate	Flat and centrally concave	Centrally wrinkled without verrucae	Absent	0	Absent
17	*A. roseum* subsp. *tourneuxii* Boiss.	Widely elliptic & elliptic	Variably polygonal (5-6)	Side-by-side	U-type undulation	Channeled	Scabrate	Convex	One large central dome with central and marginal verrucae	Small to medium	≤15	Moderately granulated
18	*A. sativum* L.	Widely elliptic	Variably polygonal (4-8)	Side-by-side	Straight to Irregularly curved	Channeled	Reticulate tissue with a broad mesh of connecting threads	convex	Dispersed verrucae without domes	Medium	>15	Sparsely granulated
19	*A. sinaiticum* Boiss.	Elliptic	Mostly widely elliptic & elliptic (some orbicular)	Jigsaw-like	U-type undulation	Channeled	Narrow mesh of thin connecting threads	convex	One large central dome with dispersed verrucae	Small	>15	Sparsely granulated
20	*A. spathaceum* Steud. ex A.Rich.	Widely ovate	Variably polygonal (4-7)	Side-by-side	S-type undulation	Channeled	Scabrate	convex	One small central striate dome with central and marginal verrucae	Small to medium	≤15	Absent
21	*A. sphaerocephalon* L.	Elliptic	Mostly widely elliptic & elliptic (some orbicular)	Jigsaw-like	U-type undulation	Channeled	Narrow mesh of thin connecting threads	convex	Many small domes with dispersed verrucae	Small to large	≤15	Absent
22	*A. trifoliatum* Cirillo	Ovate	Variably polygonal (4-8)	Side-by-side	S-type undulation	Channeled	Narrow mesh of thin connecting threads	convex	One small central dome with central and marginal verrucae	Small	>15	Sparsely granulated

On-line Suppl. Tab. 6. Principal component analysis (PCA) with eigenvalues and percentage variances for 22 *Allium* taxa based on the seed morphometric characteristics.

PC	Eigenvalue	% Variance
1	1.09E+06	87.901
2	149401	12.068
3	141.497	0.011429
4	116.706	0.0094266
5	38.8311	0.0031365
6	37.6095	0.0030378
7	19.998	0.0016153
8	11.4607	0.00092571
9	8.34677	0.00067419
10	4.17632	0.00033733
11	2.68005	0.00021647
12	1.48392	0.00011986
13	1.22689	9.91E-05
14	1.00915	8.15E-05
15	0.631364	5.10E-05
16	0.285874	2.31E-05
17	0.140951	1.14E-05
18	0.061212	4.94E-06
19	0.0280893	2.27E-06
20	0.0149838	1.21E-06
21	0.00304354	2.46E-07

On-line Suppl. Tab. 7. Character loadings of the principal component analysis (PCA) for the first two axes based on 26 quantitative seed morphological characteristics.

	Variable	PC 1	PC 2
	Seed length (mm)	0.34809	0.10312
	Seed width (mm)	0.2989	-0.062588
	Seed L/W ratio	0.016648	0.28528
	Seed area (mm^2)	0.35484	0.11554
Dorsal surface	Epidermal cell count/unit area	-0.83442	0.087439
	Epidermal cell length (µm)	0.85046	-0.25829
	Epidermal cell width (µm)	0.90521	-0.015698
	Epidermal cell L/W ratio	0.11564	-0.2586
	Epidermal cell area (μm^2)	0.94723	-0.32057
	Intercellular space length (µm)	-0.21571	0.30233
	Count of undulation elements/cell (if present)	0.21413	-0.46778
	Undulation element length (µm) (if present)	0.68102	0.31462
	Undulation element width (µm) (if present)	0.68945	0.19633
	Undulation element L/W ratio (if present)	0.39418	0.080172
	Distance between two undulation elements (µm) (if present)	0.54611	0.47814
Ventral surface	Epidermal cell count/unit area	-0.84737	0.052991
	Epidermal cell length (µm)	0.75599	0.40108
	Epidermal cell width (µm)	0.69995	0.18052
	Epidermal cell L/W ratio	0.16948	0.16332
	Epidermal cell area (μm^2)	0.92666	0.3759
	Intercellular space length (µm)	-0.21261	0.20898
	Count of undulation elements/cell (if present)	0.24594	-0.42002
	Undulation element length (µm) (if present)	0.59837	0.17359
	Undulation element width (µm) (if present)	0.41972	0.061124
	Undulation element L/W ratio (if present)	0.536	0.061392
	Distance between two undulation elements (µm) (if present)	0.5268	0.44778