Seed testa sculpture of species of *Allium* L. (Amaryllidaceae) and its taxonomic implications

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**Summary**: We investigated the seed testa sculpture of twenty-four species belonging to thirteen sections and five subgenera of *Allium* from the herbarium materials or collected from plants in living collections. Seed testa sculpture of 21 species were described for the first time in this study. According to our results, the straight anticlinal wall and one large verruca or dense granules periclinal wall were found among the species in subgenus *Amerallium*, *Cepa*, *Polyprason* and *Reticulatobulbosa*. Only *A. ochroleucum* (sect. *Daghestanica*, subg. *Polyprason*) has U-type undulation anticlinal wall, which is similar to species of subg. *Allium*. The U- to Omega-type undulation anticlinal walls and several big verrucae with marginal verrucae periclinal wall were found in subg. *Allium*. Our results suggest that seed testa sculpture is important character of species and sections level of the genus *Allium*.
**Introduction**

Seed morphology and seed testa studies have been suggested to be taxonomically useful for species and section rank detection in the genus *Allium*. Seed testa sculpture of anticlinal wall with S-, U-, Omega-, and straight type undulation and one central verruca with marginal verrucae or densely granulose periclinal wall are important characters to sections and subgenera level (Baasanmunkh et al., 2020). For instance, straight anticlinal walls were dominated in subg. *Cepa*, *Reticulatobulbosa* and *Polyprason* and the periclinal walls were distinguished by central big verruca and dense granules. The U-, Omega- and S-type undulation anticlinal walls and convex periclinal walls with several large verrucae or marginal verrucae were dominated in subg. *Allium* and *Melanocrommyum* (Celep et al., 2012; Lin, Tan, 2017; Veiskarami et al., 2018; Baasanmunkh et al., 2020). Additionally, several new taxa of *Allium* have been recognized based on their morphology including seed macro- and micro-morphological characteristics and phylogenetic studies (Deniz et al., 2015; Duman et al., 2017).

The genus *Allium* L., one of the most diverse and the largest genus of petaloid monocots (Friesen et al., 2006; Li et al., 2010), comprises more than 1000 species (Govaerts et al., 2005–2021). This genus is naturally distributed in the Northern Hemisphere (Friesen et al., 2006) and its main diversity is in the mountainous areas of southwestern and central Asia (Fritsch, Friesen, 2002; Friesen et al., 2006).

To date, seed morphology and seed testa sculpture of 460 taxa have been studied from different countries (Baasanmunkh et al., 2020). In particular, most of species were investigated from the Turkey, Iran and Central Asian countries (Celep et al., 2012; Lin, Tan, 2017; Veiskarami et al., 2018; Baasanmunkh et al., 2020). However, seed morphological studies of many species and sections of *Allium* is remaining. In particular, Friesen et al. (2006) described several new sections such as *Daghestanica* (Tschohol.) N. Friesen (subg. *Polyprason*), *Nigrimontana* N. Friesen and *Sikkimensia* (Traub) N. Friesen (subg. *Reticulatobulbosa*) based on morphological and molecular phylogenetic analysis.

The article provides descriptions of the surface sculpture of 24 species of *Allium* made by the last author 15 years ago. The descriptions of testa sculpture of most of them have not yet been published in previous works. Since 24 species represent 13 sections and 5 subgenera in the genus *Allium* (three samples are type species of sections *Daghestanica*: *Nigrimontana* and *Sikkimensia*), they complement the spectrum of species whose testa sculpture has been published so far and contribute the understanding of the evolutionary and taxonomic significance of seed surface sculpture for the classification of the genus.

**Material and Methods**

Specimens information with species/classification and origin are presented in Table 1. No special pre-treatments were applied for the preparation of scanning electron microscopy (SEM). Seeds were immersed in absolute ethanol and sputtered with a gold coating in a Sputter Coater: Polaron E5150, Polaron Equipment Ltd, Hertfordshire, England. In all cases, the seeds of at least five samples per accession were analysed, characterized, and photographed with a Zeiss DSM 926 (Zeiss, Oberkochen, Germany) scanning electron microscope at the Zoological Department of the Osnabrueck University.

Terminologies for the description of seed testa sculpture is according to Barthlott (1981), Celep et al. (2012) and Baasanmunkh et al. (2020).

**Result and Discussion**

Recently, seed testa sculpture of *Allium* have been quite well studied from different countries based on the herbarium and field collection materials (Celep et al., 2012; Lin, Tan, 2017; Veiskarami et
al., 2018; Baasanmunkh et al., 2020). In this study, we investigated seed testa sculpture of 24 species in genus Allium L. based on herbarium materials and seed collected in the living Allium collections in Institute of Plant Genetics and Crop Plant Research, Gatersleben, Germany and Botanical Garden of the Osnabrueck University, Germany (GAT and OSN accessions in the table 1, respectively). Among these, seed testa sculpture of 21 species have been studied for the first time. The seed testa micrographs are sorted in alphabetical order of subgenus, section and species names (Table 2; Figs. 1, 2). Each species and sections of the subgenera are discussed and provided below.

**Subgenus Allium**

The subg. Allium comprises more than 380 species (Khasanov, 2018) and is placed at third evolutionary line in genus Allium (Hanelt et al., 1992; Friesen et al., 2006). The U-, S-, Omega-type undulation anticlinal wall and convex periclinal wall with one central verruca or several marginal verrucae were dominated in subg. Allium (Pastor, 1981; Kruse, 1984, 1986, 1988, 1994; Neshati, Fritsch, 2009; Choi et al., 2012; Duman et al., 2017; Lin, Tan, 2017; Veiskarami et al., 2018). To date, seed morphological of 140 taxa have been studied from different sections in subg. Allium (Baasanmunkh et al., 2020). We studied six species (A. ameloaprasum L., A. acheri Boiss., A. cappadocicum Boiss. et Balansa, A. sphaerocephalum L., A. symottii G. Don and A. pictistamineum O. Schwarz) belonging to two sections (Allium and Codonoprasum) in this subgenus. Seed testa sculpture of the most species was described for the first time. The testa cells were distinguished in irregularly polygonal (Fig. 1A, C, E) and elliptic polygonal (Fig. 1B, D, F). The U-type undulation anticlinal walls were found among the species except A. acheri (Omega-type undulation, Fig. 1B). The convex or concave periclinal walls with one central or several big verrucae were dominated among the studied species.

**Subgenus Amerallium** Traub.

We described seed testa sculpture of two species A. fasciculatum Rendle (sect. Brommatorhiza) and A. stellatum Nutt. ex Ker Gawl. (sect. Lophyoprason) in this subgenus. Allium fasciculatum was investigated for the first time here. The testa cell was irregularly polygonal 3–4-edged and irregularly polygonal in A. fasciculatum (Fig. 1G) and A. stellatum (Fig. 1H), respectively. Choi and Cota-Sánchez (2010) studied straight anticlinal wall and periclinal wall with minutely roughened for A. stellatum from Canada. Our result was suggested similar result for anticlinal wall but periclinal wall somewhat differs from result of Choi and Cota-Sánchez (2010).

**Subgenus Cepa** (Mill.) Radič.

The straight, straight to arched anticlinal wall and several big verrucae with small granulate periclinal wall were dominated in this subgenus (Kruse, 1986; Bednorz et al., 2011; Baasanmunkh et al., 2020), while some species (A. cepa L. and A. atrosanguineum Schrenk) from China (Xinjiang) had the S-type undulation anticlinal walls (Lin, Tan 2017). We investigated two species (A. taquetii H. Lév. et Vaniot and A. oliganthum) belonging to two sections (Sacculiferum and Schoenoprasum) in this subgenus, respectively. Of these, A. oliganthum Kar. et Kir. has straight anticlinal wall and flat, smooth periclinal wall (Fig. 1J) described for the first time. Choi et al. (2012) studied the straight anticlinal wall and granulate periclinal wall for A. taquetii, but our result showed the several big verrucae periclinal wall (Fig. 1I). It is might be that our A. taquetii sample was misidentified. The testa cell was irregularly polygonal 4–5-edged for both species (Fig. 1I, J).

**Subgenus Polyprason** Radič.

We investigated six species (A. daghestanicum Grossh., A. gunibicum Miscz. ex Grossh., A. ochroleucum Waldst. et Kit., A. suaveolens Jacq., A. zapragajevic Kassacz. and A. stracheyi Baker) belonging to three sections (Daghestanica, Falcatifolia and Oreiprason) in this subgenus. In this study seed testa of all the species was described for the first time, except A. daghestanicum. Kruse (1984, 1988) found straight anticlinal wall and verrucae with granulose periclinal wall for A. daghestanicum (sect. Daghestanica), which is same to our result.

**Subgenus Reticulatobulbosa** (Kamelin) N. Friesen.

The straight anticlinal walls and granulose sculptures of the periclinal walls dominated in this subgenus (Kruse, 1984, 1986, 1988, 1994; Fritsch et al., 2006; Choi et al., 2012; Lin, Tan, 2017; Baasanmunkh et al., 2020). We investigated eight species (A. oreoscordum Vved., A. trachyscordum Vved., A. henryi C. H. Wright, A. drobovii Vved., A. maackii (Maxim.) Prokh. ex Kom., A. beesianum W. W. Sm., A. forrestii Diels and A. sikkimense Baker) belonging to four sections (Campananlata, Nigrimontana, Reticulatobulbosa and Sikkimensa)
in this subgenus. Seed testa of all the species was described for the first time here. The testa cell was irregularly polygonal with 3–5 edges among the species studied (Fig. 2E-L). All studied species have straight anticlinal walls whereas periclinal walls distinguished by many small granules in *A henryi* (sect. *Sikkimensia*) (Fig. 2I), one central verruca with marginal small verrucae in *A. oreoscordum*, *A. trachyscordum* (sect. *Campanulata*) (Fig. 2E, F) and *A. maackii* (sect. *Reticulatobulbosa*) (Fig. 2H), many or several verrucae in *A. drobovii* (sect. *Nigrimontana*) (Fig. 2G) and *A. beesianum* (sect. *Sikkimensia*) (Fig. 2J), and densely prominent granules in *A. forrestii* and *A. sikkimense* (sect. *Sikkimensia*) (Fig. 2K, L). Our findings agreed with previous results, that straight anticlinal walls

Fig. 1. Seed testa sculptures of *Allium*. A–F – subg. *Allium*: A – *A. ampeloprasum*; B – *A. aucheri*; C – *A. cappadocicum*; D – *A. sphaerocephalum*; E – *A. synnotii* (sect. *Allium*); F – *A. pictistamineum* (sect. *Codonoprasum*). G–H – subg. *Amerallium*: G – *A. fasciculatum* (sect. *Brommatorhiza*); H – *A. stellatum* (subg. *Amerallium*, sect. *Molium*). I–J – subg. *Cepa*: I – *A. taquetii* (sect. *Sacculiferum*); J – *A. oliganthum* (sect. *Schoenoprasum*). K–L – subg. *Polyprason*: K – *A. daghestanicum*; L – *A. gunibicum* (sect. *Daghestanica*) (Photo N. Friesen).
Seeds testa sculpture of *Allium* L. (Amaryllidaceae) dominate in the subg. *Reticulatobulbosa* (Lin, Tan 2017; Baasanmunkh et al., 2020). Especially, the periclinal walls of sect. *Sikkimensia* were clearly different from sects. *Campanulata* and *Nigrimontana* by densely prominent or many small granules, which is supported to molecular phylogenetic analysis of Friesen et al. (2006).

Finally, we provided that seed testa sculpture is important character for the species and section level of *Allium*. Especially, the straight, Omega-, U- and S-type anticlinal walls can be used to distinguish taxa on the subgenus level.

![Seed testa sculptures of Allium](image)

Fig. 2. Seed testa sculptures of *Allium*. A–D – subg. Polyprason: A – *A. ochroleucum*; B – *A. suaveolens* (sect. *Daghestanica*); C – *A. zaprjugajevii* (sect. *Falcatifolia*); D – *A. stracheyi* (sect. *Oreiprason*). E–L – subg. *Reticulatobulbosa*: E – *A. oreoscordum*; F – *A. trachyscordum* (sect. *Campanulata*); G – *A. drobovii* (sect. *Nigrimontana*); H – *A. maackii* (sect. *Reticulatobulbosa*); I – *A. henryi*; J – *A. beesianum*, K – *A. forrestii*, L – *A. sikkimense* (sect. *Sikkimensia*) (Photo N. Friesen).
### Table 1

Voucher specimen information of *Allium* species investigated (OSBU, ISTE, TASH, LE, GAT are the international herbarium acronyms and OSN are the accessions number from the living collection of the Botanical Garden of Osnabrück University)

| Subgenus/Section | Taxon | Voucher Code and Specimen data |
|------------------|-------|---------------------------------|
| *Allium*/*Allium* | *A. ampeloprasum* L. | OSBU 16840, Greece, Crete, 35°10'54"N, 24°24'10"E. N. Friesen. 26 V 2005 |
| *Allium*/*Allium* | *A. aucheri* Boiss. | ISTE, Turkey, Pelli Dagh. 1972 |
| *Allium*/*Allium* | *A. cappadocium* Boiss. et Balansa | ISTE, Turkey, Cappadocia, 1983 |
| *Allium*/*Allium* | *A. sphaerocephalum* L. | GAT 5337, Turkey, Boz Dagi, 8,5 km from Balikesi. Fritsch R. and Friesen N. 04 VI 1995 |
| *Allium*/*Allium* | *A. synnotii* G. Don (= *A. dregeanum* Kunth) | GAT 5722, South-Africa, Cape, Zandkaal, Dolomite ridge |
| *Allium*/*Codonoprasum* | *A. pictistamineum* O. Schwarz | OSN-2001-1317-W, Turkey, Spil Dagh, south of Manissa. Fritsch R. and Friesen N. 06 VI 1995 |
| *Amerallium*/*Brommatorhiza* | *A. fasciculatum* Rendle | OSBU 21046, China, Xizang, Upper Sun Kosi N of Nyalam, alt. 3960 m, 28°10N, 86°00E. G. & S. Miehe, Koch. 26 VIII 1999 |
| *Amerallium*/*Cernuum* | *A. stellatum* Nutt. ex Ker Gawl. | OSN-2002-0593-G, Devonian Bot. Garden, Edmonton, Canada |
| *Cepa*/*Sacculiferum* | *A. taquetii* H. Lév. et Vaniot | OSN-2003-1278-W, South Korea. Botanical Garden Donneko |
| *Cepa*/*Schoenoprasum* | *A. oliganthum* Kar. et Kir. | OSN-2006-1641-W, Kazakhstan, Karaganda. South Siberian Botanical Garden, Bamaul, Russia. |
| *Polyprason*/*Daghestanica* | *A. daghestanicum* Grossh. | GAT 5222, Russia, Daghestan, Danuhk |
| *Polyprason*/*Daghestanica* | *A. gunnicum* Miscz. ex Grossh. | OSN-2004-0100-W, Russia, Daghestan, Gunib |
| *Polyprason*/*Daghestanica* | *A. ochroleucum* Waldst. et Kit. | GAT 5578, Slovenia, Čaven. Botanical Garden Ljubljana |
| *Polyprason*/*Daghestanica* | *A. suaveolens* Jacq. | OSN-2005-1366-W, Austria, Niederöstereich, K. G. Bernhardt. 25 IX 2005 |
| *Polyprason*/*Rivatrafia* | *A. zaprjagajevii* Kassacz. | LE, Tadjikistan, West Pamir, Shakhdana, Siob, Kassacz 166 |
| *Polyprason*/*Rivatrafia* | *A. stracheyi* Baker | OSBU 21133, China, NW Sichuan, Upper Yalong tributary, Xianshui He, Luhuo-Gana Nof Jimda, 31°34'N, 100°43'E. G. & S. Miehe, U. Wündisch, 30 IX 1994 |
| *Reticulatobulbosa*/*Campanulata* | *A. oreoscordum* Vved. | GAT 5011, Kirgizia, Fergana Moutains, Kara-Su Valej. 1994. R. Fritsch and K. Pistrik |
| *Reticulatobulbosa*/*Campanulata* | *A. trachyscordum* Vved. | GAT 3998, Kirgizia, Talas, 1994. R. Fritsch and K. Pistrik |
| *Reticulatobulbosa*/*Nigrimontana* | *A. drobovii* Vved. | TASH, Uzbekistan, Ugamski Mountain, Bostandyk |
| *Reticulatobulbosa*/*Reticulatobulbosa* | *A. maackii* (Maxim.) Prokh. ex Kom. | BOGOs 2005-1130-Z, Russia, Ussuri. Bot Garden Samara, Russia |
| *Reticulatobulbosa*/*Sikkimensia* | *A. beesianum* W. W. Sm. | OSN-2002-0591-G, China, Tibet. Devonian Bot. Garden Uni of Alberta, Edmonton, Canada |
| *Reticulatobulbosa*/*Sikkimensia* | *A. forrestii* Diels | OSBU 21060, China NW Sichuan, Upper Yalong basin, Chola Shan, Dege-Garze, Manigango, 31°52'N, 99°7'E. G. & S. Miehe, U. Wündisch. 24 IX 1994 |
| *Reticulatobulbosa*/*Sikkimensia* | *A. henryi* C. H. Wright | OSBU 21072, China, NW Sichuan, Southern Qionglai Shan, E of Chengdu Wolong, 30°52N, 102°57'E. G. & S. Miehe, U. Wündisch, 09 X 1994 |
| *Reticulatobulbosa*/*Sikkimensia* | *A. sikkimense* Baker | OSBU 21175, China, Qinghai, Tschebsang, S of Xinghai, N 35°32'17.1", E 99°51'00.5". K. Koch, Sunancu. 01 VIII 2002 |
| Subgenus / section | Taxon                          | Testa cell shape          | Anticlinal walls       | Periclinal walls                                      | Figure |
|---------------------|--------------------------------|---------------------------|------------------------|-------------------------------------------------------|--------|
| *Allium*/Allium     | *A. ampeloprasum*              | Irregularly polygonal     | U-undulation           | Convex, several big verrucae with smooth               | 1A     |
| *Allium*/Allium     | *A. aucheri*                   | Elliptic polygonal        | U, Ω-undulation        | Convex to convex, verrucae with smooth                 | 1B     |
| *Allium*/Allium     | *A. capпадоцicum*              | Irregularly polygonal     | U-undulation           | Convex, intermediate verrucae                         | 1C     |
| *Allium*/Allium     | *A. sphaerocephalum*           | Elliptic polygonal        | U-undulation           | Convex, one central verruca with marginal granulose   | 1D     |
| *Allium*/Allium     | *A. synnotii*                  | Irregularly polygonal     | U-undulation           | Convex, several big verrucae                          | 1E     |
| *Allium*/Codonoprasum| *A. pictistamineum*          | Elliptic polygonal        | U-undulation           | Convex, intermediate verrucae with several small granulose | 1F     |
| *Amerallium*/Brommarthiza | *A. fasciculatum*               | Irregularly polygonal 3-4-edged | Straight             | Flat, many small granules                           | 1G     |
| *Amerallium*/Lophioprason (*Cernuum alliances*) | *A. stellatum* | Irregularly polygonal | Straight             | Flat to convex, many small granules                   | 1H     |
| *Cepa*/Sacculiferum | *A. taquetii*                  | Irregularly polygonal 4-5-edged | Straight             | Flat, several big verrucae                           | 1I     |
| *Cepa*/Schoenoprasum| *A. oliganthum*                | Irregularly polygonal 4-5-edged | Straight             | Flat, smooth                                        | 1J     |
| *Polyprason*/Daghestanica | *A. daghestanicum*              | Irregularly polygonal 4-5-edged | Straight             | Convex, densely indistinct granules                   | 1K     |
| *Polyprason*/Daghestanica | *A. guabicum*                   | Irregularly polygonal 4-5-edged | Straight             | Convex, densely indistinct granules                   | 1L     |
| *Polyprason*/Daghestanica | *A. ochroleucum*                | Irregularly polygonal     | U-undulation           | Convex, several big verrucae                         | 2A     |
| *Polyprason*/Daghestanica | *A. suaveolens*                  | Elliptic polygonal        | Straight             | Flat, several intermediate granule                    | 2B     |
| *Polyprason*/Falcatifolia | *A. zapjragajevii*              | Irregularly polygonal     | Straight             | Flat, several intermediate verrucae                   | 2C     |
| *Polyprason*/Oreiprason | *A. stracheyi*                  | Irregularly polygonal 4-5-edged | Straight             | Flat, smooth                                        | 2D     |
| *Reticulatobulbosa*/Campanulata | *A. oreoscordum*                | Irregularly polygonal 4-5-edged | Straight             | Convex, one central verrucae with marginal small verrucae | 2E     |
| *Reticulatobulbosa*/Campanulata | *A. trachycordum*               | Irregularly polygonal 3-4-edged | Straight             | Convex, one central granulose with marginal verrucae | 2F     |
| *Reticulatobulbosa*/Nigrimontana | *A. drobovi**                   | Irregularly polygonal 3-4-edged | Straight             | Convex, several verrucae                             | 2G     |
| *Reticulatobulbosa*/Reticulatobulbosa | *A. maackii*                   | Irregularly polygonal 3-4-edged | Straight             | Convex, one central verrucae with marginal small granules | 2H     |
| *Reticulatobulbosa*/Sikkimensia | *A. henryi*                     | Irregularly polygonal 4-5-edged | Straight             | Convex, many small granules                          | 2I     |
| *Reticulatobulbosa*/Sikkimensia | *A. beesianum*                  | Irregularly polygonal 3-4-edged | Straight             | Convex, many verrucae                                | 2J     |
| *Reticulatobulbosa*/Sikkimensia | *A. forrestii*                  | Irregularly polygonal 3-4-edged | Straight             | Convex, densely prominent granules                    | 2K     |
| *Reticulatobulbosa*/Sikkimensia | *A. sikkimense*                 | Irregularly polygonal 3-4-edged | Straight             | Convex, densely prominent granules                    | 2L     |
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