

УДК 582.572.225:581.48

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

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**Keywords:** herbarium collection, section, seed macro-morphology, subgenus, taxonomic signification.

**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 *Reticulobulbosa*. 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*.

## Скульптура поверхности семян видов рода *Allium* (Amaryllidaceae) и её таксономическое значение

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**Ключевые слова:** гербарная коллекция, секция, скульптура поверхности семян, таксономическое значение.

**Аннотация.** Изучена скульптура поверхности семян 24 видов, относящихся к 13 секциям и пяти под родам рода *Allium*. Семена взяты с гербарных образцов или с растений из живых коллекций. Нами впервые описана скульптура поверхности семенной оболочки у 21 вида. Согласно полученным результатам, виды под родов *Amerallium*, *Cepa*, *Polyprason* и *Reticulobulbosa* имеют прямую антиклинальную стенку и один крупный бугорок или периклинальную стенку с плотными гранулами на поверхности. Только у *A. ochroleucum* (sect. *Daghestanica*, subg. *Polyprason*) выявлена волнистая антиклинальная стенка U-типа, как у видов подрода *Allium*. Волнистые антиклинальные стенки от U- до Omega-типа и несколько больших бугорков с периклинальной стенкой были выявлены в подрode *Allium*. Наши результаты показывают, что скульптура поверхности семян является важным таксономическим признаком на уровне видов и секций рода *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 granulate periclinal wall are important characters to sections and subgenera level (Baasanmunkh et al., 2020). For instance, straight anticlinal walls were dominated in subg. *Cepa*, *Reticulobulbosa* 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* (Tscholok.)

N. Friesen (subg. *Polyprason*), *Nigrimontana* N. Friesen and *Sikkimensia* (Traub) N. Friesen (subg. *Reticulobulbosa*) 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. ampeloprasum* L., *A. aucheri* Boiss., *A. cappadocicum* Boiss. et Balansa, *A. sphaerocephalum* L., *A. synnotii* 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. aucheri* (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. *Lophyoprasum*) 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.) Radić.

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* Radić.

We investigated six species (*A. daghestanicum* Grossh., *A. gunibicum* Misch. ex Grossh., *A. ochroleucum* Waldst. et Kit., *A. suaveolens* Jacq., *A. zaprjagajevii* Kassacz. and *A. stracheyi* Baker) belonging to three sections (*Daghestanica*, *Falcatifolia* and *Oreiprasum*) 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 (*Campanulata*, *Nigrimontana*, *Reticulatobulbosa* and *Sikkimensia*)

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. *Reticulato bulbosa*) (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

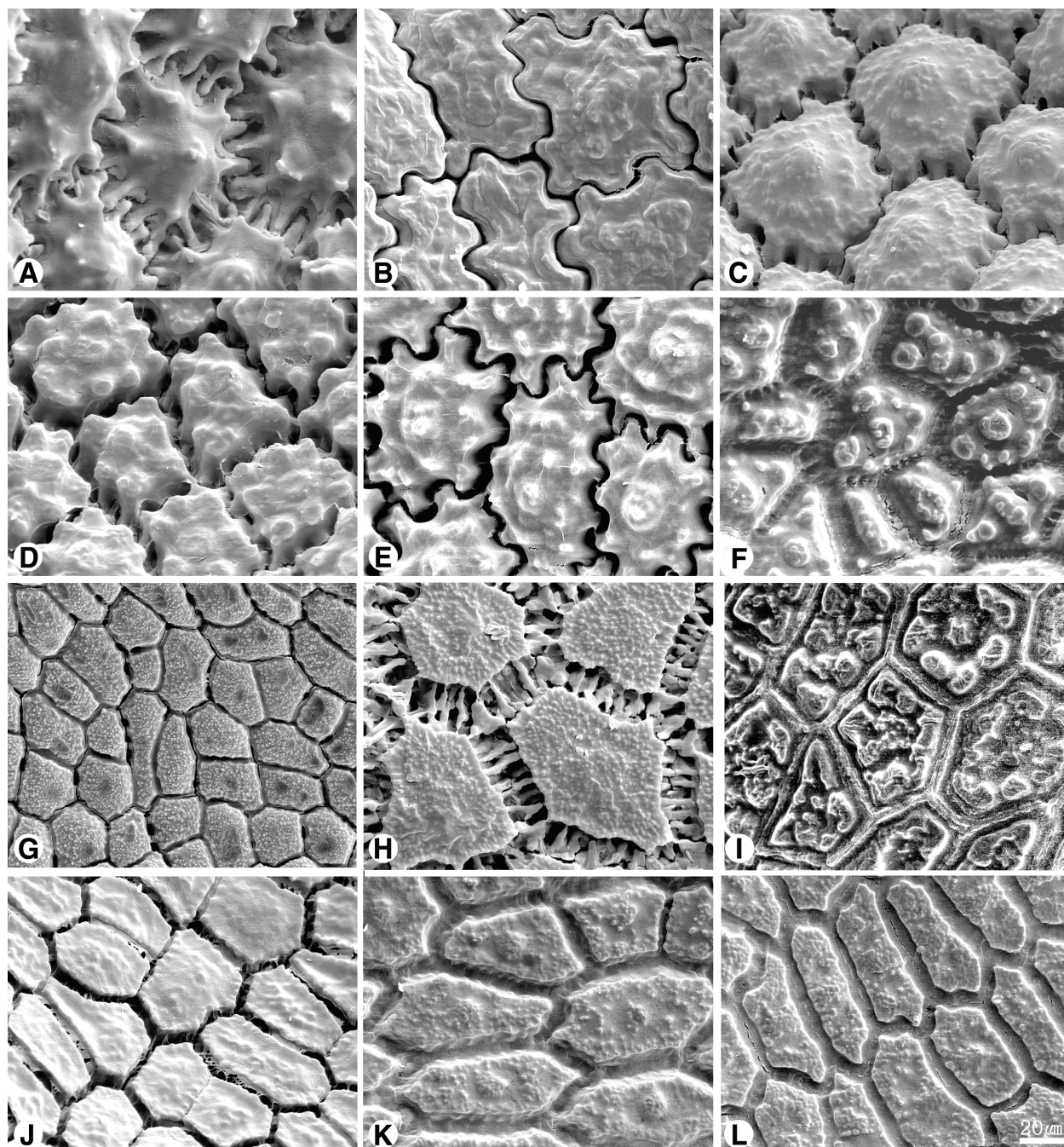


Fig. 1. Seed testa sculptures of *Allium*. A–F – subg. *Allium*: A – *A. ampeloprasum*; B – *A. aucheri*; C – *A. cappadocicum*; D – *A. sphaerocephalum*; E – *A. synnotii* (sect. *Allium*); F – *A. pictistamineum* (sect. *Codonoprasum*). G–H – subg. *Amerallium*: G – *A. fasciculatum* (sect. *Brommatorhiza*); 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).

dominate in the subg. *Reticulotubulosa* (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.

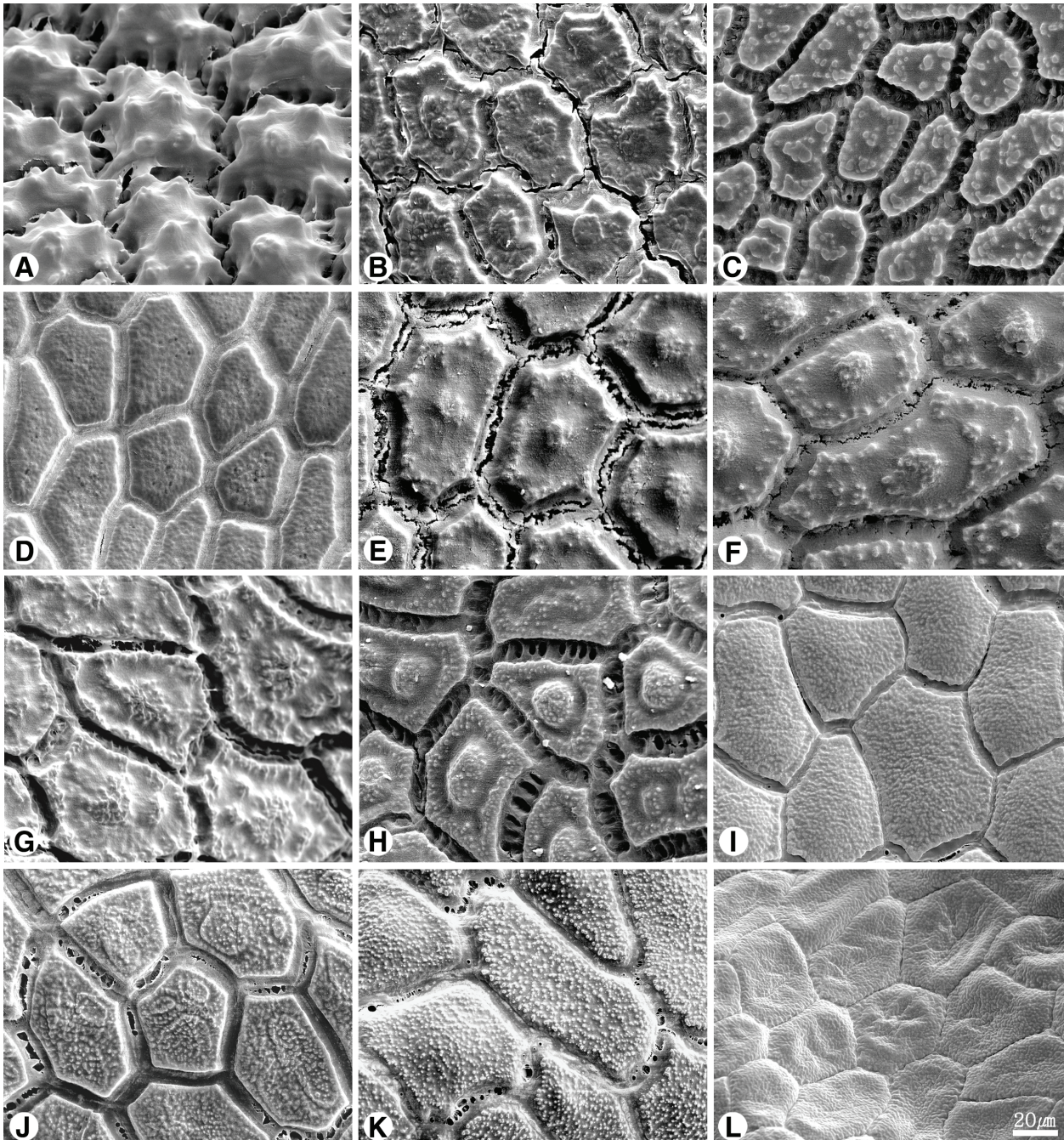


Fig. 2. Seed testa sculptures of *Allium*. A–D – subg. *Polyprason*: A – *A. ochroleucum*; B – *A. suaveolens* (sect. *Daghestanica*); C – *A. zaprjagajevii* (sect. *Falcatifolia*); D – *A. stracheyi* (sect. *Oreiprason*). E–L – subg. *Reticulotubulosa*: E – *A. oreoscordum*; F – *A. trachyscordum* (sect. *Campanulata*); G – *A. drobovii* (sect. *Nigrimontana*); H – *A. maackii* (sect. *Reticulotubulosa*); 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
<i>Allium/Allium</i>	<i>A. ampeloprasum</i> L.	OSBU 16840, Greece, Crete, 35°10'54"N, 24°24'10"E. N. Friesen. 26 V 2005
<i>Allium/Allium</i>	<i>A. aucheri</i> Boiss.	ISTE, Turkey, Pelli Dagh. 1972
<i>Allium/Allium</i>	<i>A. cappadocicum</i> Boiss. et Balansa	ISTE, Turkey, Cappadocia. 1983
<i>Allium/Allium</i>	<i>A. sphaerocephalum</i> L.	GAT 5337, Turkey, Boz Dagi, 8,5 km from Balikisi. Fritsch R. and Friesen N. 04 VI 1995
<i>Allium/Allium</i>	<i>A. synnotii</i> G. Don (= <i>A. dregeanum</i> Kunth)	GAT 5722, South-Africa, Cape, Zandkraal, Dolomite ridge
<i>Allium/Codonoprasum</i>	<i>A. pictistamineum</i> O. Schwarz	OSN-2001-1317-W, Turkey, Spil Dagh, south of Manissa. Fritsch R. and Friesen N. 06 VI 1995
<i>Amerallium/Brommatorhiza</i>	<i>A. fasciculatum</i> Rendle	OSBU 21046, China, Xizang, Upper Sun Kosi N of Nyalam, alt. 3960 m, 28°10'N, 86°00'E. G. & S. Miehe, Koch. 26 VIII 1999
<i>Amerallium/Cernuum</i>	<i>A. stellatum</i> Nutt. ex Ker Gawl.	OSN-2002-0593-G, Devonian Bot. Garden, Edmonton, Canada
<i>Cepa/Sacculiferum</i>	<i>A. taquetii</i> H. Lév. et Vaniot	OSN-2003-1278-W, South Korea. Botanical Garden Donneko
<i>Cepa/Schoenoprasum</i>	<i>A. oliganthum</i> Kar. et Kir.	OSN-2006-1641-W, Kazakhstan, Karaganda. South Siberian Botanical Garden, Barnaul, Russia.
<i>Polyprason/Daghestanica</i>	<i>A. daghestanicum</i> Grossh.	GAT 5222, Russia, Daghestan, Danukh
<i>Polyprason/Daghestanica</i>	<i>A. gunibicum</i> Miscz. ex Grossh.	OSN-2004-0100-W, Russia, Daghestan, Gunib
<i>Polyprason/Daghestanica</i>	<i>A. ochroleucum</i> Waldst. et Kit.	GAT 5578, Slovenia, Čaven. Botanical Garden Ljubljana
<i>Polyprason/Daghestanica</i>	<i>A. suaveolens</i> Jacq.	OSN-2005-1366-W, Austria, Niederösterreich, K. G. Bernhardt. 25 IX 2005
<i>Polyprason/Falcatifolia</i>	<i>A. zaprjagjevii</i> Kassacz.	LE, Tadjikistan, West Pamir, Shakh dara, Siob. Kassacz 166
<i>Polyprason/Oreiprason</i>	<i>A. stracheyi</i> 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
<i>Reticulatobulbosa/Campamulata</i>	<i>A. oreoscordum</i> Vved.	GAT 5011, Kirgizia, Fergana Moutams, Kara-Su Valey. 1994. R. Fritsch and K. Pistrick
<i>Reticulatobulbosa/Campamulata</i>	<i>A. trachyscordum</i> Vved.	GAT 3998, Kirgizia, Talas, 1994. R. Fritsch and K. Pistrick
<i>Reticulatobulbosa/Nigrimontana</i>	<i>A. drobovii</i> Vved.	TASH, Uzbekistan, Ugamski Mountain, Bostandyk
<i>Reticulatobulbosa/Reticulatobulbosa</i>	<i>A. maackii</i> (Maxim.) Prokh. ex Kom.	BOGos 2005-1130-Z, Russia, Ussuri. Bot Garden Samara, Russia
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. beesianum</i> W. W. Sm.	OSN-2002-0591-G, China, Tibet. Devonian Bot. Garden Uni of Alberta, Edmonton, Canada
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. forrestii</i> 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
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. henryi</i> C. H. Wright	OSBU 21072, China, NW Sichuan, Southern Qionglai Shan, E of Chengdu Wolong, 30°52'N, 102°57'E. G. & S. Miehe, U. Wündisch, 09 X 1994.
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. sikkimensense</i> 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

Table 2

Micro-morphological characters of seed in *Allium* species investigated. The type species of section is marked by asterisk (\*)

Subgenus / section	Taxon	Testa cell	Anticlinal walls	Periclinal walls	Figure
<i>Allium/Allium</i>	<i>A. ameloprasum</i>	Irregularly polygonal	U-undulation	Convex, several big verrucae with smooth	1A
<i>Allium/Allium</i>	<i>A. aucheri</i>	Elliptic polygonal	U, Ω-undulation	Concave to convex, verrucae with smooth	1B
<i>Allium/Allium</i>	<i>A. cappadocicum</i>	Irregularly polygonal	U-undulation	Convex, intermediate verrucae	1C
<i>Allium/Allium</i>	<i>A. sphaerocephalum</i>	Elliptic polygonal	U-undulation	Convex, one central verruca with marginal granulose	1D
<i>Allium/Allium</i>	<i>A. synnotii</i>	Irregularly polygonal	U-undulation	Convex, several big verrucae	1E
<i>Allium/Codonoprasum</i>	<i>A. pictistamineum</i>	Elliptic polygonal	U-undulation	Convex, intermediate verrucae with several small granulose	1F
<i>Amerallium/Brommatorhiza</i>	<i>A. fasciculatum</i>	Irregularly polygonal 3-4-edged	Straight	Flat, many small granules	1G
<i>Amerallium/Lophioprasum (Cernuum alliances)</i>	<i>A. stellatum</i>	Irregularly polygonal	Straight	Flat to convex, many small granules	1H
<i>Cepa/Sacculiferum</i>	<i>A. taquetii</i>	Irregularly polygonal 4-5-edged	Straight	Flat, several big verrucae	1I
<i>Cepa/Schoenoprasum</i>	<i>A. oliganthum</i>	Irregularly polygonal 4-5-edged	Straight	Flat, smooth	1J
<i>Polyprason/Daghestanica</i>	<i>A. daghestanicum*</i>	Irregularly polygonal 4-5-edged	Straight	Convex, densely indistinct granules	1K
<i>Polyprason/Daghestanica</i>	<i>A. gumbicum</i>	Irregularly polygonal 4-5-edged	Straight	Convex, densely indistinct granules	1L
<i>Polyprason/Daghestanica</i>	<i>A. ochroleucum</i>	Irregularly polygonal	U-undulation	Convex, several big verrucae	2A
<i>Polyprason/Daghestanica</i>	<i>A. suaveolens</i>	Elliptic polygonal	Straight	Flat, several intermediate granulose	2B
<i>Polyprason/Falcatifolia</i>	<i>A. zapryagajevii</i>	Irregularly polygonal	Straight	Flat, several intermediate verrucae	2C
<i>Polyprason/Oreiprason</i>	<i>A. stracheyi</i>	Irregularly polygonal 4-5-edged	Straight	Flat, smooth	2D
<i>Reticulatobulbosa/Campamulata</i>	<i>A. oreoscordum</i>	Irregularly polygonal 4-5-edged	Straight	Convex, one central verrucae with marginal small verrucae	2E
<i>Reticulatobulbosa/Campamulata</i>	<i>A. trachyscordum</i>	Irregularly polygonal 3-4-edged	Straight	Convex, one central granulose with marginal verrucae	2F
<i>Reticulatobulbosa/Nigrimontana</i>	<i>A. drobovii*</i>	Irregularly polygonal 3-4-edged	Straight	Convex, several verrucae	2G
<i>Reticulatobulbosa/Reticulatobulbosa</i>	<i>A. maackii</i>	Irregularly polygonal 3-4-edged	Straight	Convex, one central verrucae with marginal small granules	2H
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. henryi</i>	Irregularly polygonal 4-5-edged	Straight	Convex, many small granules	2I
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. beesianum</i>	Irregularly polygonal 3-4-edged	Straight	Convex, many verrucae	2J
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. forrestii</i>	Irregularly polygonal 3-4-edged	Straight	Convex, densely prominent granules	2K
<i>Reticulatobulbosa/Sikkimensia</i>	<i>A. sikkimense*</i>	Irregularly polygonal 3-4-edged	Straight	Convex, densely prominent granules	2L

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