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Seed morphology of the genus *Astragalus* L. from North Asia

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Abstract: *Astragalus* is one of the largest genera of angiosperms and a characteristic component of the steppes and mountains of North Asia. Here, we used scanning electron microscopy to investigate the seed morphology of 56 species of the genus from North Asia. In *Astragalus*, seed color varies from yellow–green, greenish brown, reddish brown to grayish brown. Seed shapes include reniform–globose, rombiform, and oblong–elliptical. Seed sizes vary from 1.25 × 0.88 mm to 4.94 × 3.29 mm. Anticlinal walls are straight, undulate, or slightly thickened, and the periclinal walls are aveolate, stellate, pectinate, or rugose. We recognized two main types of seed surface in the genus: reticulate (sect. *Cystium*, *Uliginosi*, and *Heterodontus*) and indistinct primary sculpture (sect. *Caprini*, *Craccina*, *Alopecuroidei*, *Glycyphyllos*, and *Komaroviella*). This study describes macro- and micromorphological characters of seeds that would be useful for studying systematics, taxonomy, and evolution within *Astragalus* in the future.

Key words: *Astragalus*, seed surface, seed morphology, North Asia

1. Introduction

The genus *Astragalus* L. is one of the largest genera of flowering plants and encompasses about 2500–3000 species that grow mainly in cold arid and semiarid mountain regions of the Northern Hemisphere and South America (Podlech, 2013). The genus is a characteristic component of the steppes and mountains of Asia (Polhill, 1981; Lock and Schrire, 2005), and about 110 species of *Astragalus* occur in North Asia.

In 1971, Heywood drew attention to the importance of the scanning electron microscope as a tool to study systematic problems. Many taxonomists (Nikolaevskaja and Petrova, 1989; Tantawy et al., 2004; Ovczinnikova, 2007; Svetlova, 2008; Lomonosova, 2009; Kaya et al., 2016; etc.) assert that the data on macro- and microstructure of seeds are crucial for classification of angiosperm taxa. Several authors have studied the seed surface ultrasculpture of species of *Astragalus*. Engel (1990) reported that taxa from *Astragalus* have reticulate, multireticulate, and foveolate and multifoveolate seed surface sculpture. Ekici et al. (2005) noted regulate–granulate pitted seed surfaces for *Astragalus ovalis* Boiss. & Balansa (sect. *Ammodendron* Bunge). Vural et al. (2008) studied the morphology of seeds from 48 species of the sections *Onobrychoidei* DC, *Uliginosi* Gray, and *Ornithopodium* Bunge, and found two main types of seed surface ultrasculpture: rugose and rugose–reticulate.

This study aimed to investigate the species of *Astragalus* growing in North Asia to examine the diversity of surface sculpture and assess its taxonomic significance.

2. Materials and methods

A comparative analysis of the microrelief of the seed surface of 56 species from 20 sections of the genus *Astragalus* growing in the Asian part of Russia was carried out using a scanning electron microscope (SEM). Mature seeds of *Astragalus* were collected from herbarium specimens stored in the following herbaria: NS and NSK (Table 1). Additionally, some materials were collected from the field during 2009–2011. The sample number for each species was not less than 20 seeds.

To remove the cuticle, seeds were stored in a solution of chloroform and methanol at a ratio of 1:1 for 48 h. After that, the seeds were transferred to a series of alcohols (70% and 90%). Processed dry seeds were fixed to a SEM stub using double-sided insulation tape. The

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Table 1. Material examined: species, collector, date, country, province/region, locality, coordinates, altitude, and herbaria.

№	Section /species	Collector	Date	Country	Province/region	Locality	Coordinates	Altitude, m	Herbarium
	***Caprini* DC.**								
1.	*A. schanginianus* Pall.	Shaulo, D. Krasnikov, A.	22/07/1983	Russia	Altai Republic, Ust-Koksinsky district	Tungur Village	50°10′N, 86°18′E	1345	NS
2.	*A. wolgensis*	Fedotov, K.	17/06/1984	Russia	Kurgan Oblast, Pritobolsky district	Berezovka River, Ukrainets Village	54°23′N, 64°48′E	97	NS
	***Laguropsis* Bunge**								NS
3.	*A. arkalycensis* Bunge	Zvereva, G.	27/07/1966	Russia	Khakassia Republic, Shirinsky district	Shira Lake	54°28′N, 90°12′E	459	NS
4.	*A. laguroides* Pall.	Korolyuk, A.	13/07/2007	Russia	Buryatia Republic, Dzhidinsky district	Dyrestui Village	50°38′N, 106°03′E	585	NS
5.	*A. follicularis* Pall.	Myakshina, T.	23/08/2010	Russia	Altai Republic, Kosh-Agachsky district	Taldura River	49°57′N, 87°54′E	2069	NS
6.	*A. lupulinus* Pall.	Talalaeva, M., Galaziy, G.	08/12/1954	Russia	Irkutsk Oblast, Olkhon district	Baikal Lake, Zunduk Cape	54°94′N, 83°02′E	652	NSK
	***Craccina* (Srev.) Bunge**								
7.	*A. sulcatus* L.	Krasnoborov, I., Shaulo, D.	06/10/1999	Russia	Altai Krai, Slavgorodsky district	Podsosnovo Village	53°22′N, 78°57′E	130	NS
	***Cystium* Bunge**								
8.	*A. physocarpus* Ledeb.	Vandakurova, E.	31/05/1946	Russia	Altai Krai. Uglovsky district	Shadriha Village	51°31′N, 79°49′E	181	NS
	***Uliginosi* Gray**								
9.	*A. schelichovii* Turcz.	Koroleva, A.	04/08/1970	Russia	Yakutya Republic, Bulunsky district	Jarjan Village	68°52′N, 124°07′E	98	NS
10.	*A. uliginosus* L.	Shaulo, D., Artemov, I.	18/09/2002	Russia	Novosibirsk Oblast, Suzunsky district	Inya River	53°31′N, 82°26′E	125	NS
	***Helmia* Bunge**								
11.	*A. depauperatus* Ledeb.	Krasnoborov, I., German, D.	22/06/2000	Russia	Altai Krai, Loktevsky district	Aley River, Lugovkaya Village	51°10′N, 81°18′E	240	NS
	***Onobrychoidei* DC.**								
12.	*A. adsurgens* Pall.	Shaulo, D., Nalpina, T.	05/08/1980	Russia	Krasnoyarsk Krai	Zolotaya River	52°02′N, 92°42′E	715	NS
13.	*A. austrosibiricus* Schischk.	Shaulo, D., Tuller, D.	24/07/1983	Russia	Altai Republic, Ust-Koksinsky district	Katanda Village	50°15′N, 86°10′E	1489	NS
14.	*A. inopinatus* Boriss.	Korolyuk, A., Korolyuk, E.	09/07/2007	Russia	Buryatia Republic, Dzhidinskiy district	Niznii Torei Mountains	50°32′N, 104°48′E	758	NS
15.	*A. onobrychis* L.	Krasnoborov, I., Zhirova, O.	04/09/1996	Russia	Novosibirsk Oblast, Karasuksky district	Morozovka Village	53°55′N, 78°20′E	112	NS
	***Tanythrix* Bunge**								
16	*A. roseus* Ledeb.	Anonim	-/-/1841	Kazakhstan	East Kazakhstan Oblast	Ust-Kamenogorsk City	50°00′N, 82°36′E	306	NS
	***Trachycercis* Bunge**								
17.	*A. scaberrimus* Bunge	Korolyuk, A., Korolyuk, E.	09/07/2007	Russia	Buryatia Republic, Dzhidinskiy district	Niznii Toray Mountains	50°32′N, 104°48′E	758	NS
18.	*A. testiculatus* Pall.	Krasnoborov, I., German, D.	20/05/2000	Russia	Altai Krai, Krasnoshchekovsky district	Maraliha Village	51°38′N, 82°56′E	350	NS
19.	*A. monophyllus* Bunge	Kuminova, A., Linde, S.	31/07/1975	Russia	Tuva Republic, Barun-Khemchiksky district	Kyzyl-Mazhalyk Village	51°08′N, 90°35′E	864	NS

Table 1. (Continued).

	Dissitiflori DC.								
20.	*A. angarensis* Turcz. ex Bunge	Peshkova, R.	28/06/1956	Russia	Irkutskoblast', Eherit-Bulagatsky district	Kuda River, Ust-Orda Village	52°50′N, 104°43′E	536	NSK
21.	*A. tephrolobus* Bunge	Krasnoborov, I., Luzhetsky, V.	03/07/1966	Russia	Tuva Republic	Kyzyl City	51°41′N, 94°27′E	647	NS
22.	*A. lenensis* Shemetova, Shaulo et Lomon.	Koroleva, A.	18/07/1970	Russia	Yakutya Republic, Yakut district	Yakutsk City	61°59′N, 129°43′E	72	NS
23.	*A. ionae* Palibin.	Shaulo, D., Erst, A., Myakshina,T.	20/06/2009	Russia	Khakassia Republic, Ordzhonikidzevsky district	Upper Sutik Village	55°00′N, 89°52′E	388	NS
24	*A. suffruticosus* DC.	Myakshina, T.	27/08/2010	Russia	Altai Republic, Kosh-Agachsky district	Dzazator Village	49°44′N, 87°18′ E	1593	NS
25.	*A. arbuscula* Pall.	Vereshchagin V.	17/06/1925	Kazakhstan	Katonkaragay district	Malokrasnoyarsk City	53°30′N, 77°23′E	110	NS
26.	*A. stenoceras* C.A. Mey.	Shaulo, D., Shaulo, S.	04/07/2010	Russia	Tuva Republic. Piy-Hemsky district	Uyuk Ridge, Kamenistyi kluch brook	51°54′N, 94°25′E	642	NS
27.	*A. macroceras* Bong.	Shaulo, D., Erst, A., Myakshina, T.	25/06/2009	Russia	Tuva Republic	Uyuk Ridge, Seserlig River	51°52′N, 94°15′E	591	NS
	Alopecuroidei DC.								
28.	*A. alopecurus* Pall.	Yakubova, A., Smirnov, M.	08/10/1953	Russia	Altai Republic, Onguday district	Chuya River, Belyi Bom Village	50°22′N, 87°02′E	929	NS
	Heterodontus Bunge								
29.	*A. dahuricus* (Pall.) DC.	Kuminova, A.	08/08/1976	Russia	Tuva Republic, Dzun-Khemchiksky district	Khemchik River, Ak-Dash Village	51°16′N, 91°05′E	763	NSK
	Hypoglottidei DC.								
30.	*A. danicus* Retz.	Myakshina, T	17/08/2010	Russia	Altai Republic, Kosh-Agachsky district	Kokorya Village	49°56′N, 88°58′E	2006	NS
31.	*A. agrestis* G.Don	Krasnoborov, I.	07/07/1993	Russia	Novosibirsk Oblast, Krasnozyarsk district	Mayskoe Village	54°05′N, 79°50′E	120	NS
32.	*A. cicer* L.	Shaulo, D.	20/08/2008	Russia	Novosibirsk Oblast, Novosibirsk district	Novosibirsk City	54°50′N, 83°05′E	152	NS
33.	*A. tibetanus* Benth. ex Bunge	Danilov, M., Meshkova, E.	19/07/1981	Russia	Altai Republic, Kosh-Agachsky district	Kokorya Village	50°N, 89°E	1843	NS
	Cenantrum Bunge								
34.	*A. frigidus* (L.) A.Gray	Verkhozina, A.	11/08/2002	Russia	Buryatia Republic, Tunkinsky district	Margasan River	51°42′N, 103°33′E	1992	NSK
35.	*A. propinquus* Schisch.	Lomonosova, M., Mironov L.	12/08/1981	Russia	Altai Republic, Kosh-Agachsky district	Kokorya Village	49°55′N, 88°59′E	1855	NSK
36.	*A. membranaceus* (Fisch.) Bunge	Onoeva, E.	07/09/1966	Russia	Irkutsk oblast'	Baikal Lake, Zavorotnaya Bay	54°17′N, 108°27′E	448	NSK
37.	*A. saralensis* Gontsch.	Malyshev, L.	08/21/1961	Russia	Buryatia Republic	Udinsky Spine, Uda River	52°19′N, 111°05′E	180	NSK
38.	*A. sericeocanus* Gontsch.	Granina, G.	08/08/1974	Russia	Buryatia Republic	Upper-AngaraRiver, Dagary	55°42′N, 109°55′E	455	NSK
	Glycyphyllos Bunge								
39.	*A. glycyphyllos* L.	Krasnoborov, I.	24/07/1999	Russia	Novosibirsk Oblast, Novosibirsky district	Klychi Village	54°50′N, 83°08′E	150	NS
	Hemiphaca Gontsch.								

Table 1. (Continued).

40.	*A. macropterus* DC.	Shaulo, D., Shaulo, I.	01/07/1991	Russia	Krasnoyarsk Krai, Beysky district	Joysky Ridge, Sabinka Village	53°20′N, 91°01′E	550	NS
41.	*A. multicaulis* Ledeb.	Danilov, M., Ostanin, I.	22/07/1984	Russia	Altai Republic, Ulagansky district	Ildugem River	50°18′N, 88°15′E	2153	NS
42.	*A. rytidocarpus* Ledeb.	Krasnoborov, I.	07/07/1999	Russia	Khakassia Republic, Shirinsky district	Itkul Lake	54°30′N, 90°10′E	450	NS
43.	*A. versicolor* Pall.	Koroleva, A.; Massalikina, M.	25/07/1971	Russia	Khakassia Republic, Askizsky district	Saksary Village	54°34′N, 89°47′E	474	NS
44.	*A.bifidus* Turcz.	Malyshev, L.	19/07/1986	Russia	Buryatia Republic	White Irkut River	51°57′N, 100°57′E	1987	NSK
45.	*A. olchonensis* Gontsch.	Malyshev, L., Vodopyanov, N.	25/08/1973	Russia	Irkutsk Oblast.	Baikal Lake, Olchon Island, Peschanaya Bay	52°15′N, 105°42′E	427	NSK
	Hemiphragmium (Koch) Bunge								
46.	*A. chorinensis* Bunge	Krasnoborov, I.	02/07/1979	Russia	Irkutsk Oblast	Baikal Lake, Zugduk Cape	53°10′N, 106°57′E	472	NS
47.	*A. kaufmannii* Krylov	Lomonosova, M.	13/08/1984	Russia	Altai Republic	Terektinsky Ridge, Ust-Koksa Village	50°12′N, 85°38′E	1587	NS
48.	*A. pseudoaustralis* Fisch. et C.A. Mey.	Kuznetsov, G.	05/08/1963	Russia	Altai Republic	Kurai Ridge, Mezhtuyaryk Village	50°49′N, 88°19′E	2500	NS
49.	*A. tschuensis* Bunge	Danilov, M.	30/07/1982	Russia	Altai Republic, Kosh-Agachsky district	Uzuntotygem River	50°6′N, 89°10′E	2500	NS
50.	*A. vaginatus* Pall.	Krasnoborov, I.	14/07/1989	Russia	Altai Republic, Ulaganskiy district	Chibit Village	50°20′N, 87°30′E	1217	NS
51.	*A. trigonocarpus* (Turcz.) Bunge	Karnaukhov, D., Selyutin, I.	22/07/2005	Russia	Irkutsk Oblast	Baikal Lake, Olchon Island, Khoboy Cape	53°24′N, 107°47′E	607	NSK
52.	*A. kolymensis* Jurtzev	Berkutenko, A.	21/07/1974	Russia	Magadan Oblast, Yagodinsky district	Izvestkovyi Village, Tascan River	62°47′N, 150°41′E	312	NSK
	Komaroviella Gontsch.								
53.	*A. alpinus* L.	Shaulo, D., Kovalev, I.	19/07/1979	Russia	Krasnoyarsk Krai	Kurtushibinsky Ridge, Tyhaya River	52°37′N, 93°46′E	1161	NS
	Melilotopsis Gontsch.								
54.	*A. tenuis* Turcz.	Peshkova, G., Ovchinnikova L.	05/08/1964	Russia	Transbaikal Krai	Duldurga Village	50°40′N, 113°34′E	831	NSK
	Orobella Gontsch.								
55.	*A. norvegicus* Grauer	Lomonosova, M., Khanminchun, V.	20/07/1981	Russia	Altai Republic, Kosh-Agachsky district	Aktal Village	51°10′N, 93°24′E	1061	NS
56.	*A. politovii* Krylov	Kuminova, V., Listova, N	26/07/1955	Russia	Altai Republic	Ukok Plateau, Cholok-Chad Mountains	49°15′N, 87°35′E	2578	NS

samples were sprayed with gold using the SPI MODULE unit and examined using a Philips SEM 515 scanning electron microscope (Eindhoven, The Netherlands) at Tomsk Materials Science Center (Tomsk State University). Scanning was performed on a lateral part of each seed at 55×, 800×, and 2000× magnification. The present paper provides images with 2000× magnification only. Digital images were processed using Adobe Photoshop CS 4 (San Jose, CA, USA).

The terminology proposed by Barthlott (1981) was used to describe surface sculpture. His approach distinguishes three sculpture levels: primary, secondary, and tertiary. Primary sculpture encompasses the outline of exotestal cells—general appearance, the type of anticlinal walls (AW), the relief of cellular boundaries, and the curvature of the outer periclinal walls (OPW). Secondary sculpture considers the features of the OPW surface (reticulate, tuberculate, smooth, etc.). Tertiary sculpture caused by various epicuticular secretions is quite rare on the seed surface (Shemetova, 2014) and was not found in the surveyed species.

3. Results and discussion

The seed shape, color, size, surface sculpture, and hilum position are taxonomically informative. The present study examined the seed morphology from 56 species of *Astragalus*. The surveyed species are characterized by multiseeded, puberulous, or less often glabrous fruits (sect. *Caprini* DC., *Glycyphyllos* Bunge, *Hemiphragmium* (Koch.) Bunge, *Hemiphaca* Gontsch., and *Melilotopsis* Gontsch.). The beans are of various shapes: narrow, oblong or elliptical, ovate, or semiglobose.

The seeds of the studied species from the genus *Astragalus* are yellow–green, greenish brown, reddish brown, or grayish brown, sometimes with darker lines in the region of the hilum, which is oval or rounded. The seeds are mostly reniform–globose and slightly flattened near the hilum. Rombiform seeds were observed in a few species (*A. depauperatus* Ledeb., *A. onobrychis* L., *A. tephrolobus* Bunge, *A. macroceras* Bong., *A. dahuricus* (Pall.) DC., *A. glycyphyllos* L., and *A. multicaulis* Ledeb.), and in three species (*A. angarensis* Turcz. Ex Bunge, *A. aveolated* Pall., and *A. olchonensis* Gontsch.) the seeds are oblong–elliptical in shape, with the apex elongated and acute, and the radicle protruding (Figure 1; Table 2).

Seed sizes vary from 1.25 × 0.88 mm (*A. tenuis* Turcz.) to 4.94 × 3.29 mm (*A. wolgensis* Bunge). The average seed size is 3.84 × 3.02 mm. This category includes species of the section *Caprini* DC. (*A. schanginianus* Pall., *A. wolgensis*), section *Alopecuroidei* DC. (*A. alopecurus* Pall.), and two species from the section *Cenantrum* Bunge (*A. propinquus* Schischk. and *A. sericeocanus* Gontsch.). The seeds of most species are of medium size (with an average of 2.44 × 1.87 mm) and 23 species have small seeds (with an average of 1.62 × 1.33 mm) (sect. *Onobrychoidei* DC., *Hemiphaca*, *Komaroviella* Gontsch., *Melilotopsis*, and some species from other sections).

The morphological features of *Astragalus* seed surface depend on the shape of the main epidermal cells, the thickness and curvature of their anticlinal walls, and the relief of the periclinal wall surface. Anticlinal walls in the seeds of species from the surveyed sections can be straight (*A. arkalycensis* Bunge, *A. shelichovii* Turcz., *A. depauperatus* Ledeb., *A. tephrolobus*, and others), slightly undulate (*A. tenuis*, *A. physocarpus*, *A. frigidus*, and others), strongly undulate (*A. trigonocarpus*, *A. saralensis* Gontsch., *A. chorinensis*), slightly thickened, flush with or raised above the periclinal wall surface (Figures 2–4). The relief of the periclinal walls (PW) can be aveolate, stellate, pectinate, or rugose.

In all the studied species, two main types of seed surface ultrasculpture were observed: with a reticulate pattern of seed surface (Type 1) and with an indistinct reticulate surface (Type 2).

In Type 1 morphology, the primary sculpture of seeds is well defined and consists of isodiametric cells of the exotesta. Most species possess straight or slightly sinuous anticlinal walls. Thin, indistinct anticlinal walls are found in *A. suffruticosus* DC., *A. stenoceras* C.A. Mey., *A. macroceras* (sect. *Dissitiflori* DC.), *A. tibetanus* Benth. Ex Bunge (sect. *Hypoglottidei* DC.), and *A. kolymensis* Jurtzev. (sect. *Hemiphragmium*). Anticlinal walls are thick in three species of different sections: *A. onobrychis* L., *A. angarensis*, and *A. chorinensis* Bunge (Figures 2 and 3). A particular relief of anticlinal walls can be observed in *A. arkalycensis*, *A. monophyllus* Bunge, *A. tephrolobus*, *A. ionae* Palib., and *A. politovii* Krylov; in these species, well-defined anticlinal walls with a double-convex relief were observed, unlike the other species. The secondary level of sculpture is not easily distinguished.

In a small number of species, the seed surface had anticlinal walls with indistinct relief (Type 2) and well-defined secondary sculpture (Figure 4). Type 2 species displayed four types of secondary sculpture: stellate–pectinate (*A. laguroides* Pall., *A. follicularis* Pall., *A. sulcatus* L., *A. inopinatus* Boriss., *A. lenensis* Shemetova, Schaulo et Lomon., *A. danicus* Retz., *A. agrestis* Douglas ex Hook., and *A. alpinus* L.), faveolate (*A. schanginianus*, *A. alopecurus*, and *A. propinquus*), rugose (*A. lupulinus* Pall., *A. testiculatus* Pall., *A. glycyphyllos* L., and *A. olchonensis*), and pectinate (*A. wolgensis*, *A. versicolor* Pall., and *A. kaufmannii* Krylov).

Surface characters are of little value within the sections and in some cases, seed sculpture was similar between

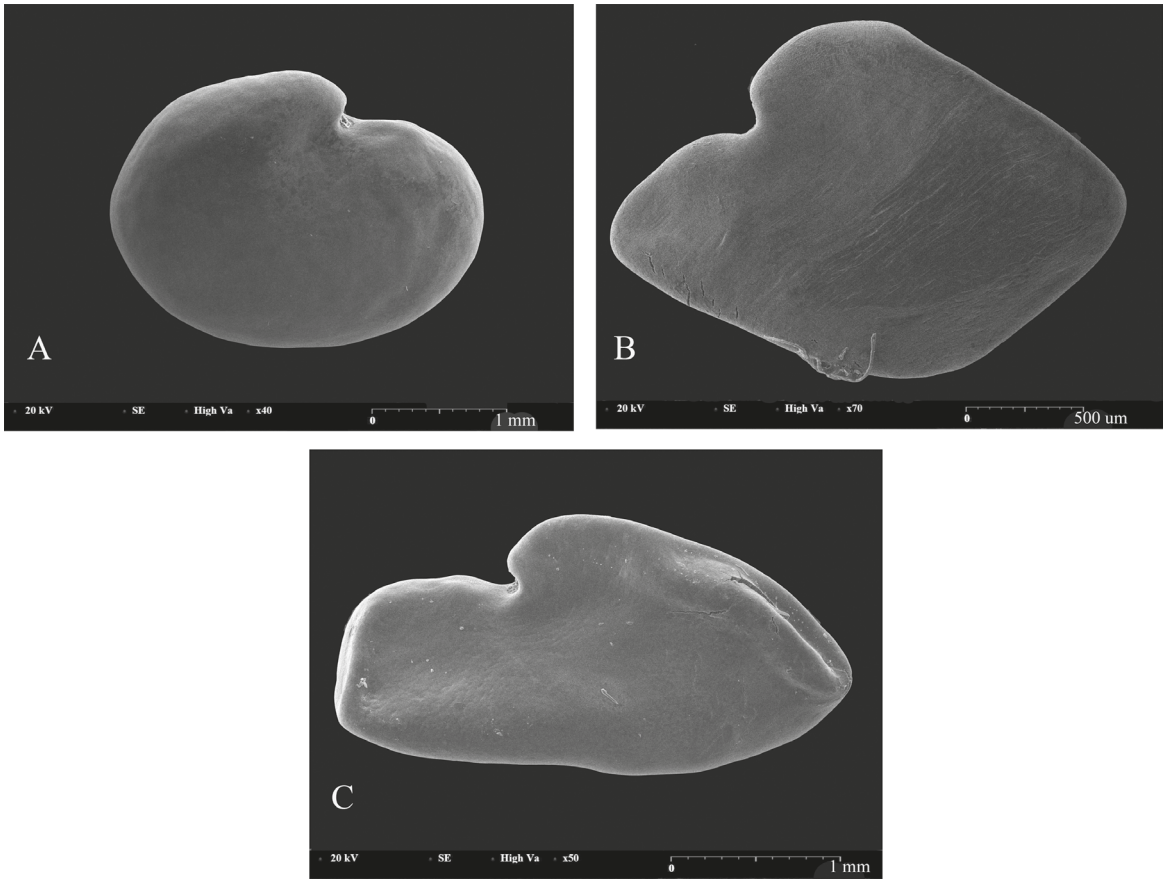

Figure 1. SEM-micrographs of seeds in species of the genus *Astragalus*: (A) *A. arkalycensis* (reniform–globose), (B) *A. depauperatus* (rombiform), and (C) *A. arbuscula* (oblong–elliptical).

sections. In all surveyed species of sections *Cystium* Bunge (*A. physocarpus* Ledeb.), *Uliginosi* Gray. (*A. schelichovii* and *A. uliginosus* L.), *Helmia* Bunge (*A. depauperatus*), *Heterodontus* Bunge (*A. dahuricus*), *Melilotopsis* (*A. tenuis* Turcz.), and *Orobella* Gray. (*A. norvegicus* Grauer and *A. politovii* Krylov), the primary sculpture is of isodiametric cells with a reticulate relief. Conversely, a reticulate pattern of seed surface was not seen in species of sections *Caprini* (*A. schanginianus* and *A. wolgensis*), *Craccina* (Stev.) Bunge (*A. sulcatus* L.), *Alopecuroidei* (*A. alopecurus*), *Glycyphyllos* (*A. glycyphyllos*), and *Komaroviella* (*A. alpinus*).

Various types of sculpture can be found in species of sections *Laguropsis* Bunge, *Onobrychoidei*, *Trachycercis* Bunge, *Dissitiflori*, *Hypoglottidei* DC., *Cenantrum*, *Hemiphaca*, and *Hemiphragmium*. Species with reticulate surface sculpture predominate among other species of these sections. The primary sculpture cannot be distinguished in some species, such as *A. inopinatus* (*Onobrychoidei*), *A. testiculatus* (*Trachycercis*), *A. lenensis* (*Dissitiflori*), *A. danicus* and *A. agrestis* (*Hypoglottidei*), *A. propinquus* (*Cenantrum*), *A. versicolor* and *A. olchonensis* (*Hemiphaca*), and *A. kaufmanni* (*Hemiphragmium*). Only *A. arkalycensis* Bunge of section *Laguropsis* exhibits a reticulate pattern of seed surface. The primary sculpture of the other three species (*A. laguroides*, *A. follicularis*, *A. lupulinus*) is indistinct.

Our data are consistent with those of other studies on seed surface sculpture in the Fabaceae. Similar types of seed surface sculpture in other species of *Astragalus* were described by Engel (1990), Ekici et al. (2005), and Vural et al. (2008), and were observed in species of the genus *Ebenus* L. (Bayrakdar et al., 2010). For the surveyed species, the authors noted reticulate, multireticulate, striate, and rugose seed patterns.

Our results indicate that seed shapes, colors, sizes, surface sculptures, and hilum positions are very diverse. Some characters seem to have systematic value, such as the types of seed surface, whereas others are apparently associated with particular habitats. However, the systematic importance of seed characters needs to be evaluated in a phylogenetic context. Unfortunately, there is still a lack of robust phylogenetic framework for *Astragalus*. In the

Table 2. Size and ultrasculpture of seed surface in *Astragalus* L.

Species	Seed length	Seed width	Seed shape	Seed surface sculpture
Sect. *Caprini*				
A. schanginianus	3.38 ± 0.21	3.49 ± 0.16	Reniform–globose	Faveolate
A. wolgensis	4.94 ± 0.03	3.29 ± 0.11	Reniform–globose	Pectinate
Sect. *Laguropsis*				
A. arkalycensis	2.64 ± 0.23	1.98 ± 0.14	Reniform–globose	Reticulate
A. laguroides	2.24 ± 0.09	1.88 ± 0.07	Reniform–globose	Stellate–pectinate
A. follicularis	2.66 ± 0.19	1.83 ± 0.07	Reniform–globose	Stellate–pectinate
A. lupulinus	3.01 ± 0.18	2.21 ± 0.21	Reniform–globose	Rugose
Sect. *Craccina*				
A. sulcatus	1.75 ± 0.36	1.21 ± 0.03	Reniform–globose	Stellate–pectinate
Sect. *Cystium*				
A. physocarpus	2.27 ± 0.07	1.77 ± 0.09	Reniform–globose	Reticulate
Sect. *Uliginosi*				
A. schelichovii	1.9 ± 0.21	1.3 ± 0.14	Reniform–globose	Reticulate
A. uliginosus	1.51 ± 0.14	1.59 ± 0.12	Reniform–globose	Reticulate
Sect. *Helmia*				
A. depauperatus	1.36 ± 0.06	1.4 ± 0.17	Rombiform	Reticulate
Sect. *Onobrychoidei*				
A. adsurgens	1.51 ± 0.11	1.29 ± 0.11	Reniform–globose	Reticulate
A. austrosibiricus	1.75 ± 0.17	1.54 ± 0.12	Reniform–globose	Reticulate
A. inopinatus	1.61 ± 0.12	1.65 ± 0.10	Reniform–globose	Stellate–pectinate
A. onobrychis	1.38 ± 0.05	1.25 ± 0.03	Rombiform	Reticulate
Sect. *Tanythrix*				
A. roseus	2.06 ± 0.02	1.59 ± 0.01	Reniform–globose	Reticulate
Sect. *Trachycercis*				
A. scaberrimus	1.63 ± 0.23	1.29 ± 0.19	Reniform–globose	Reticulate
A. testiculatus	1.65 ± 0.13	1.55 ± 0.11	Reniform–globose	Rugose
A. monophyllus	2.41 ± 0.19	1.76 ± 0.06	Reniform–globose	Reticulate
Sect. *Dissitiflori*				
A. angarensis	2.09 ± 0.13	1.36 ± 0.11	Oblong–elliptical	Reticulate
A. tephrolobus	1.77 ± 0,08	1.38 ± 0.12	Rombiform	Reticulate
A. lenensis	2.16 ± 0.06	1.53 ± 0.13	Reniform–globose	Stellate–pectinate
A. ionae	2.59 ± 0.32	1.64 ± 0.21	Reniform–globose	Reticulate
A. suffruticosus	2.26 ± 0.13	1.58 ± 0.07	Reniform–globose	Reticulate
A. arbuscula	2.88 ± 0.29	1.44 ± 0.19	Oblong–elliptical	Reticulate
A. stenoceras	3.13 ± 0.11	1.09 ± 0.11	Oblong–elliptical	Reticulate
A. macroceras	2.44 ± 0.17	1.77 ± 0.09	Rombiform	Reticulate
Sect. *Alopecuroidei*				
A. alopecurus	3.75 ± 0.22	2.58 ± 0.021	Reniform–globose	Faveolate
Sect. *Heterodontus*				
A. dahuricus	1.27 ± 0.18	1.02 ± 0.03	Rombiform	Reticulate

Table 2. (Continued).

Sect. *Hypoglottidei*				
A. danicus	1.49 ± 0.27	1.13 ± 0.19	Reniform–globose	Stellate–pectinate
A. agrestis	1.37 ± 0.15	1.25 ± 0.17	Reniform–globose	Stellate–pectinate
A. cicer	2.31 ± 0.14	1.87 ± 0.07	Reniform–globose	Reticulate
A. tibetanus	2.1 ± 0.37	1.45 ± 0.026	Reniform–globose	Reticulate
Sect. *Cenantrum*				
A. frigidus	2.35 ± 0.19	2.01 ± 0.14	Reniform–globose	Reticulate
A. propinquus	3.63 ± 0.24	3.49 ± 0.13	Reniform–globose	Faveolate
A. membranaceus	2.53 ± 0.23	1.76 ± 0.21	Reniform–globose	Reticulate
A. saralensis	2.36 ± 0.15	1.66 ± 0.05	Reniform–globose	Reticulate
A. sericeocanus	3.49 ± 0.12	2.25 ± 0.08	Reniform–globose	Reticulate
Sect. *Glycyphyllos*				
A. glycyphyllos	2.06 ± 0.36	1.98 ± 0.17	Rombiform	Rugose
Sect. *Hemiphaca*				
A. macropterus	1.58 ± 0.19	1.25 ± 0.13	Reniform–globose	Reticulate
A. multicaulis	1.72 ± 0.09	1.66 ± 0.06	Rombiform	Reticulate
A. rytidocarpus	2.04 ± 0.11	1.12 ± 0.13	Reniform–globose	Reticulate
A. versicolor	1.51 ± 0.17	1.41 ± 0.11	Reniform–globose	Pectinate
A. bifidus	1.42 ± 0.21	1.07 ± 0.17	Reniform–globose	Reticulate
A. olchonensis	2.66 ± 0.28	1.55 ± 0.17	Oblong–elliptical	Rugose
Sect. *Hemiphragmium*				
A. chorinensis	2.13 ± 0.16	1.93 ± 0.09	Reniform–globose	Reticulate
A. kaufmannii	2.33 ± 0.07	2.26 ± 0.10	Reniform–globose	Pectinate
A. pseudoaustralis	2.43 ± 0.31	2.5 ± 0.23	Reniform–globose	Reticulate
A. tschuensis	2.27 ± 0.29	2.21 ± 0.27	Reniform–globose	Reticulate
A. vaginatus	2.36 ± 0.09	2.43 ± 0.03	Reniform–globose	Reticulate
A. trigonocarpus	2.42 ± 0.12	2.14 ± 0.13	Reniform–globose	Reticulate
A. kolymensis	2.57 ± 0.25	2.49 ± 0.18	Reniform–globose	Reticulate
Sect. *Komaroviella*				
A. alpinus	1.83 ± 0.12	1.42 ± 0.14	Reniform–globose	Stellate–pectinate
Sect. *Melilotopsis*				
A. tenuis	1.25 ± 0.17	0.88 ± 0.5	Reniform–globose	Reticulate
Sect. *Orobella*				
A. norvegicus	2.07 ± 0.19	1.66 ± 0.10	Reniform–globose	Reticulate
A. politovii	2.97 ± 0.26	2.43 ± 0.19	Reniform–globose	Reticulate

Mean value ± standard deviation.

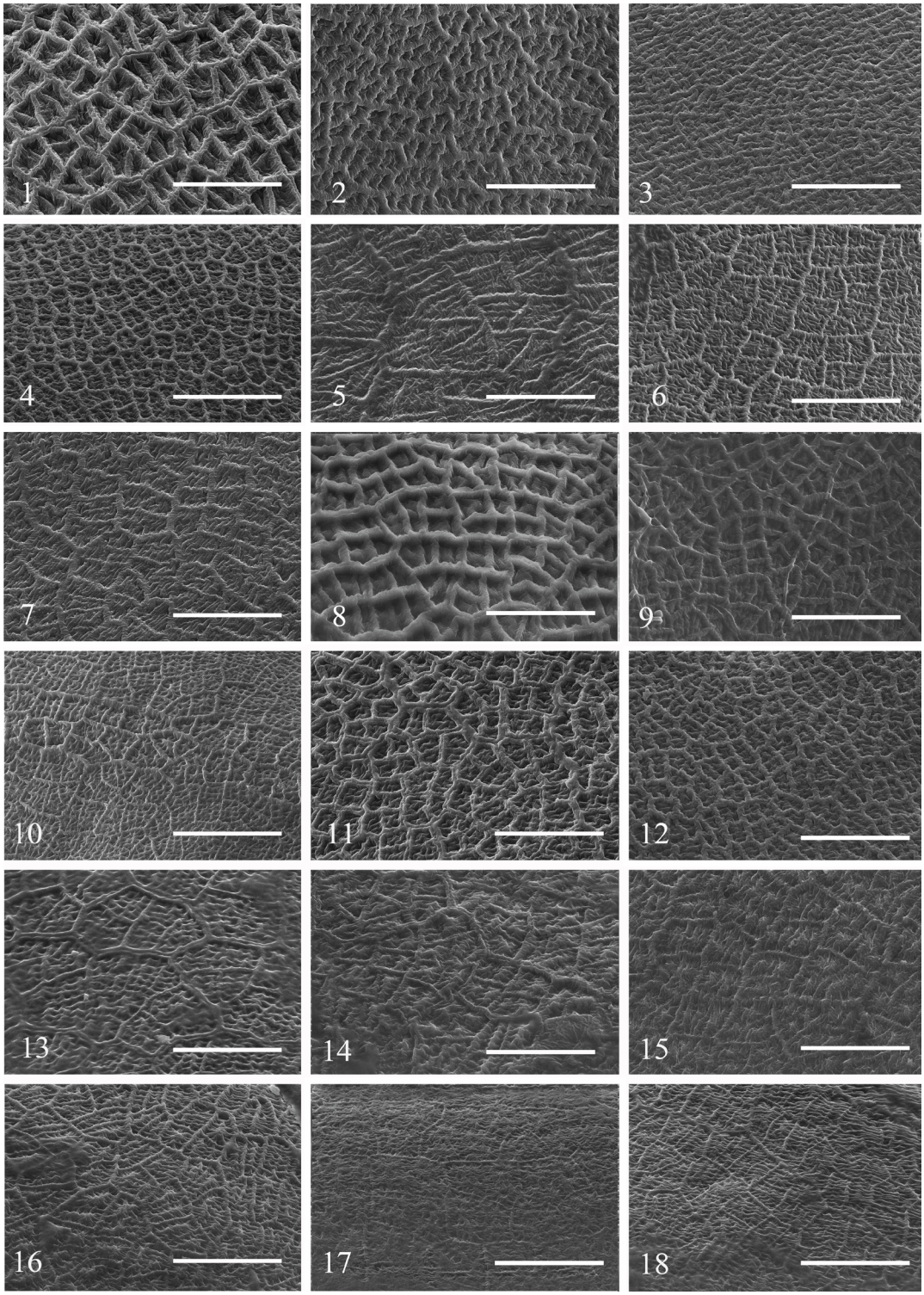

Figure 2. SEM-micrographs of seed surfaces in species of the genus *Astragalus*: (1) *A. arkalycensis*, (2) *A. physocarpus*, (3) *A. schelichovii*, (4) *A. uliginosus*, (5) *A. depauperatus*, (6) *A. adsurgens*, (7) *A. austrosibiricus*, (8) *A. onobrychis*, (9) *A. roseus*, (10) *A. scaberrimus*, (11) *A. monophyllus*, (12) *A. angarensis*, (13) *A. tephrolobus*, (14) *A. ionae*, (15) *A. suffruticosus*, (16) *A. arbuscula*, (17) *A. stenoceras*, and (18) *A. macroceras*. Scale bar is 30 μm.

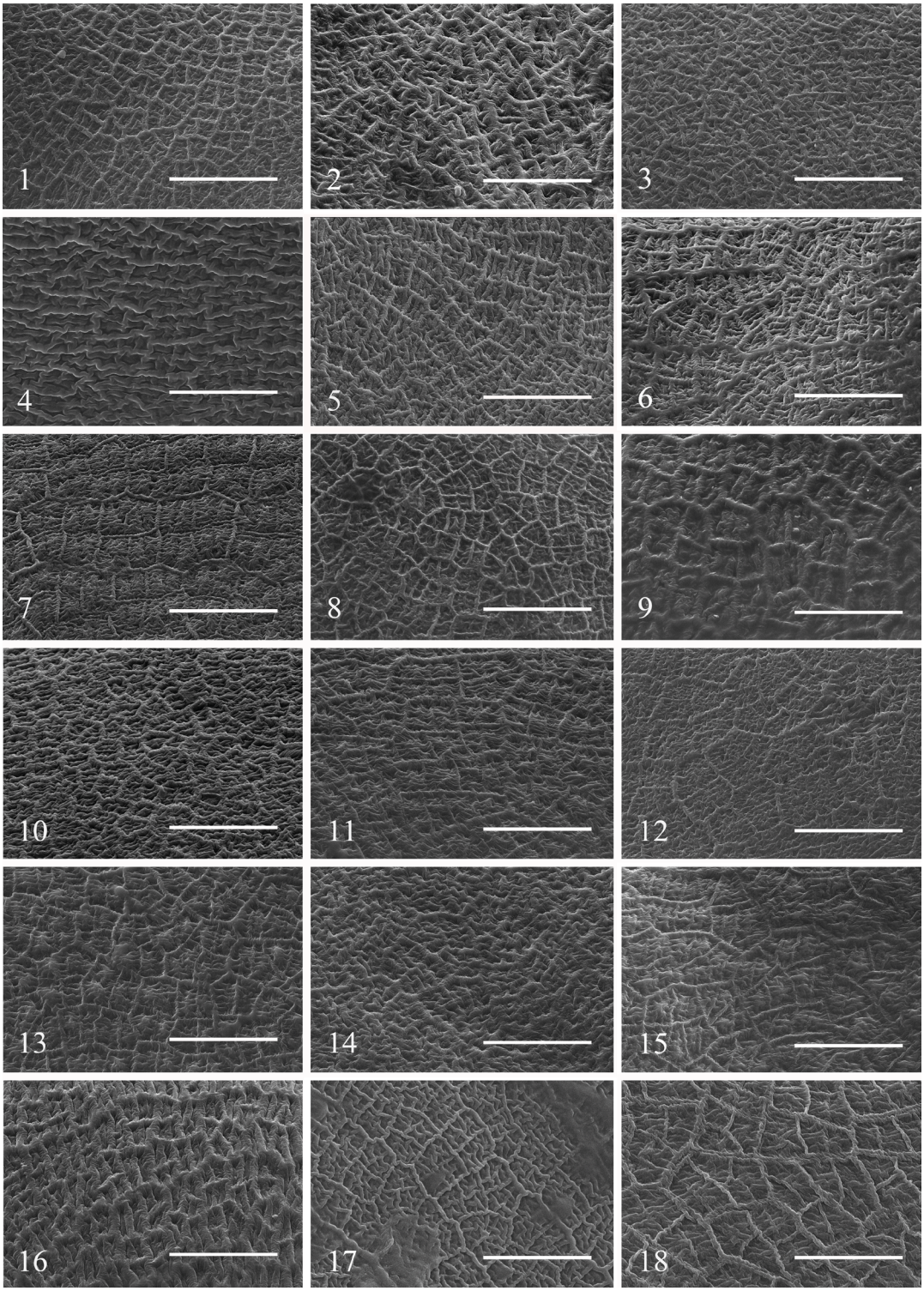

Figure 3. SEM-micrographs of seed surfaces in species of the genus *Astragalus*: (1) *A. dahuricus*, (2) *A. cicer*, (3) *A. tibetanus*, (4) *A. frigidus*, (5) *A. sericeocanus*, (6) *A. macropterus*, (7) *A. multicaulis*, (8) *A. rytidocarpus*, (9) *A. bifidus*, (10) *A. chorinensis*, (11) *A. pseudoaustralis*, (12) *A. tschuensis*, (13) *A. vaginatus*, (14) *A. trigonocarpus*, (15) *A. kolimensis*, (16) *A. tenuis*, (17) *A. norvegicus*, and (18) *A. politovii*. Scale bar is 30 μm.

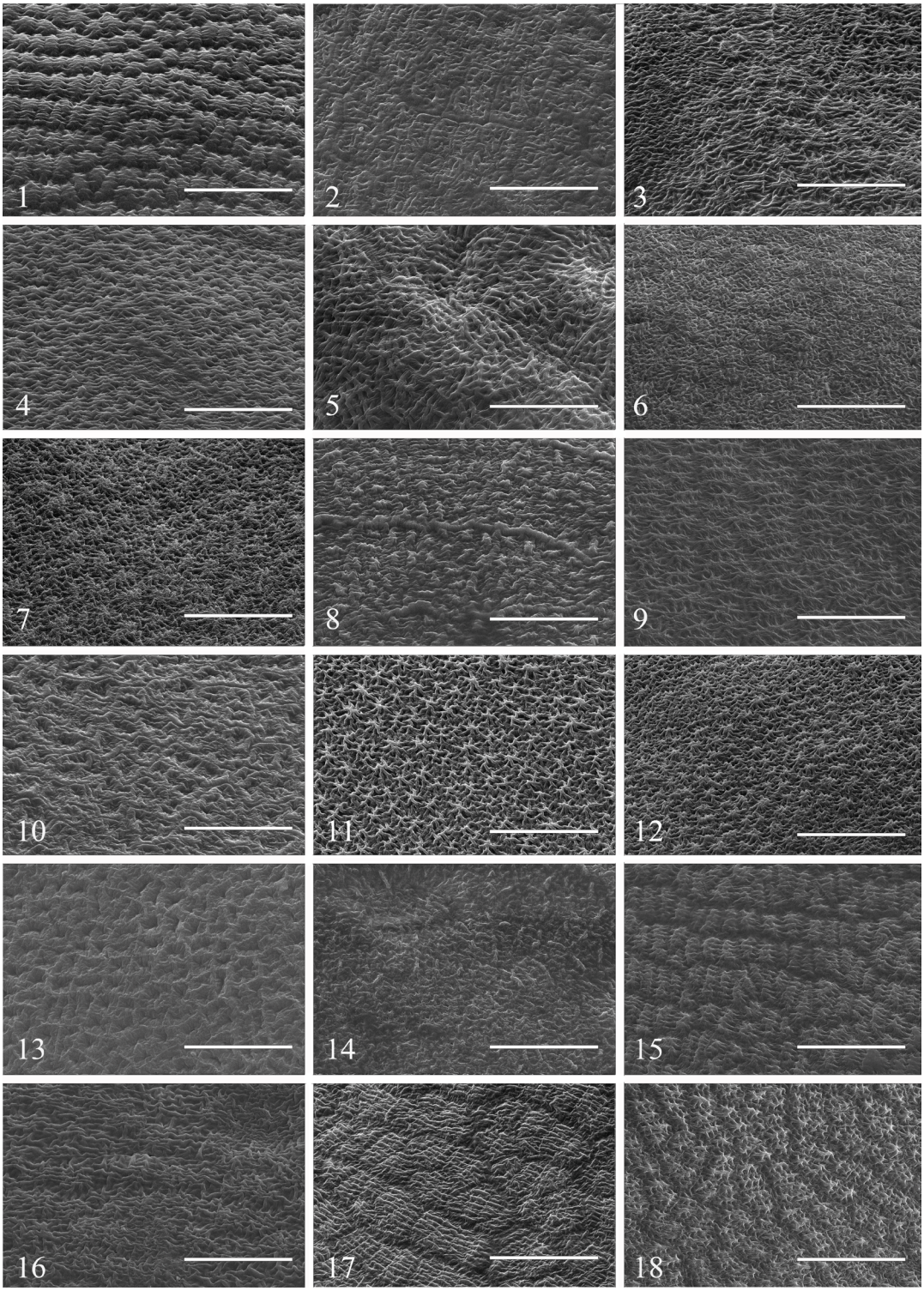

Figure 4. SEM-micrographs of seed surfaces in species of the genus *Astragalus*: (1) *A. wolgensis*, (2) *A. schanginianus*, (3) *A. laguroides*, (4) *A. follicularis*, (5) *A. lupulinus*, (6) *A. sulcatus*, (7) *A. inopinatus*, (8) *A. testiculatus*, (9) *A. lenensis*, (10) *A. alopecurus*, (11) *A. danicus*, (12) *A. agrestis*, (13) *A. propinquus*, (14) *A. glycyphyllos*, (15) *A. versicolor*, (16) *A. olchonensis*, (17) *A. kaufmannii*, and (18) *A. alpinus*. Scale bar is 30 μm.

future, an integration of seed morphology and molecular phylogenetics will lead to a better understanding of the evolutionary history of *Astragalus*.

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