

POLLEN MORPHOLOGY OF SOME ASIATIC SPECIES OF GENUS *SALSOLA* (CHENOPODIACEAE) AND ITS TAXONOMIC RELATIONSHIPS

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Abstract

Comparative studies on the pollen grain morphology of 27 Asiatic species of the genus *Salsola* were conducted by using scanning electron microscope (SEM analysis) in order to assess the taxonomic value of pollen traits. The pollen are radially symmetrical isopolar, pantopolyporate, spherical or subspheroid. The pollen characters like size, pore number, chord (C/D ratio), pore diameter, exine thickness, level of sinking of pore, convexness of mesoporial exine, spinule and minute-hole densities and number of spines on pore membrane appeared to be useful characters in distinguishing the species. Interesting intraspecific variations in pollen grain morphology were recorded for the C/D ratio. This parameter is highly specific, supporting the delimitation of *Salsola* species, and appears to be more conservative than some flower and fruit characters. The numerical value of form index comprising the ratio between the length of polar axis and diameter (P/E) also was an informative trait for delimitation of the species investigated here. Three pollen types were recognized. Euclidean distance was used to compute the dissimilarity matrix and a cladogram prepared. The quantitative characters of pollen morphology allowed clustering of groups and ordination analyses of species from different sections/subsections within genus *Salsola*. These features indicated that overall pollen traits reflect the current taxonomic boundaries, except for the *Salsola* species allocated to *Climacoptera* and *Halothamnus*, which should be accepted as separate genera.

Introduction

Chenopodiaceae has attracted the attention of several investigators from different disciplines including pollen morphology; notable among them being Akhani (1996, 2003), Akhani *et al.*, (1997, 2003, 2005, 2007, 2009), Perveen (2000), Khan *et al.*, (2002), Shepherd *et al.*, (2005), Kadereit *et al.*, (2003, 2006), Khan and Qaiser (2006), Keshavarzi and Zare (2006), Mehrun-Nisa *et al.*, (2007), Murakeozy *et al.*, (2007), Christine *et al.*, (2007), Voznesenskaya *et al.*, (2007), Zare and Keshavarzi (2007), Sukhorukov (2007, 2008), Olvera *et al.*, (2008), Akopian *et al.*, (2008), Cabrera *et al.*, (2009), Smith *et al.*, (2009), Doulatyari *et al.*, (2009), and Guma *et al.*, (2010). In spite of all these investigations still many difficulties are experienced in distinguishing the pollen of Chenopodiaceae even from those of some very closely related families of order *Centrospermae*, like *Amaranthaceae*, *Caryophyllaceae*, *Dysphanaceae* and *Phytolacaceae* because of strong similarity in their floral and pollen morphology.

Moquin-Tandon (1849) was the first to describe pollen of this family. A general description of the pollen morphology of some chenopods is also found in the classical works of Averdieck (1958) and Erdtman (1966), who described Chenopodiaceae as a stenopalynous family with (oligo-) polyporate pollen grain type. In some studies importance of taxonomical significance of pollen characters, such as sizes of pollen grains and aperture configurations in Chenopodiaceae has been stressed. The pollen morphology of more than 117 species belonging to 50 genera from Chenopodiaceae both from Cyclolobeae and Spirolobeae subfamilies in the flora of former Soviet Union has been compared with the species of taxonomically closely related families from Order Centrospermae such as, Amaranthaceae and Caryophyllaceae (Monoszon, 1973). An artificial key for distinguishing *Salsola* species such as *S. kali*, *S. lanata*, *S. laricina*, *S. longistylota*, *S. ruthenica*, *S. soda*, *S. dendroides* and *S. rigida* based on palynological characters has also been given (Monoszon, 1973). However, these palynological studies were mainly based on fossil pollen and a restricted number of individuals from each species. These studies cannot fully explain the morphological characteristics of the male gametophyte if we take into consideration the conservatism associated with reproductive structures and reproduction processes (Toderich, 2008).

Tsukada (1967) was the first who distinguished Chenopodiaceae from Amaranthaceae by using electron microscopic studies based on various palynological parameters including apertures and exine sculpture, number of pores, exine perforations, form, sizes and number of spinules. Nowicke and Skvarla (1979) compared the Chenopodiaceae with Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Halophytaceae, Nyctaginaceae, Phytolaccaceae, Portulacaceae and Caryophyllaceae. According to them ultrastructure of pollen grain of Chenopodiaceae resembles Amaranthaceae in several aspects such as thickened tecta, the aperture structure with reduced pointed flecks of exine underlain by lamellar plates, and a thickened amorphous endexine of pollen. However, their observations were used on restricted number of genera (*Aellenia*, *Anabasis*, *Haloharis*, *Beta*, *Chenopodium*, and *Nitrophila*) and species.

Number of pores has been used as a diagnostic systematic feature by many authors, especially for families with a polyporate type of pollen grain like Chenopodiaceae (McAndrews & Swanson, 1967; Uotila, 1974; Gomez & Pedrol, 1987; Youngjae and Lee, 1995; Helena and Santos, 1999; Toderich *et al.*, 2000). The pollen morphology in genus *Salsola* was discussed only briefly in the previous publications of Nowicke and Skvarla (1979) and Toderich *et al.*, (2000). General description of pollen grain of *S. tragus* is given in the classical work of Erdtman (1966). Some palynological data of *Salsola* is also included in the monograph of Kupriyanova and Alyoshina (1972) covering the pollen flora of Russia. Some palynological data from the taxonomical point of view is also given for *Salsola komarovii* in the Korean Flora (Youngjae & Lee, 1995). However, the pollen morphology of Chenopodiaceae in particular genus *Salsola*, has not been investigated at length. Only few studies related to the pollen morphology of genus *Salsola* have been completed, which provide descriptions of very few species.

The lack of data on the pollen grain morphology has added to the taxonomic difficulties within the family. Uptill now no worldwide monograph on this genus has been published. In some species, due to the high degree of polymorphism and wide distribution, together with transcontinental dispersal as in *Salsola kali*, identification of species with the aid of local floras is posing difficulties. The aim of this paper therefore is to provide first comprehensive survey of the pollen grains of *Salsola* species from Central Asia using SEM (scanning electron microscopy) in order to detect the possible

evolutionary trends in *Salsola* pollen morphology and provide additional data for future analysis of intraspecific and intrageneric systematics and phylogenetic relationships of *Salsola* in the world. This paper has mainly paid an attention primarily at the species level. The pollen morphology presented here will provide a supplementary support in the taxonomical revision of the genus *Salsola*, tribe Salsoleae (Chenopodiaceae).

Materials and Methods

The flower samples of 27 *Salsola* taxa from Central Asia were collected from their natural habitats. Their pollen morphology and quantitative attributes were investigated. Only 1-2 populations (more than 50 flowers for each population) were evaluated for endemic species: *S. montana*, *S. aperta*, *S. gemmascens*, *S. incanescens*, *S. arbusculiformis*, *S. pachyphylla*, *S. aucheri* and *S. gossypina*. In the case of species like *S. arbuscula*, *S. richteri*, *S. paletziana*, *S. carinata*, *S. leptoclada*, *S. sclerantha*, *S. dendroides*, *S. micranthera*, *S. orientalis*, *S. laricina*, *S. iberica*, *S. praecox*, *S. ruthenica*, *S. kali*, *S. paulsenii*, *S. pestifer*, *S. lanata*, *S. crassa*, *S. subaphylla* with wide geographical distribution samples from more than 8-10 populations were collected. The nomenclature of species has been adopted according to the Flora of Uzbekistan (1953). Flowers were fixed in glutaraldehyde, postfixed in OsO₄ and dehydrated. Critical point drying was done in CPD 030 Balzers and putter-coated with gold in SCD050 Balzers. The observations were made using JEOL JSMT330 scanning electron microscope and described according to Bozolla and Russell (1998). The studies were made during 2000-2004. Comparative analysis of pollen morphology and measurement of qualitative parameters of pollen grains was done at the Laboratory of Plant Cell Structure-Kyoto University (Japan), Department of Botany-Poznan University (Poland) and Laboratory of Electron Microscopy, University of Georgia (USA).

Following quantitative and qualitative parameters were recorded: pollen diameter (D1- maximum diameter, μm); polar axis (D2- diameter perpendicular to D1, μm); chord distance between three neighboring pores, forming a triangle with sides as equal as possible near the highest focus on the grain (C, μm); C/D ratio- mean value between three neighboring pores and diameter of pollen grain; total numbers of pores and numbers of pores per 100 μm^2 ; diameter of pore (μm) and pore area (μm^2); distance of interpore (μm); exine thickness (μm); veruca numbers on mesoporial exine; echinus number on pore membrane; convexness of mesoporial exine (++, prominent; +, weak; - none{flat}) and sinking of pore (++, prominent; +, weak; - none{flat}). The values of pollen indices were taken by using computer program Digital Image Scanning System (DISS) according to Bozolla and Russell (1998). Statistics and cluster analysis was done according to Lakin (1990) by using computer Program Windows Microsoft Excel and Statistica 6 version.

Results

The palynological data showed that all investigated species of genus *Salsola* have spinulose and punctate/perforate tectum, differing mostly in the type of apertures, number and degree of pore sinking, pollen grain size, exine thickness, nanospinules number on the mesoporial exine; echinae number on pore, interpore distance and C/D ratio value. Data for examined species is presented in Table 1. Palynological features of the investigated *Salsola* species are outlined below.

Table 1. Interspecific variation of palynological traits of some Asiatic species of *Salsola*

Species	Diameter of pollen (μm)	Polar axis (μm)	Distance of interpore (C) (μm)	C/D ratio	Number of pores	Size of pore (μm)	Diameter of pore (μm)	Pore area (μm^2)	Exine thickness	Form index	Number of spinules /per $100\mu\text{m}^2$	Sinking of pore ²	Convexness of mesopore ³
Section <i>Coccosalsola</i> (Ulbrich) Botcs., subsection <i>Aarbuscula</i>													
<i>S. arbuscula</i>	13.26±0.28	13.04±0.25	2.31±0.27	0.294	22	3.41±0.26	1.93±0.13	2.99	0.88±0.12	0.977	290±8	+	+
<i>S. arbusculiformis</i>	15.35±0.24	15.03±0.20	3.57±0.11	0.414	18	2.96±0.16	2.31±0.13	4.70	0.83±0.03	0.980	191±4	+	+
<i>S. richieri</i>	15.20±0.25	14.50±0.29	2.48±0.11	0.424	20	3.26±0.07	2.61±0.06	5.37	0.79±0.03	0.957	303±17	+	+
<i>S. pachyphylla</i>	17.50	17.10	3.28±0.22	0.439	16	4.59±0.23	2.63±0.09	5.44	1.03 ±0.14	0.977	167±28	+	+
<i>S. paletzkiana</i>	15.42±0.16	14.58±0.15	2.72±0.08	0.403	19	4.19±0.15	3.33±0.18	9.10	0.93±0.03	0.946	156±16	+	++
<i>S. montana</i>	13.12±0.09	12.72±0.17	2.07±0.08	0.407	24	3.07±0.09	2.45±0.07	4.78	0.72±0.04	0.969	336±32	-	+
Section <i>Malpigita</i>													
<i>S. gemmascens</i>	13.17	12.15	2.49±0.30	0.355	24	3.63±0.16	2.036±0.06	3.26	0.68±0.02	0.922	337±67	-	+
Section <i>Cardiandra</i>													
<i>S. carinata</i>	11.94	11.70	1.77±0.22	0.463	16	3.16±0.15	2.343±0.02	4.31	0.48±0.09	0.979	305±31	-	+
<i>S. leptoclada</i>	21.28	19.38	2.86±0.25	0.359	28	5.18 ±0.43	3.060 ± 0.07	7.41	1.07 ±0.12	0.911	334±20	++	+
<i>S. sclerantha</i>	23.18	23.14	4.63±0.13	0.385	25	6.68±0.11	3.94±0.12	12.23	0.92±0.03	0.991	124±5	+	+
Section <i>Belanthera</i>													
<i>S. aucheri</i>	16.33±0.31	14.95±0.13	3.51±0.09	0.421	15	3.51±0.09	3.07±0.08	7.38	0.48±0.04	0.920	264±9	-	-
<i>S. gossypina</i>	13.09±0.12	12.43±0.13	2.38±0.07	0.462	14	4.03±0.04	3.31±0.05	8.62	0.71±0.03	0.950	253±17	-	-
Section <i>Caroxylon</i> (Thunb) Ijijn													
<i>S. dendroides</i>	14.63±0.17	13.91±0.22	1.81±0.04	0.293	47	1.96±0.04	1.48±0.03	1.97	0.76±0.05	0.950	458±60	-	+
<i>S. micranthera</i>	12.23±0.18	11.63±0.47	1.62±0.05	0.305	23	1.51±0.04	0.98±0.03	0.77	0.81±0.05	0.950	465±28	+	-
<i>S. orientalis</i>	19.83±0.18	19.33±0.08	1.96±0.11	0.263	49	2.65±0.08	1.85±0.06	1.55	0.98±0.03	0.976	427±1	+	-
<i>S. laricina</i>	19.81±0.42	19.05±0.51	2.10±0.11	0.354	48	3.13±0.08	1.86±0.06	2.74	1.33±0.07	0.962	600±52	++	+
<i>S. incanescens</i>	23.79	20.91	3.96±0.08	0.358	26	6.68 ±0.32	3.598 ±0.06	10.16	0.898±0.02	0.879	202±16	+	+
Section <i>Salsola</i> subsection <i>Kali</i>													
<i>S. iberica</i>	14.70±0.09	13.72±0.13	3.54±0.04	0.249	37	2.57±0.09	1.36±0.03	1.51	1.05±0.05	0.930	250±11	+	+
<i>S. praecox</i>	17.39±0.35	16.87±0.47	2.55±0.15	0.330	34	2.95±0.18	2.07±0.05	3.37	1.17±0.14	0.969	140±6	++	+
<i>S. ruthenica</i>	21.76±0.38	20.78±0.23	2.73±0.09	0.215	49	2.71±0.11	1.85±0.10	2.68	0.89±0.03	0.955	134±6	+	+
<i>S. kali</i>	21.88	21.76	3.39 ±0.19	0.241	50	4.25 ±0.25	1.87 ±0.10	2.75	1.16±0.14	0.990	111±5	++	+
<i>S. aperta</i>	14.79±0.42	14.39±0.37	2.13±0.27	0.452	21	3.98	2.180	6.86	0.96	0.972	303±12	+	+
<i>S. paulsenii</i>	17.73	17.37	2.56±0.38	0.34	29	3.85 ±0.43	2.94 ±0.19	4.34	0.63±0.05	0.983	258±13	-	-
<i>S. pestifer</i>	19.64±0.16	19.32±0.18	1.85±0.05	0.195	53	2.88±0.04	1.95±0.08	2.99	1.03±0.031	0.984	247±1	+	+
Section <i>Physurus</i> Ijijn													
<i>S. lanata</i>	25.53±0.11	24.47±0.10	3.06±0.03	0.260	30	5.03±0.14	3.44±0.11	9.26	1.36±0.03	0.960	247±12	++	-
<i>S. crassa</i>	29.31	27.91	2.69±0.55	0.223	36	4.75±0.48	3.70 ±0.35	10.85	1.20 ±0.07	0.953	236±9	++	++
<i>S. subaphylla</i>	18.12±0.19	17.24±0.33	2.42±0.13	0.352	24	4.17±0.22	3.72±0.09	10.87	1.12±0.02	0.950	0	++	++

1- include size of pore and its area.

2- level of sinking of pore, ++ prominent, + weak, - smooth.

3- degree of convexness of mesopore exine, ++ prominent, + weak, - smooth.

I-Species of section *Salsola* subsection Kali

***S. praecox*:** Pollen: radial symmetrical, isopolar, pantoporate, spheroidal or nearly so; pollen size: 14.86-18.42 μm in diameter with a polar axis of 13.42-18.21 μm ; exine is 0.25-2.27 μm ; ornamentation 123-160 spinules per 100 μm^2 ; tectal spinules conical, 0.1 x 0.1; pores numerous: 44-69, small 0.91-1.07 μm in diameter, circular, protuberant, rounded-ovate, semi-sunken; operculum 1.3 x 0.5 μm with 16-22 short, conical spinules; interpore distance: 2.03-3.58 μm ; C/D value 0.330, size of pore 1.55-4.43 μm , form index 0.90-0.99; exine 1.2 x 1.4 μm thick; tectum subtectate 0.56 μm thick, collumellae foot layer continuous, endexine irregular.

***S. paulsenii*:** Palynological characters almost indistinguishable from *S. praecox*. Size of pollen grain: polar axis: 17.37 μm , diameter of pollen: 17.73 μm ; number of pores 24-32; interpore distance 1.51-2.32 μm ; pore area 3.20-5.31 μm^2 ; size of pore 2.02-2.60 μm ; nanospinules number on the mesoporial exine 22-34; echinus number on pore membrane 20- 31; C/D value 0.337; size of pore: 2.12-2.88 μm , index form: 0.983; thickness of exine: 0.48- 0.77 μm ; number of spinules per 100 μm^2 : 232-284.

***S. iberica*:** Differs from two species described above by its smaller anthers, divergent in lower part at least to the middle. Each anther terminates in a minute dot-like or ovate, flattened, sessile appendage. Size of pollen grain: polar axis: 13.01-14.28 μm , diameter of pollen: 14.29-15.20 μm ; number of pores: 31-41; interpore distance: 1.97-2.41 μm ; C/D value: 0.226-0.278; size of pore: 0.82-1.88 μm ; pore area: 0.53-2.77 μm^2 ; size of pore: 1.45- 3.96 μm ; form index: 0.89-0.99; thickness of exine: 0.79-1.27 μm ; number of spinules per 100 μm^2 : 234-258.

***S. ruthenica*:** Characterized by unusual linear, basifixed and long stamen filaments. Anthers are oblong-ovate, with locules free in lower one-third and connected by the rather small firm semioval, sessile appendage, which merges imperceptibly with the locules. Polar axis: 19.97-22.21 μm ; diameter of pollen: 20.67-22.88 μm ; interpore distance 2.14-2.91 μm ; exine thickness 0.74-1.02 μm ; pores numerous 40-58, circular, 1.39-2.46 μm , not sunken; C/D 0.187-0.235; pore area: 1.98-3.55 μm^2 ; size of pore: 2.06-3.18 μm ; form index: 0.92-0.98; number of spinules per 100 μm^2 : 130-140.

S. pestifer- punctate exine surface. Polar axis 18.54-20.24 μm ; diameter 18.71-20.61 μm ; Pores 48-56; thickness of exine 0.92-1.16 μm ; interpore distance 1.57-2.06 μm ; diameter of pore 1.61-2.51 μm ; pore area: 2.99 μm^2 ; size of pore: 2.30-3.44 μm ; spinules on operculum 25-32; nanospinules on ectexine 18-24; C/D value 0.163-0.212; number of spinules per 100 μm^2 : 222-259.

***S. aperta*:** Some palynological features common with the species described above but is strongly distinguishable from them by long, free, linear-tape form filaments and oblong lengthened small 0.9-2. 0 mm long anthers with locules free almost at summit and connected by rather small firm semioval, rostriform, sessile appendage 0.1-0.15mm long, which merges imperceptibly with the locules. Pollen grains have pores that are larger in size, reduced is number and symmetrically placed on the scarcely perforated, punctate tectum. The most notable feature is number of pores which are 22-33. C/D ratio value 0.452 is more related to the woody species of subsection *Arbusculae*, section *Coccosalsola* than to species of section *Salsola*. Polar axis: 14.39 μm ; diameter: 14.79 μm ; interpore distance: 1.93-2.54 μm ; thickness of exine: 0.96 μm ; size of pore: 2.18 μm ; pore area: 6.19-7.40 μm^2 ; size of pore: 4.39-5.18 μm ; number of spinules per 100 μm^2 :

279-327. Pollen morphology of woody perennial *Salsola* is less specialized than for above analyzed annual *Salsola* species.

II-Section *Coccosalsola* subsection *Arbusculae*

***S. arbuscula* Pall.:** Pollen are spherical or nearly so, 11.77-14.11 μm in polar axis and 12.01-14.41 μm in diameter. The exine is 0.72-1.41 μm thick. The C/D ratio ranges from 0.304-0.392, corresponding to 18-24 pores. Pore diameter varies between 1.36-2.54 μm . The pores have fairly circular outlines (small ones are sometimes elongate); the inner walls of the pores are generally fairly steep. Each pore has an operculum, and the nanospinules (echinus) on the operculum are usually shorter or equal and more varied in size and shape than those on the mesoporial exine. A prominent sinking of pores is common for this species. A distinguishing feature of the exine sculpture of *S. arbuscula* is a fairly high density of nanospinules. The tectal perforations are practically invisible even at high magnification. Nanospinules are long, usually fairly sharp and somewhat curved. Nanospinule density is as 274-307 spinules per 100 μm^2 .

***S. arbusculiformis*:** Filaments broadly linear, pointed to the connective, basifixed to the saucer-shaped glabrous ovoid lobes, hypogynous disc. Anthers (2.0-2.8 mm long) separated to the middle or deeper, terminating in a sessile oblong to subovate appendage (0.4 mm long). Polar axis: 14.11-16.03 μm ; diameter: 14.50-16.20 μm ; interpore distance: 3.09-3.85 μm ; C/D ratio: 0.414; number of pores: 12-26; thickness of exine: 0.74- 1.002 μm ; size of pore: 1.94-3.64 μm ; pore area: 3.23-8.57 μm^2 ; number of spinules per 100 μm^2 : 186-193.

***S. richteri*:** Pollen polar axis: 1.28-15.08 μm ; diameter: 13.32-15.70 μm ; interpore distance 2.15-3.18 μm ; number of pores 18-24; thickness of exine 0.57-0.94 μm ; diameter of pore 2.09-2.99 μm ; size of pore: 2.81-3.61 μm ; pore area 3.77-6.64 μm^2 ; C/D value 0.424; number of spinules per 100 μm^2 : 269-337.

***S. Paletziana*:** anthers (very large 2.9-3.8 mm long) strongly divergent beyond the middle, borne on flat linear filaments, terminating in a narrowly lanceolate pale appendage upto 1mm long. Size of pollen grains: diameter: 14.62-15.09 μm ; polar axis: 13.97-15.04 μm ; number of pores 21-33; thickness of exine 0.77-1.13 μm ; size of pore 2.45-4.39 μm ; pore area 4.14-15.39 μm^2 ; distance of interpore 2.17-3.96 μm ; nanospinules number on the mesoporial exine 19-26; echinus number on pore membrane 25-37; C/D value 0.332-0.431; number of spinules per 100 μm^2 : 140-172.

***S. Montana*:** Polar axis 11.93-13.56 μm ; diameter: 12.94-13.67 μm ; number of pores: 20-28; pore area: 3.26-6.61 μm^2 ; thickness of exine: 0.61-0.91 μm ; interpore distance: 1.85-2.48 μm ; size of pore: 1.85- 2.99 μm ; number of spinules per 100 μm^2 : 300-386.

***S. Pachyphylla*:** Polar axis: 17.10 μm ; diameter 17.97 μm ; number of pores 16-24; diameter of pore 2.50-2.79 μm ; pore area 4.91-6.11 μm^2 ; interpore distance 2.60-3.85 μm ; thickness of exine 0.67-1.35 μm ; C/D value 0.439; size of pore: 4.16-5.00 μm ; number of spinules per 100 μm^2 : 133-189.

III. Section *Malpigila*

***S. gemmascens*:** Polar axis: 12.15 μm ; diameter: 13.17 μm ; number of pores: 24; interpore distance: 2.16-2.77 μm ; - Nanospinulus on operculum range between 36-48. Thickness of exine: 0.677 μm ; pore area: 2.99-3.41 μm^2 ; diameter of pore: 2.036 μm ; size of pore: 3.63 μm ; C/D value: 0.355; number of spinules per 100 μm^2 : 266-399.

IV. Section *Belanthera*

Very little variation was recorded among the species of Section *Belanthera*.

***S. aucheri*:** Polar axis: 14.68-15.41 μm ; diameter: 15.33-18.37 μm ; number of pores: 12-18; thickness of exine: 0.36-0.77 μm ; pore area: 4.95-6.91 μm^2 ; interpore distance: 3.05-3.89 μm ; diameter of pore: 3.09-3.63 μm ; size of pore: 3.22-3.73 μm ; C/D value: 0.421; number of spinules per 100 μm^2 : 255-273.

***S. gossypina*:** Anthers divergent throughout, appendage lanceolate, acuminate, white, about as long as anther; size of pollen grains: polar axis 12.25-12.80 μm ; diameter 13.27-13.55 μm ; number of pores 12-24; pore area 3.89-6.06; thickness of exine 0.68-0.79 μm ; interpore distance 2.24-2.97 μm ; size of pore: 3.91-4.20 μm ; diameter of pore 3.00-3.48 μm ; C/D value 0.462; number of spinules per 100 μm^2 : 236-270.

V. Section *Cardiandra*

Species belonging to Section *Cardiandra* are characterized by punctate spinulose exine.

***S. sclerantha*:** Polar axis: 23.14 μm ; diameter: 23.18 μm ; number of pores: 25; interpore distance: 8.925 μm ; thickness of exine: 0.918 μm ; pore area: 12.23 μm^2 ; diameter of pore: 3.94 μm ; size of pore: 0.85-1.00 μm ; C/D value: 0.385; number of spinules per 100 μm^2 : 113-134.

***S. carinata*:** Sessile appendage, several times shorter than anthers; interpore distance 1.77 μm ; diameter of pore 2.95 μm ; thickness of exine 0.48 μm ; size of pollen grains: polar axis: 11.69 μm ; diameter: 11.94 μm ; number of pores: 16; interpore distance: 1.50-2.13 μm ; thickness of exine: 0.48 μm ; pore area: 4.31 μm^2 ; size of pore: 2.34 μm ; C/D value: 0.463; number of spinules per 100 μm^2 : 274-335.

VI. Section *Caroxylon*

Species of section *Caroxylon* form a very homogenous group and have a very similar, sometimes indistinguishable pollen morphology except *S. micranthera*, whose anthers are extremely small.

***S. orientalis*:** Polar axis 18.00-20.01 μm ; diameter 19.41-20.27 μm ; interpore distance: 1.6-2.23 μm ; diameter of pore: 2.34 μm ; size of pore: 2.09-2.31 μm ; pore area: 1.87-4.73 μm^2 ; exine thickness 0.82-1.10 μm ; number of pores 34-58. C/D value: 0.09; number of spinules per 100 μm^2 : 406-469.

***S. laricina*:** Polar axis: 17.24-21.56 μm ; diameter: 17.73-22.80 μm ; form index: 0.940-0.992; interpore distance: 1.30-2.69 μm ; number of pores: 44-56; diameter of pore: 1.39-2.38 μm ; size of pore: 0.32-1.76 μm ; pore area: 1.77-3.55 μm^2 ; exine thickness 0.32-1.76 μm ; number of pores: 36-52; C/D value: 0.354; number of spinules per 100 μm^2 : 571-675.

***S. micranthera*:** Polar axis 11.12-11.816 μm ; diameter: 11.47-12.80 μm ; number of pores: 36-54; diameter of pore: 0.83-1.32 μm ; size of pore: 1.20-1.90 μm ; pore area: 0.57-1.97 μm^2 ; thickness of exine: 0.62-0.96 μm ; interpore distance: 1.36-1.71 μm ; C/D value: 0.305; number of spinules per 100 μm^2 : 429-483.

***S. dendroides*:** Polar axis 12.92-14.97 μm ; diameter: 13.96-15.01 μm ; number of pores: 44-52; pore area: 1.43-2.27 μm^2 ; thickness of exine: 0.64-1.02 μm ; interpore area: 1.51-1.87 μm ; diameter of pore: 1.29-1.65 μm ; size of pore: 1.55-2.56 μm ; C/D value: 0.293; number of spinules per 100 μm^2 : 362-531.

S. incanescens: Polar axis 20.91 μm ; diameter: 23.79 μm ; index form: 0.88; number of pores: 26; diameter of pore: 3.60 μm ; size of pore: 0.84-0.93 μm ; thickness of exine: 0.90 μm ; interpore distance: 8.01 μm ; pore area: 10.16 μm^2 ; C/D value: 0.358, number of spinules per 100 μm^2 : 161-238.

VII. Section *Physurus*

Species of this section have the widest range of variation in pollen grain sizes and are clearly distinguishable from all examined *Salsola* sections; very large, almost spherical pollen grains, ca –28-30 μm in diameter, numerous large pores, very thick walls and non-perforate tectum with short, sparsely distributed nanospinules on the mesoporial exine. The operculum pore membrane is covered by numerous short, hard to distinguish echini.

S. lanata: Anthers polar axis: 21.08-25.90 μm ; number of pores: 28-32; diameter 26.21-24.15 μm ; index form: 0.96; interpore distance 2.21-3.77 μm ; diameter of pore: 3.02-4.12 μm ; thickness of exine 1.12-1.61 μm ; C/D value 0.260; pore area: 9.26 μm^2 ; number of spinules per 100 μm^2 : 198-321.

S. crassa: anthers polar axis 24.45-26.88 μm ; diameter 26.72-30.21 μm ; number of pores: 36-48; interpore distance 2.78-3.13 μm ; pore large: 3.13-3.65 μm ; pore area: 9.45-13.65 μm^2 ; flat, prominent sunken with well defined circular outline; exine thickness 1.14-1.52 μm ; C/D value: 0.233; index form: 0.95; number of spinules per 100 μm^2 : 228-245.

S. subaphylla: The pollen differs strikingly from that of all examined species in lacking spinules on the exine. The distal part of the tectum may be smooth or rough (scabrous). A few larger, slightly sunken, symmetrically distributed pores, which in combination produce a polyhedral like shape of mesoporial exine is peculiar for this species. Operculum is protuberant and uniformly covered by short rounded ovate echinus. Number of pores varies between 22-33. Pollen grain: polar axis: 17.24 μm ; diameter: 18.12 μm ; index form: 0.95. Interpore distance 1.98-2.89 μm ; C/D value: 0.352. Pores circular, large in diameter 3.72 μm than those of species from section *Salsola*, *Caroxylon*, *Belanthera* and even *Coccosalsola*. Pore area: 10.87 μm^2 ; size of pore: 4.17 μm . thickness of exine: 1.12 μm ; no spinules on pollen surface.

Diversity statistics and canonical discriminate analysis were used to determine the relationship between different sections of genus *Salsola*. The palynological study of 28 Asian and European *Salsola* taxa has shown that this genus is rather stenopolynous with a few exceptions.

The palynological results presented in this study show that the pollen are radially symmetrical, isopolar, pantoporate, spherical or subspheroidal. The pollen characters comprising size, pore number, chord (C/D ratio), diameter of pore, exine thickness, level of sinking of pore, convexness of mesoporial exine, spinule and minute-hole densities and number of spines on pore membrane appeared to be useful in distinguishing each species.

The C/D ratio shows interesting intraspecific variation in pollen grain morphology (Fig. 3). This parameter seems to be highly specialized supporting the delimitation of the *Salsola* species and appears to be more conservative than some flower and fruit characters.

The tectal perforations, even at high magnification (x10.000) are minute or absent. Nanospinules are 0.12-0.38 μm long, usually fairly sharp and sometimes somewhat curved with relatively narrower base. The pores have fairly circular outlines (small ones are sometimes elongate). Each pore has an operculum and the spinules on the operculum

are often longer, stronger and more varied in size and shape than those in the exine surface. Three pollen types are recognized.

The comparative morphology of pollen of *Salsola* species is shown in the figures 1-4.

Type I: *S. orientalis*, *S. leptoclada*, *S. ruthenica*, *S. pestifer*, *S. paulseni* belong to this type. It is characterised by large (17.41-20.76 μm) pollen grains with numerous pores (40-58) and lack convex mezoporial exine.

Type II: *S. arbuscula*, *S. arbusculiformis*, *S. paletziana*, less *S. gemmascens* are included in this type. They are characterized by small size of pollen grains (11.78-16.20 μm) with sunken pores (16-28) and distinctly convex mesoporial exine.

Type III: *S. praecox*, *S. sclerantha*, *S. leptoclada* are included in this group. They almost occupy intermediate position between type I and II as far as the number of pores (30-38) is concerned and extexine spinule/punctate density. However, conspicuous link exists between *S. subaphylla* (recently considered as *Halothamnus*) and species of section *Physurus*, such as *S. lanata* and *S. crassa* (recently reclassified as *Climacoptera*). All investigated species have large (3.60-5.04 μm), sunken, well configured pores with densely spinulose aperture membrane. Pollen morphology differs clearly from other species of *Salsola* in C/D ratio (0.14; 0.06; 0.32), fairly large grains (19.3-25.49 μm) and almost absence/or presence of minute ectexine perforations.

Euclidean distance was used to compute the dissimilarity matrix, and a cladogram prepared. Based on the pollen morphology, quantitative characters clustering groups and ordination analysis of species from different sections/subsections within genus *Salsola* indicated that overall pollen traits (features) almost reflect current taxonomic boundaries (Fig. 6). Majority of the species belong to the same section and are grouped together. This is the case for woody-shrubby species of subsection *Arbusculae* of section *Coccosalsola*, which form a taxonomically separate monotypic subsection. Similar situation is observed in the species of section *Physurus*, recently separated as *Climacoptera*. Annual herbaceous Asian and European taxa from section *Salsola* subsection *Kali* Ulbrich (Idzikowska, 2005), are predominantly grouped together, while some other annual species of the same subsection are positioned between both clusters. This is the case for *S. aperta* and *S. paulsenii*, which typically belong to the sect. *Kali* (*Salsola*) and are much close to woody species of sect. *Arbuscula* and *Belanthera*.

Discriminate analysis based on pollen character variations has shown an evident separation of species of section *Physurus* into the separate genus *Climacoptera*. Our palynological and ultrastructural studies of grains of various groups of *Salsola* confirm and fully support the separation of genus *Climacoptera* from *Salsola* done by Botschantzev (1969) and Prato (1986). Discriminate analysis based on pollen character variations has provided convincing proof for separation of species of section *Physurus*.

The tectum in the genus *Salsola* is either punctate, perforated or smooth non-perforated however, this feature cannot be related to a clear taxonomic grouping. A similar continuous gradation between the two pollen types based on sexine sculpture has been noted within some sections of genus *Silene* (Caryophyllaceae) Ghazanfar (1984).

The dendrogram suggests that there are trends from finely to coarsely tubuliferous/punctate ectexine sculpture. The punctate type is most clearly defined. Examination of exine from the various species of *Salsola* (Chenopodiaceae), although highly limited, provides a more comprehensive knowledge of the pollen morphology and a better understanding of the relationship within genus *Salsola* and different representatives of the order Centrospermae as well.

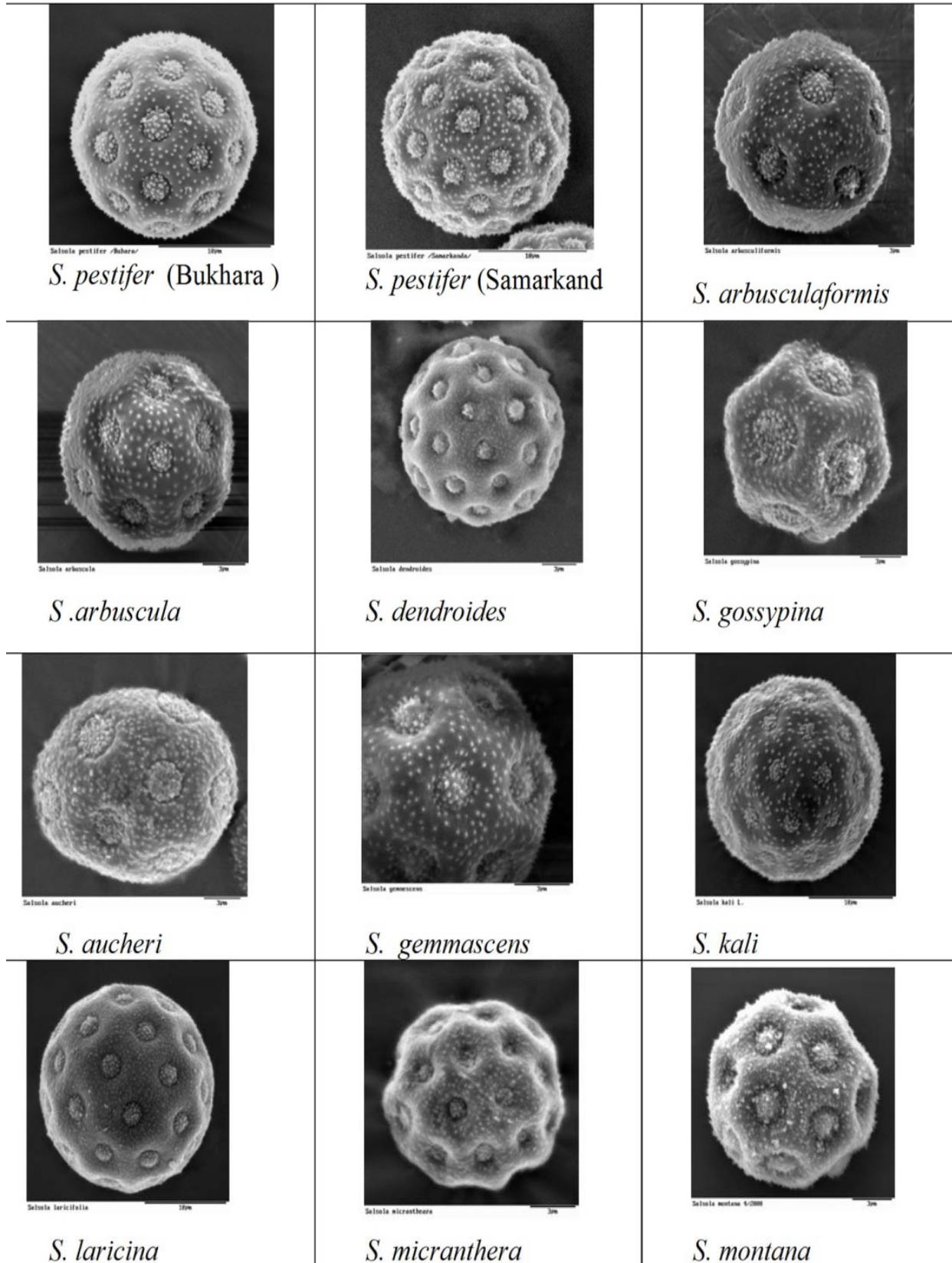


Fig. 1. Scanning electron micrographs showing pollen grain morphology of some Central Asian *Salsola* species (all magnifications $\times 5000$).

Discussion

The pollen morphology of the *Salsola* species in general shows uniform type characteristics. This is evident from the ultrastructural pollen morphology of 27 species investigated by us during this investigation which too basically show same features. However, a number of structural and general evolutionary trends were observed within the genus. Scanning electron micrographs of the species from different sections (Botschantzev, 1969) investigated here provided further information on the pollen morphology and complemented the light microscopic observations. Number of pores, size and shape of pores and pollen grains, thickness of exine, C/D ratio, interpore distance, and echinae number on pore membranes and verruca number on mesoporial exine were of great diagnostic significance. There is a strong correlation with changes towards semiangular and oblate forms. The evolutionary trends in mesoporial exine and pore membrane sculpture is somewhat unclear. This character is either absent (as in *Halothamnus subaphyllus*) or weakly developed or structurally complex within the genus *Salsola*. Majority of the species have well distinguished spinules and minute tectal perforations. Later are rather poorly differentiated and can be observed only at high magnification (above x 10.000). The transformation in the sculptural patterns that are well developed in different *Salsola* sections appears to be a distinct specialization within the genus. The pollen grains of *S. lanata* and *S. crassa* may represent increase in the size of pollen and reduction in number of pores. Moreover the pollen morphology of *S. aperta* from the section *Salsola* subsection *Kali* suggests its close taxonomic relation to species of section *Cardiandra*. From pollen morphological point of view *Salsola* species are closely related to genus *Suaeda*, *Camphorosma*, *Chenopodium*, *Haloharis*, *Sarcobatus*, *Traganum* from Chenopodiaceae, as well as to the type II pollen morphology found in Caryophyllaceae, Portulacaceae, Phytolacaceae and Amaranthaceae (Tsukada, 1967; Uotila, 1974; Skvarla & Nowicke, 1976; Youngjae & Lee, 1995; Pinar & Inceoglu, 1999).

Increase in grain size is a general trend that has been described in a number of unrelated families by various authors. This peculiarity is clearly evident in *Salsola* particularly in the pollen of *S. pestifer*, *S. lanata* and *S. crassa*. *Salsola* taxa are characterized by comparatively larger pollen in the family. The pollen grains of these species occasionally tend to have thicker exine than any other centrospermous representatives. However, the exine thickness in the sect. *Physurus* is not increased significantly despite a very conspicuous increase in grain size. There is a correlation between length of the polar and equatorial axes and size of the flower; the largest grain being found in most members of section *Physurus*, *Cardiandra* and *S. subaphyllus* which have some of the largest flowers. Trends related to sculpturing are all derived by modifications of the basic uniformly reticulate/tectate condition. It was observed that representatives of *Salsola* species from *Physurus* section (recently *Climacoptera*) and *S. subaphyllus* (recently *Halothamnus subaphyllus*) are well distinctive in the genus and family and clearly represent a unique specialization (Freitag *et al.*, 1986; Toderich *et al.*, 2000). However, as pointed out by Turner and Heywood (Mabry, 1973), phyletic rather than taxonomic relationships are of major significance. We can briefly summarize our results by emphasizing that exine with the spinulose and tubuliferous/punctate surface pattern are structurally very similar in all examined taxa and in other

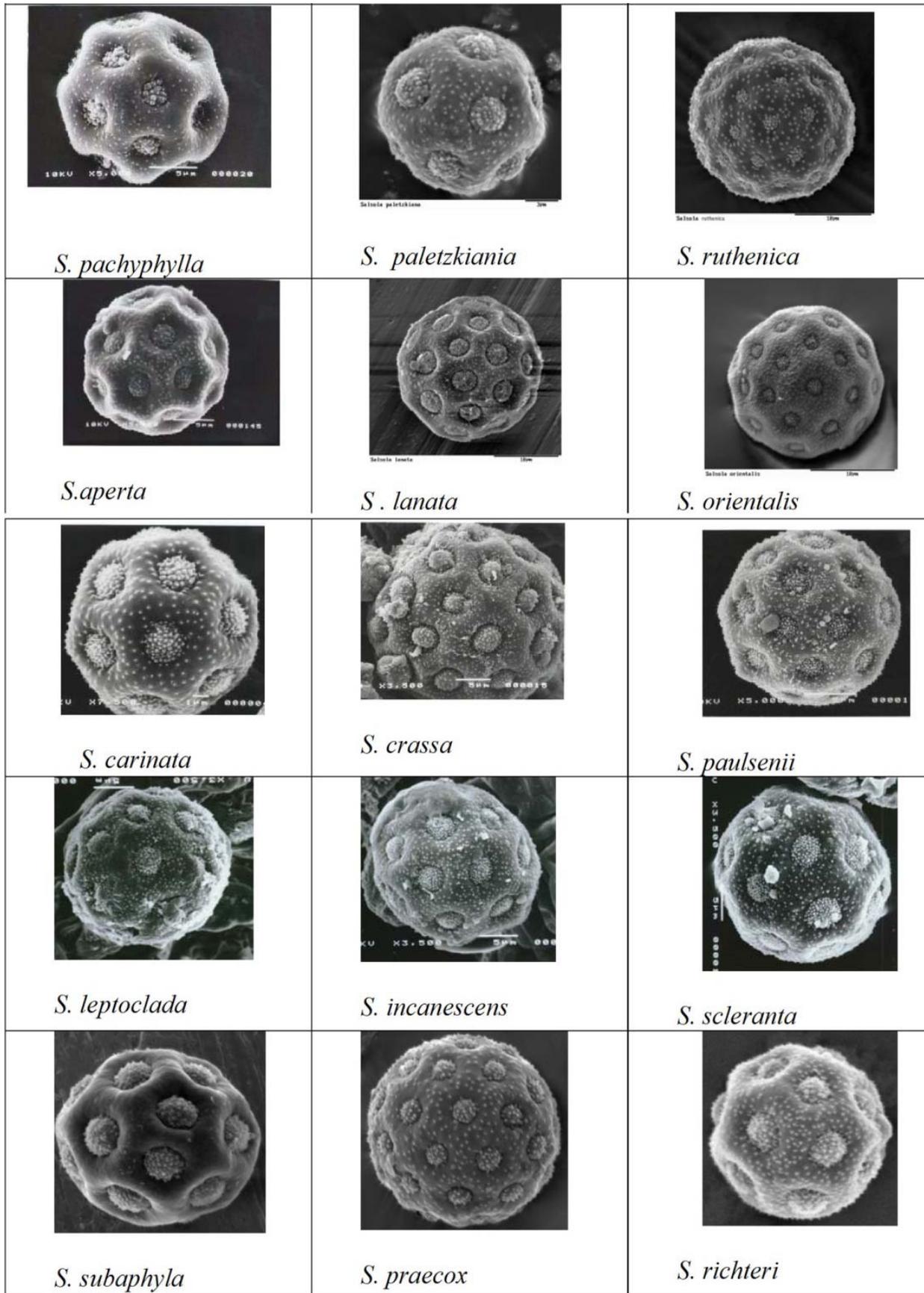


Fig. 2. Scanning electron micrographs showing pollen grain morphology of some Central Asian *Salsola* species (all magnifications $\times 5000$).

representatives of *Centrospermae*, indicating a close phylogenetic association. A greater sampling is required for a more comprehensive understanding of the endexine, but it seems quite evident that the species of genus *Salsola* as in the majority of the representatives of order *Centrospermae* possess pollen with reduced endexine. A presumed reduction of the reticulum dimensions has resulted in very finely reticulate to tectate-perforate grains in the species of *Salsola*. Pollen grains of *Salsola* are clearly the most distinct in the family and seemingly have evolved along a line of evolution away from the rest of the family. The essentially spherical, moderately small, pentaporate is regarded as a primitive condition for the family. This type of pollen is widespread in Chenopodiaceae, and is a basic type in dicotyledons as a whole. The widespread occurrence of the pentaporate pollen grain type throughout the families of *Centrospermae* with a rather simple reticulate/or punctate exine sculpture suggests that this is the basic type in this order. Major evolutionary advancement within the genus *Salsola* can be observed as:

1. A change in shape from spherical or subspherical to oblate; reduction in number of pores; increase in grain size; change in sculpturing of various modifications of tectum and presumed reduction to very finely reticulate and tectate perforate (this type in *Salsola* comprises an advancing character), many of these specialization's can be correlated with advancements in other group of flowering species of plants; similar morphological trends have been described in the families like Amaranthaceae (Riollet & Bonnefille, 1976; Ugrorogho & Oyelana, 1992) and Caryophyllaceae (Ghazanfar, 1984).
2. The formation of well-developed and structurally more complex endo-apertures would appear to represent an additional trend in the Chenopodiaceae family, however, more detailed study and documentation is necessary to fully understand the development of endoapertural ultrastructure in different systematically unrelated genera.

Change in pollen grain outline from circular to semiangular has occurred independently in a number of chenopod genera and other representatives of *Centrospermae*. For example many species of *Salsola* represent a concomitant change in grain shape from nearly spherical to varying slightly degrees of oblateness. The evolution within the *Salsola* group has probably started from the basic type, characterized by a smooth to finely reticulate uniform sculpture. The main developments have followed this basic one, leading to increased differentiation in couple of species with increase in coarseness of the reticulate sculpture on the mesocolpia. Other developments have lead to a uniform increase in the coarseness of the reticulate sculpture over the whole pollen surface. It is of interest that the basic type is seen in most genera, whereas specialized types are restricted to *S. subaphyllus* (revised as *Aellenia* or *Halothamnus*), as well to the section *Physurus*. It is also obvious that the evolutionary trends in the genus *Salsola* and Chenopodiaceae family related to other families in *Centrospermae* have progressed in a parallel manner. The evolutionary sequence of *Salsola* pollen types thus appears much more completely preserved in Chenopodiaceae to a limited extent in Amaranthaceae and Caryophyllaceae families in which many isolated and strongly specialized types are found (Borsch and Bartholott, 1998). Although differences in internal morphology were observed at inter-and intra-family level these can be interpreted as reflecting variations rather than major differences. The ultrastructure of pollen grain of Chenopodiaceae in general resembles Amaranthaceae in several aspects such as thickened tecta, the aperture structure, which consists of reduced pointed flecks of exine underlain by lamellar plates.

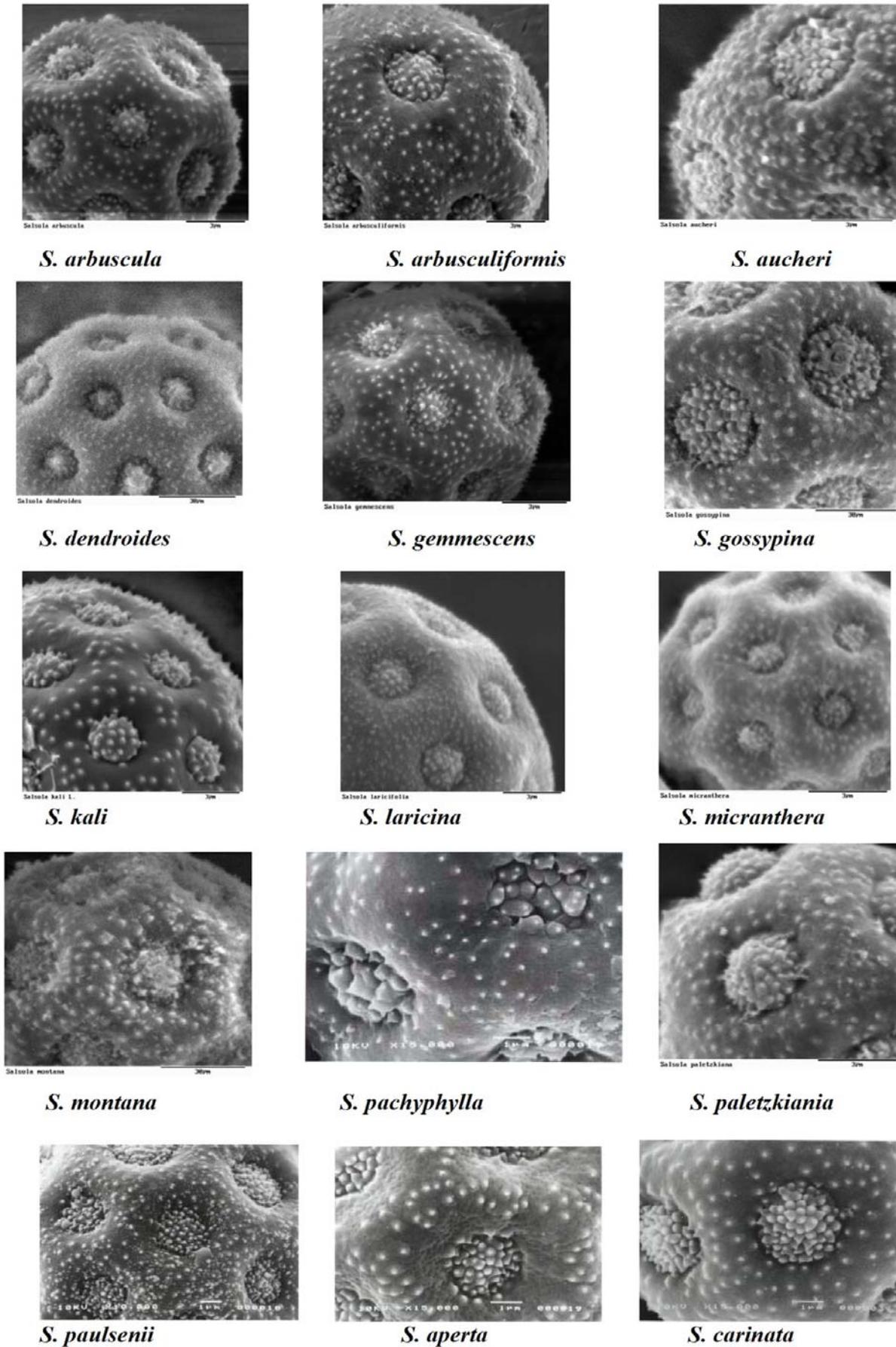


Fig. 3. Scanning microphotographs showing mesoporial structure in some *Salsola* species.

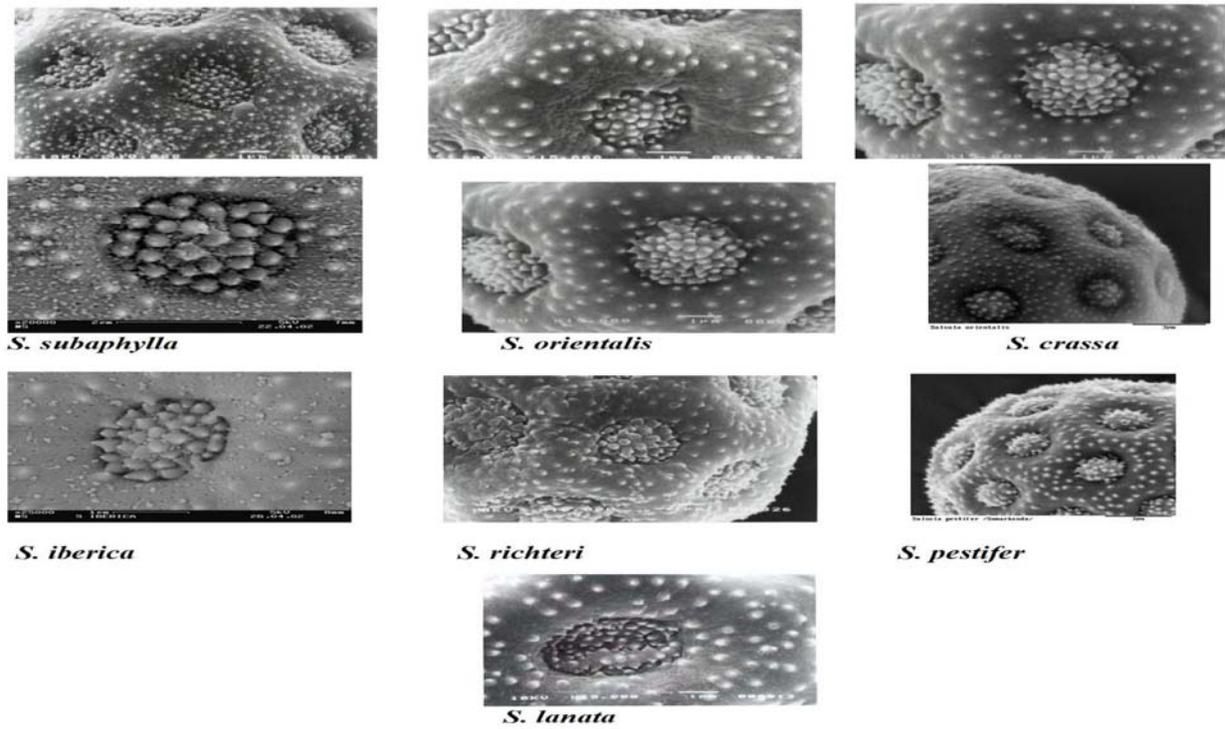


Fig. 4. Scanning microphotographs showing mesoporial structure in some *Salsola* species.

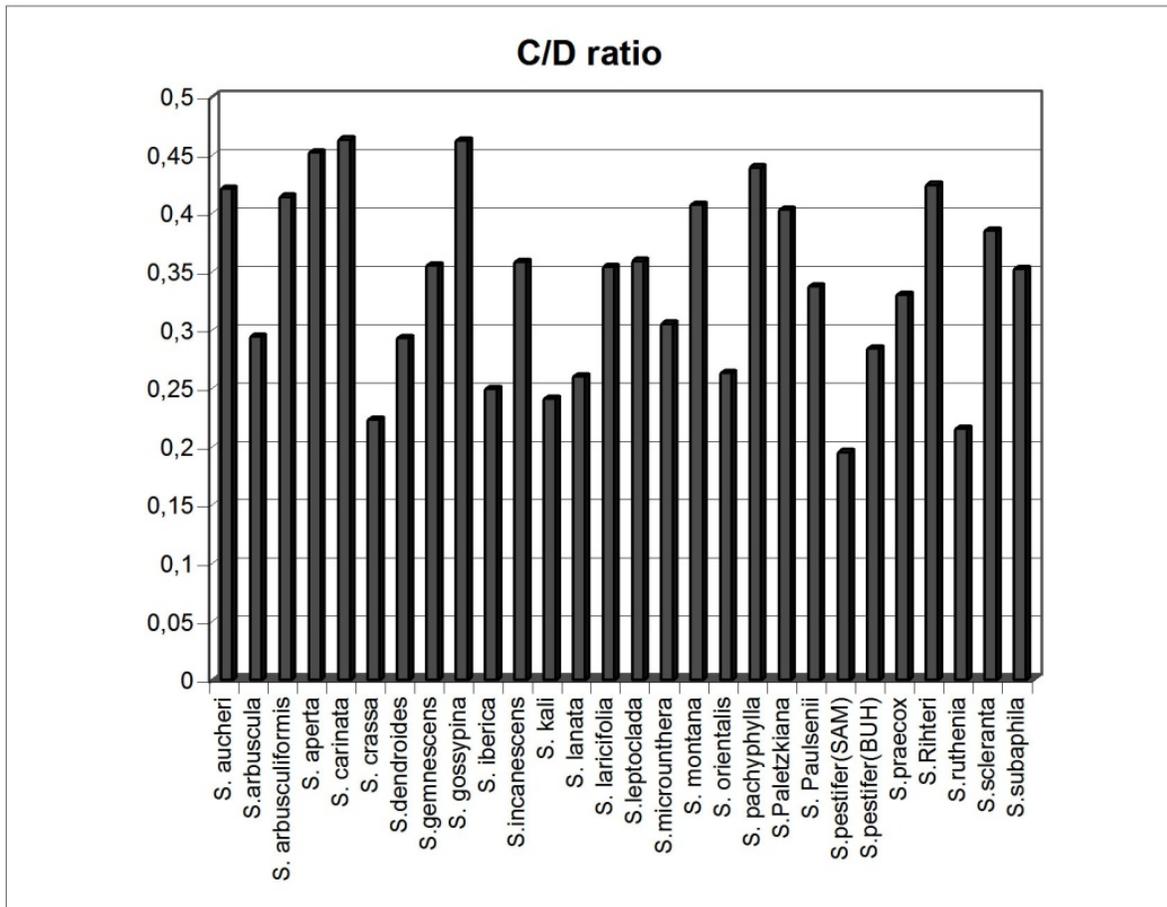


Fig.5. Variability of C/D ratios within examined species of *Salsola*.

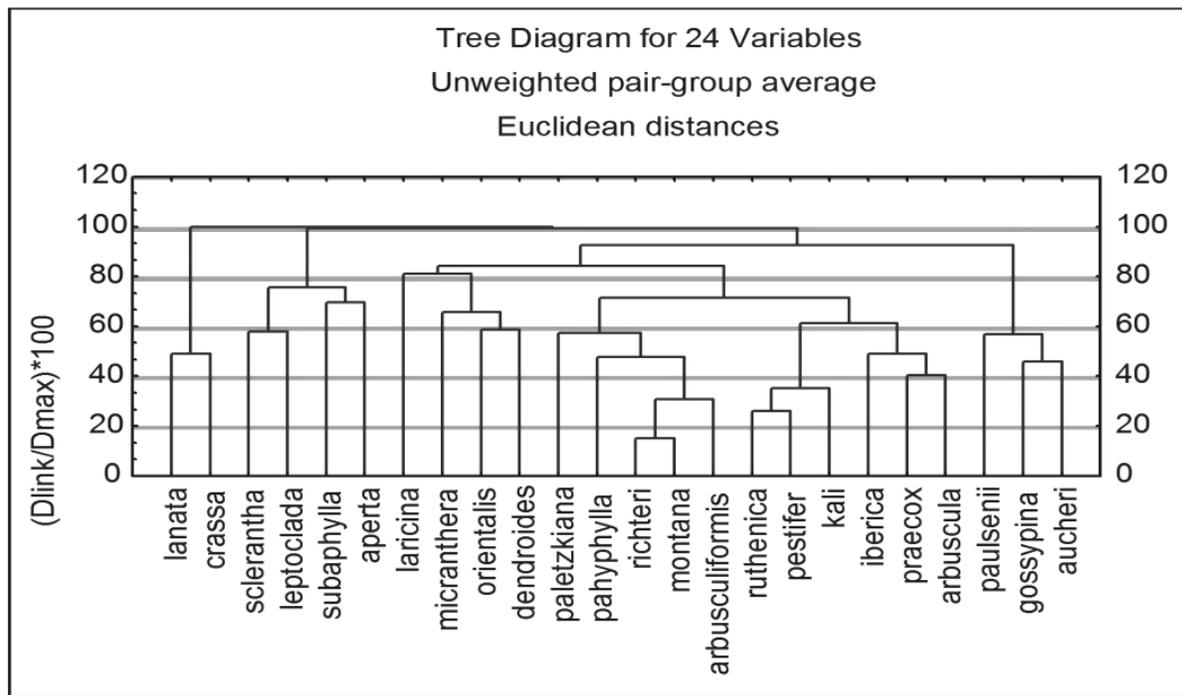


Fig. 6. The dendrogram based on palynological distance data showing relationship 21 Central Asian species of genus *Salsola*.

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