Genus *Salsola* of the Central Asian Flora; Its structure and adaptive evolutionary trends
(中央アジアの植物相*Salsola*属の構造と適応進化の傾向）

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Genus *Salsola* of Central Asian Flora: structure, function, adaptive evolutionary trends, and effects to insects

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CHAPTER 1. INTRODUCTION

1.1 Introduction

Uzbekistan, in the Central Asian region, is a landlocked country covering 447,400 square kilometers. Two-thirds of its land consists of steppe, desert, and semi-desert areas with the remainder as fertile valleys with abundant natural resources: oil, natural gas, gold, polymetals and so on. Dramatic political changes after the collapse of the Soviet Union have impacted all areas of human life, including the relationship between humans and natural resources. Over-exploitation of natural resources particularly through unsustainable agricultural practices is central to the issue. Some of the adverse actions of considerable importance are irrigation, alteration of natural rivers, mining, drilling, oil and mineral exploration, poor infrastructure development (roads, markets and railways), urban development, fuelwood collection, over-stocking and overgrazing by livestock. The poor management or destruction of appropriate native woody-shrub/ dwarf shrub vegetation in many arid areas of Uzbekistan is leading to land degradation with the development of wind and water erosion, preventing natural regeneration of rangeland plants. Shifting sands are one of the major problems of land degradation in the Kyzylkum Desert. Shifting sand dunes are almost devoid of vegetation and make up about 0, 5 million hectare (Kharin, 1995). Grazing and trampling by livestock, agricultural use, and mining industries destroy the vegetation cover and enhance sand mobility. Sand dune movement is a threat to irrigated farmlands, villages, railways, highways and others infrastructures.

The leading factors of anthropogenic degradation of cover vegetation in the Kyzylkum deserts are: a) agricultural land use (grazing, cutting and up-rooting of shrubs and undershrub), b) hay making and c) industries impact (mining, construction activity, transport, etc).

Salinization is one of the major ecological and production problems currently facing the agricultural sector in arid and semiarid areas of the Central Asian countries. Recent use by the former USSR of the major rivers of Central Asia (Amudarya, Zerafshan, Syrdarya) for the production of exports, including cotton, oil, and minerals, has resulted in rising water tables, waterlogging, and the well known ecological disaster of the saline lands around the receding Aral Sea. In particular, secondary salinization (human caused) is increasing rapidly and crop production under these conditions is becoming less sustainable in this region. Drought and salinity are capable of having a far greater effect on food security in Central Asian than in other areas.

Besides salinization, contamination by heavy metals and chemical compounds released by agriculture, uranium, oil and gas industries has been frequently reported for Kyzylkum sandy Desert (Walter and Box, 1983; Goldshtein 1997; Solodov 1998; Toderich et al 2001, 2002, 2004a, b; Tsukatani et al 2001). Initial explorations of the natural plant cellular mechanisms affecting the bioremediation of elemental and/or organic pollutants suggest great promise for the use of desert plants in large-scale environmental clean-up efforts. Factors that relate to take-up of chemical compounds, such as tannins, nitrates, metals, and oxalates (some of which may be toxic for plant development) have not been adequately studied for the arid flora of Central Asia. Native desert plants, however, have the advantage of being highly adapted to the hyper-arid climatic and edaphic contaminated conditions.

There is firm evidence that conditions within the core areas of Kyzylkum Desert are getting worse and that some remedial effort is warranted to protect the biodiversity, urban settlement, resource extraction and communication links.

In this context the native *Salsola* (from order Centrospermae, Chenopodiaceae family) species have the advantage of being highly adapted to the local deserts edaphic and climatic conditions, which are characterized by having a strong seasonal factor.

Salsola plants, which are an innovative pioneer species for range regeneration of the sandy Central Asian deserts, serve as an excellent model to study sexual reproduction, seed dormancy and native seed bank establishment for arid fodder plants. Knowledge about *Salsola* ”plant functional reproductive system” can be useful in the evaluation and prediction of sexual reproduction, seed formation and ecology of seed germination techniques, especially for the conservation and restoration of natural saline/sandy desert ecosystems in Uzbekistan. The conservation and protection of gene pools of native arid and semiarid Asiatic flora is basic for understanding the influence of environmental factors on morphoembryological processes, as well as revealing of their plasticity and tolerance under stress conditions. Plant reproductive strategies, based on morphological, structural, physiological and biochemical features for different ecological groups of chenopods of the desert Central Asiatic flora, are not well documented in the literature (Butnik 1981; Toderich et al., 1995, 1998, 2002, 2004a; P’yankov et al., 1997; Wolfe, 1998).

Traditionally descriptive anatomical and embryological approaches were based mainly at the families or generic levels. However several key features are unreliable since polymorphism within taxa often exceeds interspecific boundaries.

In the present work our proposed concept of “plant functional reproduction system” (PFRS) is based on common plant traits both structural and functional, that are responsible for similar responses to environmental conditions and that have dominant effects on major ecosystem processes. Groups of plant species with common structural features can form a “functional plant group”. Plant traits used for the identification and level of adaptation of species include important structural embryological parameters of floral organs, pollen biology and morphology, effective pollen control and pollination system, structural fruits traits, seed set and seed germination characteristics connected with reproductive plant functional activities (Wallace et al, 1968; Werker and Many, 1974; Young et al., 1983; Yamaguchi, 1990; Takeno et al. 1995). The fertility benefit of reproductive assurance for arid plants has not been examined in the light of their seed production. The reproductive plant functional hypothesis resolves this disparity between theoretical prediction and empirical results of seed production by explaining how combination of different types of pollination/fertilization can be advantageous in species with strong ecological habitat and inbreeding depression.

Besides that, the concept of "plant functional reproduction system" of arid plants could be a universal approach for the analysis of natural plant ecosystems, their reaction to harsh climatic and ecological factors and for making predictions about reproductive success, and consequently vegetation spatial distribution and changes under natural and anthropogenic impacts.

One of the most common features of Asiatic desert/semidesert *Salsola* species is their lower reproductive ability. As a rule, these species develop a large amount of flowers, but only a few forms viable seeds. In addition, low seed germination and seedling survival rate are frequently observed. Nowadays there is a gradual, but conspicuous decrease in the number of individuals among natural populations of *S. montana, S. arbusculiformis, S. aperta, S. orientalis, S. paletzkiana and* etc. The recruitment (germination and successful establishment) of these perennial species appears to be exclusively dependent upon sexual reproduction. The general descriptive embryological data concerning pollination/fertilization, embryo and fruit development of this *Salsola* complex remains controversial (Bochantzeva, 1948; Konycheva, 1963; 1983, Demyanova, 1974; Japakova, 1995; Toderich et al, 2001, 2004b).

Genus *Salsola*, which has the most C_4 species among any of the Chenopodiaceae (Iljin, 1955; Khatib, 1959; Freitag, 1986; P'yankov et al, 1997, 1999, 2000, 2002; Sage and Monson, 1999; Black et al. 2003) provides a valuable source of species to explore the variation and evolution of C_4 anatomy and cellular natural mechanisms to salt/drought stress factors in flowering plants (Toderich et al, 2002). Studies on structural diversity of vegetative and generative organs during their ontogenesis for different groups of *Salsola* species represent a unique case to solve disputable questions as to systematic and phylogenetic relations within Chenopodiaceae, genus *Salsola* inclusive. Also, some data were found to be useful in relation to the identification of desert floras origin and spatial species dispersal. However, in this respect Asiatic *Salsola* species are not studied enough yet (Botschantzev, 1969; P'yankov et al 1997, 2002).

The nomenclature of species of genus *Salsola* used in the present work refers mostly to the Flora of Uzbekistan (1953, 1962), as well as the "Plantae Vasculares URSS" from Czerepanov (1981). The taxonomy of genus generally corresponds to the sections and subsections of Salsola sensu strict described by Botschantzev, 1969.

In this context the objective of the present work,which has been conducted from 1999 to

2007, was to study the floral morphology and sexual reproduction system of Asiatic woody tree-like species *S. richteri, S. Paletzkiana, S. arbuscula, S. arbusculiformis, S. montana and S. subaphylla ,* many perennial semishruband shrublets like *S. orientalis, S. dendroides, S. laricina, S. gemmmascens* etc. , as well as annual *Salsola* herbs as *S. iberica, S. pestifer, S. paulsenii, S. aperta, S. lanata etc.* related to their assimilation tissue anatomy, photosynthesis type, biochemistry and seed production under dryland environments. It was hoped that pollen and fruit morphological traits might contribute to a better understanding of the "plant functional reproduction system" of the *Salsola* spp. complex in their adaptive evolution to natural desert environments. In the present study, special attention was paid to seed quality and ecology of their germination that could be useful for pastoralists and farmers in agroforestry research Program both in Uzbekistan and Central Asian saline/sandy ecosystems.

1.2. Order Centrospermae and taxonomic position of genus *Salsola*

The order Centrospermae (Carryophyllales) is often described as one of the most natural orders of higher flowering plants. This order of at least eleven families and about 6.000 species has long attracted the attention of systematists. There has been much debate about the justification in including within the order some of the families. Originally the circumscription of the order was based unitarily on morphological features. The name "Centrospermae" refers to the central or basal placentation. The order is well–defined by a number of morphological and anatomical features, especially by embryological characters: the most conspicuous being campylotropous or amphitropous ovules and curved or coiled embryo with perisperm storage tissue. Later (Mabry et al, 1973, 1976; Eckard 1976) was revealed an exceptional chemical distinction, the presence of pigments, termed betalains, in almost all families allied as the Centrospermae. The mutual affinity among the Centrospermae families has been further substantiated by ultrastructural and phytochemical investigations. It was determined that sieve element plastids are of a unique type, and nine families are united among flowering families by containing betalain pigments instead of anthocyanins. Two families, the Caryophylaceae and the Molluginaceae, which have been placed in the Centrospermae by various authors (Roemer, 1920; Harms 1934; Cronquist 1968; Takhtajan 1969), lack the distinctive betalain pigments, and their placement has, as a result, been the subject of some controversy. There is evidence that these two betalains containing families arose from common centrospermous ancestor (Ehrendorfer, 1976; Mabry, 1973). Thus, the families generally accepted today as belonging to the order Centrospermae are: Aizoaceae, Amarantaceae, Basellaceae, Cactaceae, Chenopodiaceae, Carophyllaceae, Molluginaceae, Didiereaceae, Nyctaginaceae, Phytolacaceae, Portulacaceae (Harms 1934; Thorne 1968; Takhtajan 1969; Eliasson 1988).

The Chenopodiaceae of over 122 genera and about 1500 species (Cronquist 1981; Shmida, 1985; Pratov 1986; Thorne 1992; Kuhn et al., 1993) is one of the core centrospermous families, and has always been beyond dispute. The family has a cosmopolitan distribution, and comprises of herbs or shrubs, rarely small-trees or lianas. The members of Chenopodiaceae are mostly characteristic for arid to semiarid and/or saline habitats, and they form an important component of the flora and vegetation of desert environments from the northwestern Sahara and southeastern Europe to the Himalayas and the Gobi desert, and in the arid region of Australia, South Africa, the pampas of south America and the prairies and deserts of North America. The Chenopodiaceae family is divided among eight subfamilies and 14 tribes. A great number of halophytes and xerohalophytes of the world belongs to this family (Breckle 1986; Aronson, 1989; Akhani and Ghorbanli, 1993; Le Houerou, 1993). Chenopodiaceae are, however, taxonomically not well investigated due to the limitation of practical taxonomical characters, the fleshy nature of many species, late flowering and fruiting time, and the fact that a lot of species are aesthetically not attractive for most collectors and botanists. Recent contributions, however, fill many gaps in our knowledge of Chenopod taxonomy in Southeast and Africa (Williams et al, 1974; Scott, 1977, 1978; Townsend 1980; Assadi 1984; Pratov 1987; Freitag, 1989, 1991a, 1997; Kothe-Heinrich; 1993, Hedge et al. 1997).

Karyology of the family is well studied. The chromosomal set is being available for about 400 species and 53 genera (Grant 1982a; Turner 1994). About 50% of the taxa are polyploids or have polyploid races. Counts are available for all the subfamilies and 12 of the 14 tribes (absent in the tribe Nucularieae) as treated by Ulbrich. All the genera counted to date have base numbers of n=9, except for *Camphorosma* and *Spinaceae,* which have n=6 (based upon 2 n=12 for all taxa within this groups counted to date). These two genera are positioned within two closely adjacent tribes of the subfamily Atripliceae and the counts appear to be independently derived from a base number of n=9. It is possible, however, that numbers which appear to be on a base of n=9 (2n = 8, 36, 54, 72) are old derived hexaploids or higher polyploids. (Turner et al., 1994).

Apart from taxonomic and karyological difficulties in many genera of Chenopodiaceae, there are some fascinating aspects regarding the diversity of adaptive strategies and ultrastructure in many species. The occurrence of betalains in Chenopodiaceae is taxonomically significant because these compounds link the family with others of Caryophyllales, especially Amaranthhaceae. In Chenopodiaceae there is several distinctive micromorphological variability that are often considered as adaptative features to dry arid and/or salt-affected environments. For instance, some species consists of small succulent leaves with well developed indumentum (hairs, glands, pappillae) on the epidermis surface. The cuticle is usually thin, and the leaf is protected from desiccation by epicuticular wax deposits (platelets) or a thick layer of vesicular hairs. Many species also have a crystal-containing hypodermis. Various alkaloids also occur in the Chenopodiaceae, particularly the Salsoleae. Various flavonols, flavonoids and triterpenoid saponins have also been reported in the family. Members of Chenopodiaceae typically accumulate large quantities of nitrates, which are sometimes converted into toxic nitrites (Hegnauer 1964; McWhorter et al 1995; Fuller and McClintock, 1986). The spiny leaves and fruits, and the chemical constituents of other organs are known to cause skin irritation (Mitchell and Rook 1979). The pollen of various weedy chenopods, such as *Atriplex*, *Chenopodium*, *Bassia* and *Salsola* is known to be allergenic (Lewis and Imber, 1975).

Embryology of Chenopodiaceae has been fairly well studied in various genera (Rocen 1927; Cooper 1935; Maheshwari 1950; Hindmarsh 1966; Skvarla and Nowicke 1976; Devi and Rao 1976; Konycheva 1983; Johri et al 1992; Kuhn et al 1993; Nowicke 1994; Toderich 2000, 2002). It was suggested that the anther wall development is monocotyledonous, i.e., the outer secondary parietal layer division is suppressed, so that the middle layer and tapetum are developed from the inner secondary parietal layer type. This type is probably synapomorphic and mostly common for monocots. But also occurs in a few eudicot families especially within the Caryophyllales (Chenopodiaceae, Amaranthaceae, Molluginaceae, and Portulacaceae) as well as the related Polygonaceae and Droseraceae. The anther wall consists of an epidermis, fibrous endothecium, and an ephemeral middle layer. The tapetum is mostly of the secretory type, but an ameboid tapetum has been reported in *Chenopodium murale L*. Pollen grains are usually three-nucleate when shed. Members of Chenopodiaceae have similar spherical, pantoporate pollen with variable numbers of pores. The exine has a thick, minutely perforate tectum with short spinules.

The ovule is campylotropous, bitegmic and crassinucellate. As is typical of Caryophyllales, the micropile is formed by the inner integument. Megagametophyte (embryo sac) development may be of the Polygonum type as in *Chenopodium*, or of the Allium type as in *Suaeda*. The synergids have prominent hooks, and the three antipodal cells may be ephemeral or persistent. Endosperm development is at first nuclear, later cellular. Embryo development is of the Chenopodiad and/or Solanad types. Most Chenopodiaceae have curved to annula (horseshoe-shaped) embryos with perisperm persisting in the mature seed, but in members of Salsoloideae the embryo is spirally coiled and perispern is more or less absent. The fruits of Chenopodiaceae are utricles, achenes, rarely berries, or small pyxides that are often associated with persistent and/or acrescent, appendaged tepals.

One of the largest and economically very important is the almost cosmopolitan genus *Salsola*. The exact number of species is not established yet: ranging from about 100 (Kuhn 1993; Freitag 1997) to 150 (Willis, 1973) and over 300 according to. Botschantsev (1969, 1976; Judd et al., 1999). The wide geographical distribution of *Salsola* can be divided into two regions: the largest region stretches across the deserts of the Old World from the Canary Islands through North Africa and south-west Asia to Central Asia. The second region is in South and southwest Africa, where over 80 species have been reported (Arnold 1972; Botschantsev 1976). Being most diverse in Asia, Europe, and Africa, many *Salsola* species now are widely naturalized in North and South America and Australia. In the flora of Uzbekistan about 47 species of *Salsola* are mostly described in the typical desert and semidesert zones and account for up to *45*% of the Chenopodiaceae family species.

Tribe Salsoleae and genus *Salsola* in particular includes shrubs, subshrubs and herbs both perennial and annual with C_3, C_4 or C_3-C_4 intermediate photosynthesis species (Akhani et al. 1997; P'yankov, 2001; Voznesenskaya, 2001).

The perennial species are usually woody at the base with a lifespan of 7-12 years. Plant surfaces are glabrous or with a minutely hirtellous indumentum. They have a pivotal (5-10 m deep) and superficial (8-12 m radial) root system. Annual species are usually represented by herbs with superficial roots.

It is well known that from the taxonomic point of view genus *Salsola* (subfam. Salsoloideae) is generally considered extremely difficult. As reviewed by (Ulbrich 1934; Ilijn 1936; Botsanschev 1969, 1975a,b; Winter 1981; Pratov 1986; Rilke 1996; Hedge et al 1997; Toderich, 2000; P'yankov, 2002) there is considerable disagreement on species delimitation and itrageneric relationships within the genus *Salsola*.

Despite extensive systematic treatments of *Salsola* and its relatives (Flora Uzbekistan 1952, 1963; Aellen, 1968, 1979; Botschantzev, 1969; Aellen and Akeroyd, 1993; Freitag 1997; P'yankov et al 1997, 2001) the number of species and species groups within this genus remains uncertain.

To make evident the large species diversity that is assembled in the classical *Salsola* concept, the genus description was enlarged to cover the more important variations of characters. Moreover, for a better handling of the numerous species, the genus has been split into a number of sections, which are in fact comparable to some other traditionally recognized genera of Chenopodiaceae family. The detailed revision of most species groups of the genus *Salsola* was carried out by Botschantsev, 1989. Based on the earlier works of Fenzl (1851), Ulbrich (1934) and Iljin (1936), as well as on morphological features of vegetative organs Botschantzev, 1989 recognized six systematic sections of *Salsola*.

The taxonomic system of genus Salsola worked by Botschantsev, 1989 is still widely accepted and in the present study we also use it as a base:

Section *Caroxylon* (Thunb.) Fenzl.

Section *Malpigila* Botsch.

Section *Cardiandra* Aellen

Section *Belanthera* Iljin

Section *Coccosalsola* ,sub. *Arbuscula* (Fenzl.

Section *Salsola*, sub. Kali (Ulbrich.)

The sections of genus *Salsola* used in the system of Freitag and Rilke (cited in Hedge, 1997) appear for the most part to be natural groups, although it was clear to the authors that their taxonomic ranks are unequal. With minor variation their system is based on the most remarkable account of Iljin, 1936, 1937 and the revision of Botschantzev, 1969. The big number of species, however, (more than 42) treated by Botschantzev,1969 and Pratov, 1986 as genus *Climacoptera* has been placed by Freitag and Rilke, 1997 into the genus *Salsola* as a separate Section "*Physurus*". Though in recent years evidence has accumulated that only these subgeneric units (8 recognized sections) form the natural monophyletic groups represent the different evolutionary lineage within Salsoloideae. Above-cited authors, however, were analyzed mainly *Salsola* species growing in Africa, Iran, Mediterranean region, Europe and little attention was given to the Central Asiatic *Salsola* complex. So, it become clear that several evolutionary lines start and is developed in the genus *Salsola.* Many of them continue in more advanced subgenus units. Thus, the traditional delimitation is already evident, but the intraspecies diversity is not described in the botanic literature yet. Some refinements of a new revision and classification of genus *Salsola* need investigation of other species from outside the Flora Iranica, African and Mediterranean areas. The heterogeneous character of genus *Salsola* is best expressed by the attempts to raise whole sections or parts of sections to segregated genera *Physandra, Aellenia* and *Climacoptera* by Botschantsev (1956), *Eremochion* by Gilli (1959), *Nitrosalsola* and *Xylosalsola* by Tzvelev (1993).

Still now a major point of disagreement exists in relation to the species of section *Salsola,* sub. *Kali* (Ulbrich). According to literature about 20 species of the total number of species of genus *Salsola* belong to section *Salsola,* sub. *Kali* (Ulbrich). Difficulties in the identification of species belonging to section *Salsola* sensu lato have existed for a long time, even for the trained taxonomist. The members of this section are morphologically very similar and relatively poor in key features. This delimitation of species is not only caused by the notorious lack of easily recognizable characters, but often by insufficient plant material and a confusing nomenclature. The situation is also complicated by the exceedingly high degree of polymorphism in certain widespread species. Besides the chenopod experts themselves have produced many problems, by adhering to a too narrow species concept, overestimation of weak characters and insufficient consideration of the relevant literature. This section which mostly consists of annual herbs, is characterized by leaves ending in a bristle or short point, absence of true hairs, and filiform stigmas that are longer that the style .The inconspicuous appendage of anthers, flattened fruits, and horizontal seeds of *S. kali, S. paulsenii, S. pestifer, S. praecox, S. collina* and others lead to their placement in series Ruteniceae Iljin (Iljin, 1936). But specific limits are often difficult within this section. The greatest difficulties are the morphological resemblance between various species of this section. For example, *S. pestifer* has been misidentified as *S. tragus* L., S. *iberica* Sennen*, S. paulsenii* and *S. australis* R. Br (Judd et al., 1999). A morphological and structural similarity is noted between *S. pestifer*, *S. praecox* and *S. kali* subsp. *ruthenica* (Iljin), the latter of which is widespread in Europe. A lot of studies on the biogeographical distribution, morpho-embryological and eco-physiological specificity of annual species of genus *Salsola s*ection Salsola sub. *Kali* (Ulbrich) in terms of its systematic relations within genus *Salsola* have been performed and published in the botanical literature (Aellen 1968; Botschantsev 1969; Winter 1981; Butnik 1984; Voznesenskaya 1986; Rilke, 1977a, 1998, 1999; Rilke and Reiman, 1996; Freitag 1996; Toderich 2001). Members of section *Salsola*, predominantly *S. kali,* which is widespread in more or less saline, littoral habitats throughout Europe (subsp.kali) and along the Mediterranean Sea (subsp.tragus), are usually recognized as three subspecies: *Salsola* k *ali, subsp. iberica* (Sennen Pau) *(subsp. ruthenica* (Ilin) and *subsp. tragus* (L.) Nyman (Aellen 1968, Aellen; Aneroid, 1993). In particular, *S. kali* and *S. tragus* are hard to separate. The characters used by Iliin (1936); Aellen (1968); Rilke, 1996; Freitag, 1996 to delimitate the subspecies within the framework of European species of this section are habitat, shape and various morphological traits of leaves and fruits. High intra-population variation was observed with respect to color, thickness of leaves and bracts, indumentum, tepal lobes and wings development Rilke and Reimann 1996; Rilke 1999. Recently a detailed taxonomic survey and revision of section *Salsola* sensu lato has been presented by Rilke, 1999. Within species of section *Salsola* she recognized 18 species, assembled into two subsections: *Salsola* and *Kali* Dumort based mostly on presence and/or absence of chlorenchyma in the stem cortex, as well as in the distribution of unicellular papilla-like hairs, anther structure and fruit types

Despite comprehensive analysis of section *Salsola* given by S. Rilke, 1999 the taxonomic status of Asiatic members of this section remains still very contradictory. The correct name for the widespread annual *Salsola* species and the problem of synonymy in this section was also discussed (Mosyakin, 1996). The following have been used as synonims*: S. australis* R.Br. *S. iberica* Sennen and Pau., *S. kali* L. *var. tenuifolia* Tausch., *S. pestifer* A. Nelson and *S. kali* L. *subsp. ruthenica* (Iljin) Soo. Systematical keys have been prepared to identify the different species of *Salsola* grown in northern America. A systematic study of annual *Salsola* species in Utah characterized *S. pestifer* as well as two varieties of *S. paulsenii,* one with spinose perianth tip and a second with a lax perianth tip. Some distinguishing morphological and karyological characters were reported for these taxa as well. Plants of *S. paulsenii* have both 2n –18 and 2n- 36, 54 numbers of chromosomes, while *S. pestifer* is mostly characterized by 2n-36. (Crompton and Bassett, 1985)

Many members of this section, such as *S. pestifer, S. praecox, S. paulsenii, S. aperta, S. soda, S. androssowii, S. sogdiana, S. acutifolia, S. tamaricina* growing mostly in open inland salt marshes, marshy-steppe or saline sands communities of Kyzylkum Desert are also an evolutionarily young, not clearly separated taxon. *S. pestifer* and *S. praecox* with slender leaves are growing on dry, sandy, mostly under moderated saline soils. Stems with green or pale cortex, spiny leaves and bracts, small ovoid anther-appendages, which narrow gradually from the base, characterize this section. Recently it was suggested that the Asiatic group shows some affinities in floral traits, structural specificity, and pollen morphology with European species like *S. kali* and *S. ruthenica* (Toderich et al., 2000).

Obviously more detailed data on the structural and genetic variability and its relation to salinity must be considered essential to assess the taxonomical importance of genus *Salsola*, sect. *Salsola,* sub. *Kali.* Besides that there is still great interest in the structural, eco-physiological and genetic peculiarities of annual desert *Salsola* species and, hence in their taxonomy, evolution, and geographical distribution. Since the main center of distribution of this genus is in continental Asia from Kazakhstan to Mongolia and within the Irano-Turanian and the Transcaspian lowlands, the profound structural analysis of vegetative-reproductive system under natural harsh desert conditions represents a major scientific interest.

The identification of woody shrubs at different developmental ontogenetic stages (often under field conditions) is also a special problem. For example, for farmers and pastoralists it's quite crucial to differentiate between the seeds of two morphologically very similar species *S. paletzkiana* and *S. richteri* during the collection of seeds for the extraction of the alkaloid "salsolin" used for pharmaceutical purposes.

For range improvement livestock industry programs a special problem exists in the identification, often in field conditions, of many taxa of this genus at various developmental and ontogenetic stages. There are several questionable names applied to different taxa.

Contradictory infrageneric classifications and taxonomic positions still exist within *Salsola* species (about 42) that have been included by early authors in sect. *Eusalsola* (Fenzl.); sect. *Nitraria* (Ulbrich, 1934); sect. B*rachyphylla* (Iljin, 1937) or sect. *Physurus* (Beguinot 1914, Ulbrich, 1934; Iljin, 1936; Aellen 1968). The extremely high morphological and eco-physiological variability of species of this group has been known for a long time and led to the description of several species, subspecies and varieties. At the same time Botschantsev 1969; Pratov, 1986 based on differences in habit, vegetative and generative morphological characters grouped these species into a distinct genus *Climacoptera.* Lately this taxon, however, was replaced again to genus *Salsola* sect. *Physurus* (Hedje et al., 1997). From palynological point of view Toderich et al (2000) considers *S. lanata* as typical species belonging to genus *Climacoptera*, taxonomically closely related to genus *Salsola.*

From the phylogenetic point of view the history of genus *Salsola* is a striking example for the evolutionary convergence of morphological, ecological and biochemical traits. One of the adaptive strategies that are correlated with morphology, ecology and even taxonomy is photosynthetic type. Two types of CO_2-fixation, namely C_3 and C_4 are described for different representatives of genus *Salsola* (Osmond et al., 1969, 1980; Winter, 1981; Frey et al 1985; Freitag et al 1999; P’yankov et al 1997, 1999, 2001, 2002). Distinct morphological groups plus structural and biochemical lines of C_4 photosynthesis started and developed within the genus during evolutionary times are found. These taxonomic groups recently were associated with NAD- and NADP-ME biochemical types of leaf photosynthesis (P’yankov et al, 1997, 2001a, 2001b). These biochemical groups mainly coincide with systematic and evolutionary branches: the section *Caroxylon*, *Belanthera*, *Malpigila* and *Cardiandra* belong to NAD-ME, while *Cocosalsola* and *Salsola* belong to NADP-ME along with some C_3 and C_3-C_4 species (P’yankov, 1997). A unique distribution of different C_4 Chenopodiaceae structural and biochemical subtypes along the aridity gradient was recently determined (P’yankov, et al 1999, 2000, 2002).

There are no recent worldwide monographs of genus Salsola, and in some species, owing to the high degree of organ polymorphism and expansive, even transcontinental dispersal, the identification of species with the aid of local Floras is inadmissible. It was not yet been determined to what extent this variability represents genetic, developmental or environmental differences. In this context we suggest that the taxonomic status of many species of genus *Salsola* and determination of their relatives’ relation needs to be reevaluated. Probably, the lack of distinctly differentiating characters is due to the active evolution-taking place in the section *Salsola* sub. *Kal*i (Ulbrich) in both Asia and other continents.

CHAPTER 2. Material and Methods

2.1. Desert and semidesert ecosystems of Uzbekistan

A. Kyzylkum Sandy Desert and Priralie

This section represents an overview of the physics-geographical and soils characteristics of main habitats (eco-edafic zones) of *Salsola* species distribution and plants sites collection within Uzbekistan (Fig. 1).

Figure 1. Map of soil typology of Uzbekistan.

(**Source:**http://www.fao.org/AG/AGL/swlwpnr/reports/y_nr/z_uz/uz_map/uzmp221.pdf **)**

The desert soils of Uzbekistan, where halophytic plant communities are grown, evolved under semi-arid and arid conditions. They are characterized by low organic matter (< 1.0%), a high level of calcium, often associated with gypsum, and a low agricultural potential. The soils are composed of particles of varying sizes, are frequently saline, with unfavorable physico-mechanical properties; poor structural characteristics, and often a high level of compaction. Most of these soils have evolved from alluvial, colluvial or aeolian loessic deposits with little weathering of the parent rock. Three main groups of soils may be distinguished among all the soil types recorded in Uzbekistan (Gintzburger et al., 2003):

-sandy aeolian soils (13,3 million hectare), sand dunes of the Kyzylkum and some agriculturally important loess deposits (the piedmomnt of the eastern mountains);

- grey brown (11million hectare) and sierosem –grey soils (3.8million hectare) of pre-desert and steppe;

- solonchaks and solonets , azonal soils (1,6 million hectare) mostly on depressions, and takyrs

(2,8 million hectare) with a shallow water table and high mineralized underground water
The combination of sandy aeolian soils is a common formation occurred in majority arid zones of the Kyzylkum desert. The Uzbek desert ecosystem covers the Kyzylkum, the Ustyurt plateau, the Karshi steppe, as well as the separate sites in the southern part of Uzbekistan and the Fergana valley and is represented mostly by low lying lands with an elevation between 100 to 500m.
The Kyzylkum Desert occupied the areas between the two largest rivers of Middle and Central Asia, the Syr-Darya to the east and the Amu-Darya Rivers to the south and southwest. These two rivers originated from the massive Tyan'-Shan, Pamir-Alay and Turkestan mountain chains drain into the Aral Sea to the northwest. Special conditions are found in the hilly and low-mountain areas of Kyzylkum, such as Kul'dzhuktau, Muruntau, Nuratau, Auminzatau, Bukantau, and Tamdytau. Here the eastern hills of the Kyzylkum and the Ustyurt plateau, display a unique natural landscape of complex ecological niches where the richest desert flora biodiversity is found. However, we shall only concentrate on the Kyzylkum, as far as plant material of *Salsola* species used for the present study was collected from there. The eastern hills and low mountains (Nuratau, Kul'dzhuktau, Auminzatau, Tamdutau, Bucantau, Soultandag etc.) are distributed all over the Turanian lowland. Many solonchak depressions (Ayakagitma, Mingbulak, Beshbulak, Kulkuduk, Karakata, Karasugursk, Kukayaz) are located between sandy-loam/clay soil formations and large, sand-dune areas. These physico-geographical peculiarities immensely affect the unique flora of the Kyzylkum desert.

Soil conditions heightening the risk of land degradation in the whole arid/semiarid zones of Uzbekistan include salinity, sodicity, hydromorphy, soil shallowness, and risk of erosion (FAO, 2000). Among them, soil salinity and sodicity are the most severe affecting 53% of the country arable lands. Salinity induced soil in the Aral Sea Basin, where the negative environmental consequences are considered to be some of the largest caused by humanity in recent times, has increased steadily over the last few decades. The percentage of saline soils in 2005 significantly increased compared to the situation in 1990, when the share of slightly, medium and highly saline lands was 50%, 33% and 10 %, respectively. In 2000, a year of notable water shortage, the percentage of medium and highly saline soil increased significantly, whereas slightly saline soils decreased to 45%. From last decades the rapid changes in area affected by secondary salinization occurred in Karakalpakstan, Khoresm and Syrdarya regions (Mirzachuli steppe), Fergana Valley and Kashkadarya and along Amu-Darya River much of the salt-affected land occurs in the Buchara oasis (Southeast Kyzylkum), where numerous solonchak depressions (Ayakagitma, Mingbulak, Beshbulak, Kulkuduk, Karakata, Karasugursk , Kukayaz) are located. Technogenic industrial areas patchily distributed between sandy-loam/clay soils formations and the large sand dunes areas could be considered a source of degradation of fertile lands in Kyzylkum desert and

Priaralie regions both from Uzbekistan and Kazakhstan sides.

Additionally large-scale industrial development of the gold mining, gas- and oil- extracting and processing in the southeast and central Kyzylkums, for the last 15-40 years, have aggravated land degradation of these territories. Tailing piles of ores below industrial grade that were formed during the process of the deposits' development. The open and underground ways, the underground leaching (UL) mines and the tailings of the hydrometallurgical plants that processes uranium ores and technological solutions of (UL) are considered one of the main sources of environment pollution of the Kyzylkumes. Uranium production in the Kyzylkum area peaked in the 1980s when 3700 to 3800 tU/year were produced. The mine taillings of radioactive waste deposits (as well as the dumps of uranium ores below industrial grade and the mining of underground leaching areas) situated on the left bank of Zerafshan River near Navoi city is also dangerous for the ecology of the region.

More than 30 years of uranium production-related activities by Navoi mining Metallurgical Combinate (NMMC) have impacted whole Kyzylkum natural environment. This includes the areas affected by conventional mining and processing of uranium ores, as well as the operation of in situ leaching facilities. In addition to the areas directly affected by these activities, there are surface accumulations comprising an estimated 2 424 000 m^3 of sub-economic uranium-bearing material. The uranium content of this material is estimated to be 2-5 mg/kg (0.002 to 0.005 percent U). The related contaminated material recovered from the surface of these operations is about 3 500 000 m^3 (Solodov, 1998). High human impact (urban, industrial and agricultural activities, handicrafts and traffic) on the southern part of Kyzylkum deserts leads to the pollution of the sands and the irrigated lands with pesticides, nitrates, organic pollutants and various heavy metals (Goldshtein, 1997; Toderich et al, 1999; Tsukatani and Katayama, 2001; Toderich et al, 2001, 2002a, b, c, 2003, Toderich et al, 2005a,b). Thus, the areas suitable for agricultural development in Aral Sea Basin are continuously decreased.

Our currently experiments showed that soils of Kyzylkym desert and lower streams of Amudarya and Zerafshan River Basins are characterized by low productivity with a predominance of carbonates and gypsum content (Fig.2). The humus content is around 0.5% in sandy desert and ranges from 0,7% at the gray-brown sites up to 1.2 % in the virgin and newly irrigated takyrs, which are widely distributed in South-Eastern Kyzylkum.

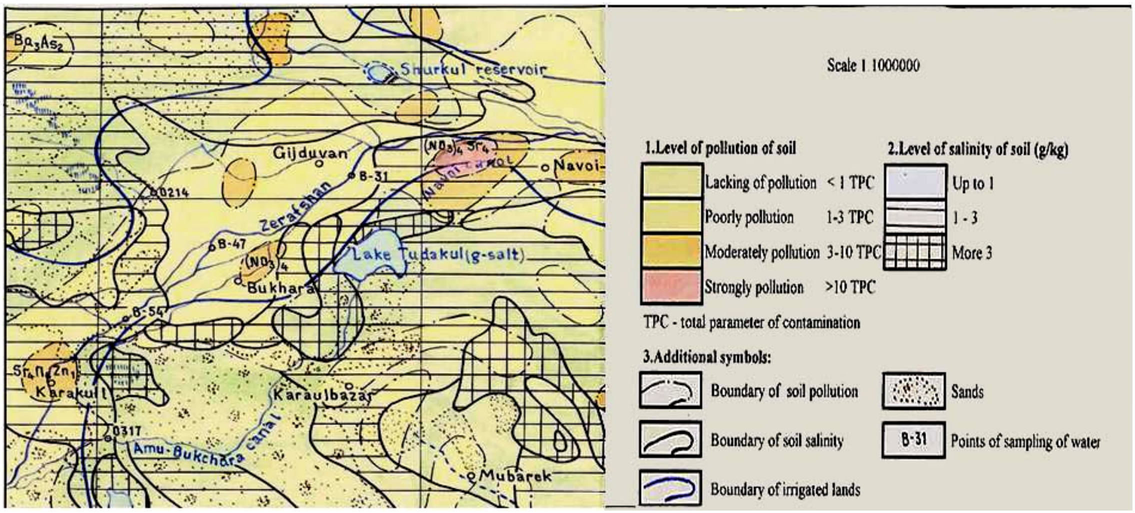
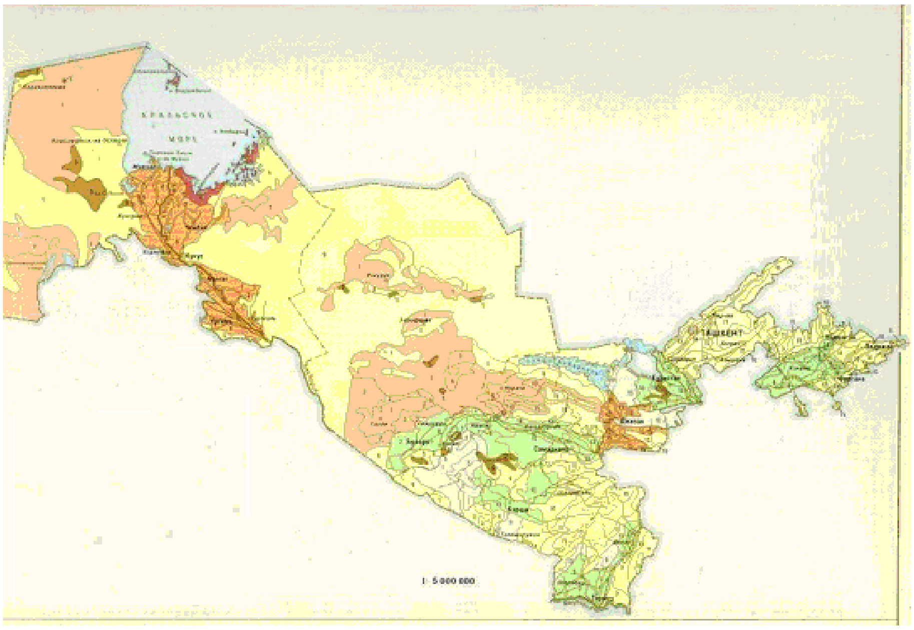


Figure 2. Extent of salinity and pollution of soils in South-east Kyzylkum region

A low productivity and high salinity (1200-2000 mg/l and rarely more than 3800 mg/l of soluble salt) characterize these soils, with a dominance of carbonates, sulfate, chloride and/or mixed types of salinisation. Sulfate-hydrocarbonate-calcium is the predominate type of soils. In the Central Kyzylkum, which is less salinized, the sulfate-potassium-sodium (and rarely chloric-potassium-sodium) types occur frequently. In the last few years there has been a tendency for fast degradation of floodplain ecosystems of the Amudarya and Zerafshan Rivers delta –marginal territories of Kyzylkum desert. It seems that human induced soil salinization remains the main triggers for degradation of land in the Aral Sea Basin (Kamalov, 1995).

Focusing on countrywide soil chemistry of surveyed salt –affected areas with shallow water table we found out that the predominant salinity type is chloride-sulfate, while sulfate -chloride type is also described (Fig.3).



Soil chemistry	Dry solonchaks	Wet solonchaks	Solonets
Chloride and sulfate - chloride			🟥
Chloride-sulfate	🟧	🟧	🟫
Sulfate	🟩	🟩	🟩

Figure 3. Map of soil salinity extension accordingly landscapes distribution in Uzbekistan

Soil type of surveyed area is silt-sandy loam, throughout the profile up to the depth of 60 cm. The soil is highly saline in the top soil and in the lower layers. Ground water salinity varies from to 2000-8200 mg/l. Sodium and magnesium are the dominating cations. It was also found that the organic matter in these soils ranges from 0.7 to 1.5%。 Total nitrogen (N) and phosphorus (P) contents in salt affected soils are low, usually ranging between 0,7-5,5 mg/kg and 10,0-18,26, mg/kg respectively. Available potassium (K) content is classified as low or moderate (Shirokova et al., 2006). Consequently, the natural fertility of the saline soils, especially in deltas of the main rivers of Uzbekistan is characterized as rather low, and cultivation of most agricultural crops requires high inputs of chemical fertilizers or applying of costly leaching practice. This strategy, however, increases the risk of re-salinization in the root zone of plants and leaching process has to be repeated every cropping season in order to avoid build-up of high salt concentration in the top soil profile. In this respect the appropriate practices for salinity control should be selected based on the quantification of water and salt movement in the soil, crops response and adaptation to water and salinity stress and how environmental conditions and management influence these interactions. In this regard, efficiently water use for irrigation couple with introduction of modern bio-remediation technologies as mentioned by Yensen et al., 2000 and Toderich et al, 2004, 2006 a,b could help to integrate all interactions and define the best management for crop production under saline environments.

Summarizing the existing information and based on the geological and hydrological characteristics, we have concluded that salt affected areas of Uzbekistan demonstrate the most characteristic features of natural continental (not marine/coastal) salinization, sodication and alkalinization. Since the most important direct source of soil salinization is the shallow groundwater level below the lowland surface, there is a chance of irrigation-related salinization in two dominant situations: when the abundant use of river waters causes waterlogging and rise of saline groundwater (salinization from below); and when typically saline tubewell-waters are used for irrigation (salinization from above) as it is a case in Kyzylkum desert.

Agro-climatic conditions, ground water salinity and soil-plant salinity relation

The target areas of *Salsola* species sampling constitutes a salt depression formed by freely-flowing saline hot artesian water (vertical drainage water), which is the only water source available for cultivation under sandy Kyzylkum desert conditions. The agro-climatic environments undergoes extreme, continental, arid conditions, limited and unreliable winter precipitation (mean of annual precipitation varies from 100 up to 180mm), a high level of evapotranspiration, extreme daily, seasonal, and annual fluctuations of air temperatures, soils with high salinity and gypsum content, and finally as a result of all theses extreme conditions, it has a sparse, but diverse, vegetation cover. Climatic conditions as is shown in Fig. 4 are given for the Kanimekh agro-ecological zone, Navoi region (Central Kyzylkum), which has been chosen as biomonitoring site of salinity trends and halophytic botanic diversity changes.

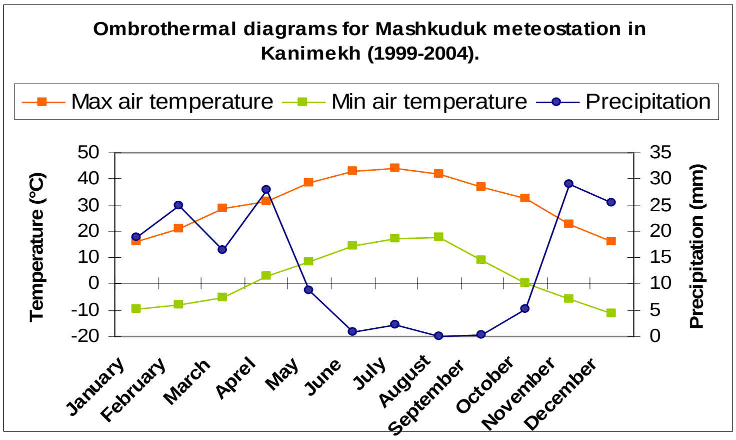


Figure 4 Dynamics of air temperature and precipitation changes

Spatial and temporal distribution (zonation) of natural vegetation of 8 visually divided zones accordingly soil salinity level were studied based on plant vegetation type and soil salinity level. The most important factor for the zonation was soil salinity and the salt tolerance limits of species. In general the width of each zone as is seen in the Fig. 5 differs according to the relief, floristic composition, and the ion concentration (haloaccumulation plant ability).

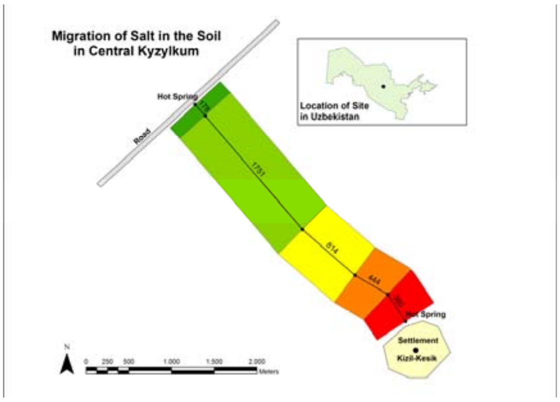
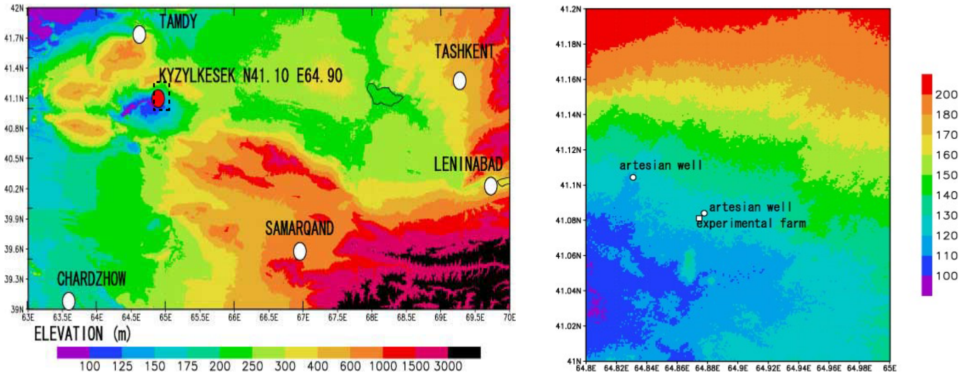


Figure 5 Spatial and temporal distribution (zonation) of natural vegetation of 8 visually divided zones

Spatial distribution (zonation) of natural desert vegetation in relation to soil salinity was studied in an area of about 10 -25 hectare located between two artesian hot springs at the Kyzylkesek site, Kanimekh district, Navoi region (Fig. 6a,b)



Figures 6 a,b. Spatial distribution (zonation) of natural desert vegetation

Our results showed that the ground water salinity taken from different sources (drainage collector, surface and underground water) varies from to 2500-12800 mg/l. Sodium and magnesium are the dominating cations. Ground water table fluctuates from 0.8-2.5 m during May-July at the experimental agricultural plot and up to 5-8 m in the desert pasture area. Dynamics of soil moisture under different plant communities, which are distributed in the degraded pastures, is shown in Fig. 7

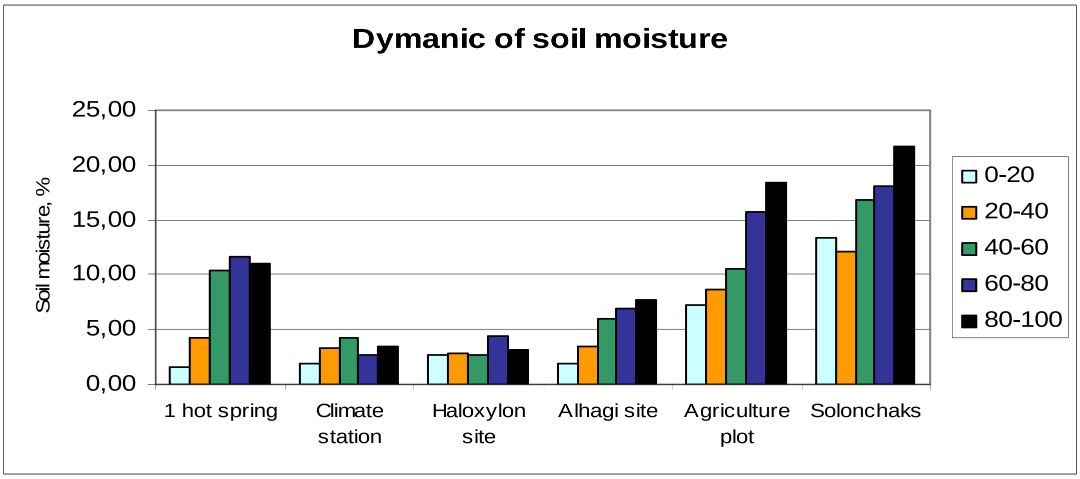


Figure 7. Dynamics of soil moisture at the different ecotopes in the Central Kyzylkum

Due to low transpiration capacity, *Alhagi* plant communities promote retention of soil moisture in the top soil (Fig.8). The same situation is also observed on saline marginal drylands, where *Climacoptera* and others annual *Salsola* species dominate. Due to low transpiration capacity, *Alhagi* pseudoalhagi-annual-*Salsola* plant communities, located near the experimental area helped in retaining soil moisture in the top soil.

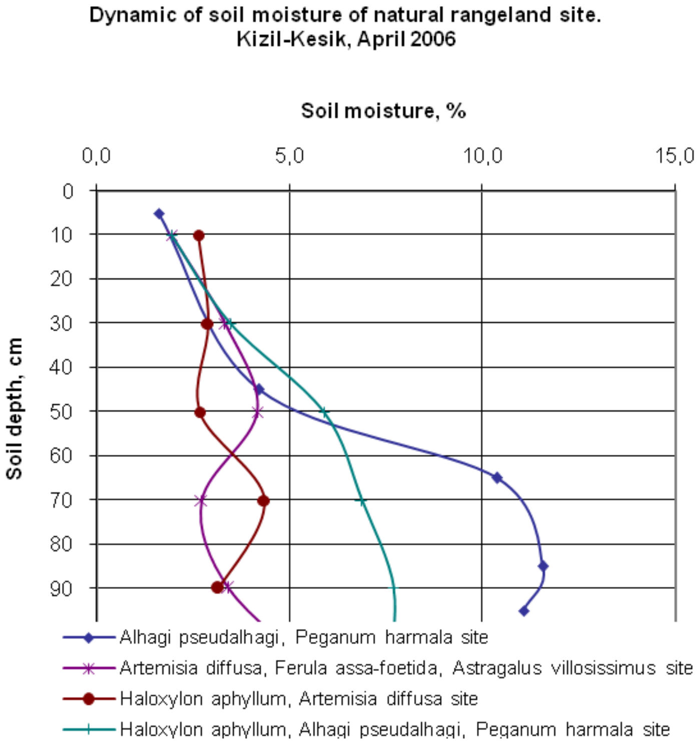


Figure 8. Dynamics of soil moisture under main desert plant communities with dominance of annual and perennial *Salsola* species

Additionally the high evaporation rates are drying the ponds in summer, making them as evaporation ponds. Poor natural drainage system of marginal cropping irrigated lands has caused an increase in the salt content at the superficial crust and groundwater that induces secondary salinization of the soils. The very intensive processes of soil salinization occur in the area located in the vicinity of the artesian wells. Therefore the studies of different ecological groups of wild halophytes have supported studies of groundwater with reference to salinity sources and irrigation management. Average electric conductivity of the irrigation water (artesian hot spring) varies between 2300 to 3100 mg/l, while pH varies between 7.3 and 8.1. The dominant cation is Na^+ and the dominant anion is SO_4^{2-}. A very intensive process of soil salinization occurs in the area located in the vicinity of the artesian wells. Chemical analysis of soil from target area showed that main type of mineralization is calcium-sodium and hydrocarbonate-sulfate. Analysis of each zone separately demonstrated significantly differences of content cations and anions. Three zones (Climate station site, Haloxylon and Alhagi sites) with the less content of soil moisture as is shown in the fig.9 is characterized by significantly amount of $Ca^{2+,}$ HCO_3^- ions and the less content of Na^+, Mg^{2+} and Cl^- compare with other sites.

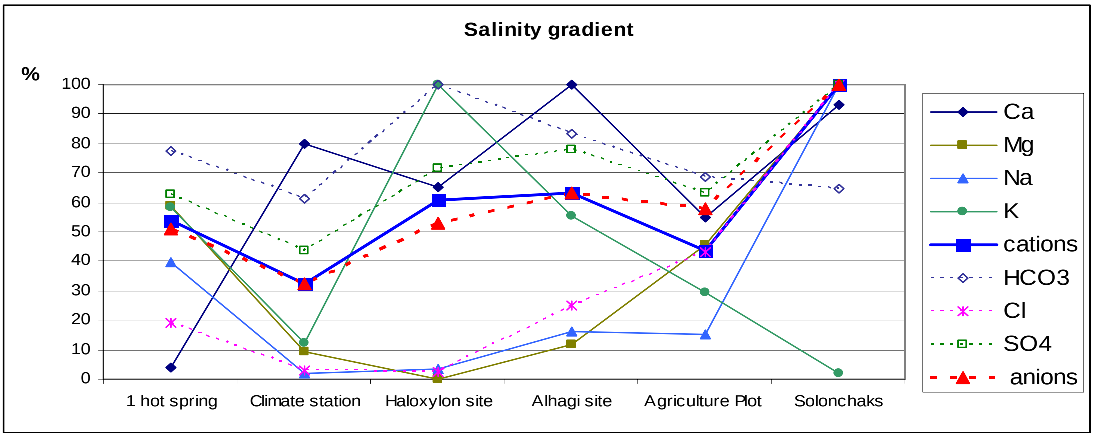
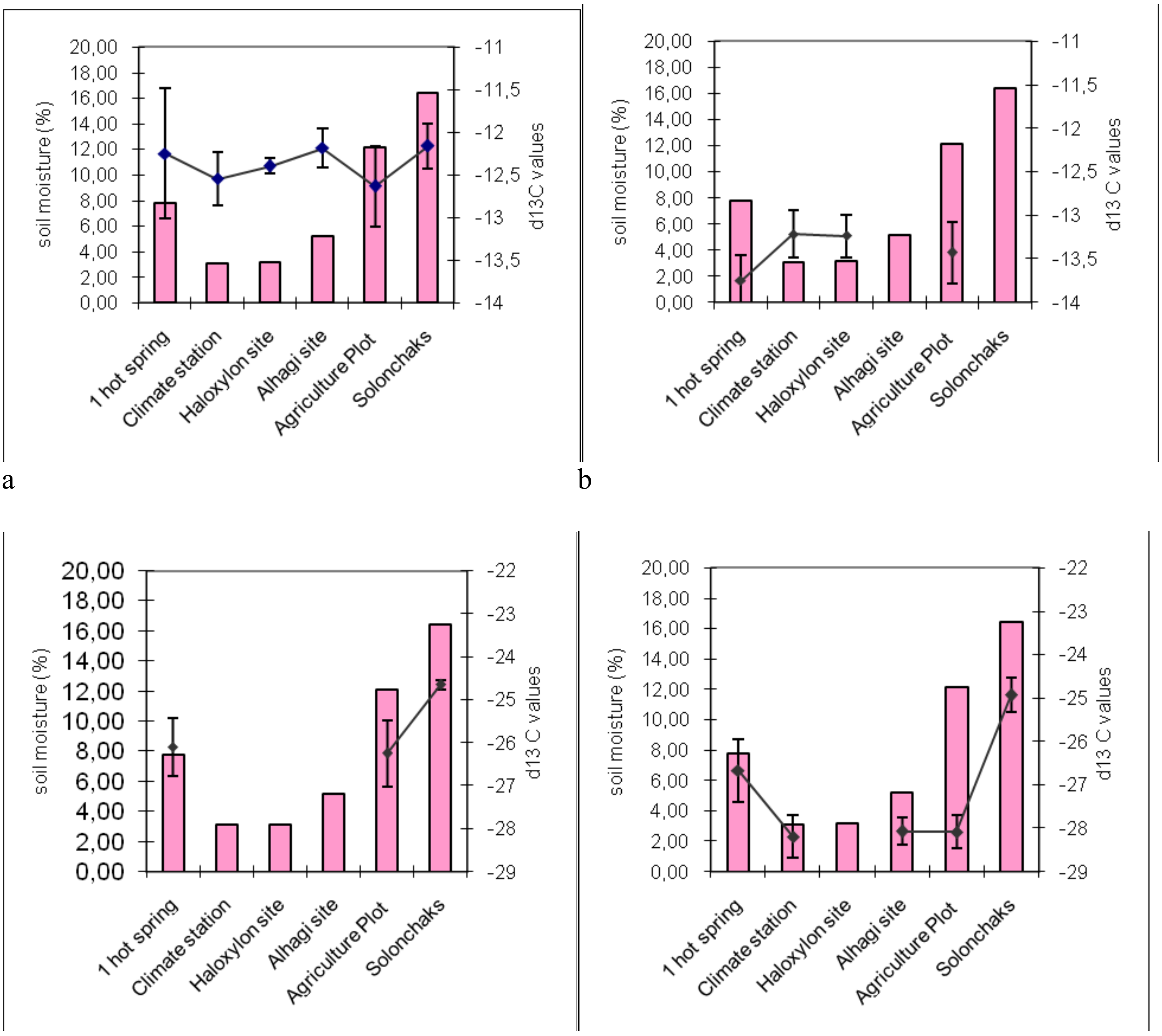


Figure 9. Relative content of different cations and anions in studied zones.

Sites 1 hot spring and Agriculture plot is characterized as a moderate zone both by content of soil moisture and composition of the majority ions (Na^+, $Mg^{2+,}$ K^+, $HCO_3^{-,}$ $SO_4^{2-,}$ Cl^-). The higher content of ions and soil moisture, was observed in olonchaks site (salt depression), moreover amount of Na^+ in this site almost in 20 times more than in Climate station site and Haloxylon site, Cl^- in 10 times and SO_4^{2-} – in about 2 times. This results showed that Climate station site, Haloxylon and Alhagi sites characterized by the less moisture soil with calcium-carbonate type of mineralization. Therefore, studied zones are represented along the gradient of mineralization changes (based on main content cations and anions) and could be distributed as following: Climate station site < Agriculture plot < 1 hot spring < Haloxylon site < Alhagi site < Solonchaks site. High soil mineralization in Haloxylon and Alhagi is characterized by high content of Ca^{2+} and HCO_3^- , i.e. gypsum content. Based on the composition and content of Na^+ and SO_4^{2-} ions (as main ions of salinity) the surveyed zones accordingly salinity gradient could be arranged as following: Climate station site < Haloxylon site < Agriculture plot < Alhagi site < 1 hot spring < Solonchaks site. Soil of Agriculture plot site is characterized by less level of salinity because of irrigation, which leads to wash out salts.

As is seen from the Figs. 10a, b, c, d the high contents of salts in the soils indicates that water became less available for plants, especially for xerophyte species. Halophyte and hyperhalophyte due to adaptive mechanisms to grow on salinity soils can better use water from such type of soil (fig. 10 a,b,c,d).



a b

c d

Figures 10 a,b,c,d. Soil moisture (histogram) and a) *Haloxylon aphyllum* (line), b) *Salsola paulsenii* (line),c) *Tamarix hispida* (line), d*) Alhagi pseudalhagi* (line) related to C isotope values.

We have also identified that along the increasing mineralization gradient (based on contents of mean cations and anions) leaf carbon isotope rations of C_3 species tended to increase (Fig. 10 a, b, c, d). The crucial role in this tendency plays Na^+, SO_4^{2-} and Cl^- ions. Difference between leaf carbon isotope rations in *Tamarix hispida* from 1 hot spring site (middle value of soil salinity) and solonchaks (maximum value of soil salinity) is 1.6 ‰, while difference in the leaf carbon isotope rations of the *Alhagi pseudalhagi* plant community grown near the Climate station site (minimum value of soil salinity) and solonchaks (maximum value of soil salinity) – 3.3 ‰. These data indicate that water-use efficiency increase with increasing soil salinity level and correspondingly decreasing soil water availability. For comparison, a 2 ‰ differences in discrimination C_3 species indicates a difference in water-use efficiency of about 30% (Shuyskaya and Toderich unpublished data).

B.Semidesert and Foot hills Zone (Zarafshan River Valley and Mirzachuli-Karnab-Karshi steppes)

The second major site of *Salsola* species collection occupied the areas of middle stream of Zerafshan River Valley including part of Karnabchuli steppe, territories of Karshi steppe, northwestern Kyzylkum desert, floodplains of Aydarkul-Arnasay lakes systems, partly extended to Mirzachuli steppes (in the Syrdarya River Valley), where the clay and loessic deposits and different halophytic plant communities consisting from *Salsola* species are dominant (Fig. 11).

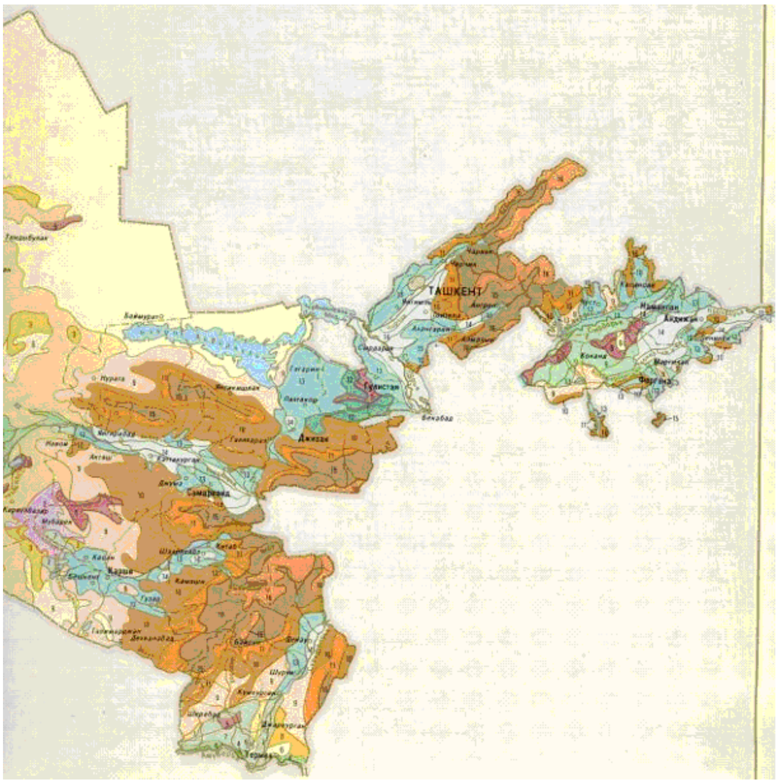


Figure 11. Map of main types of soil at the Mirzachuli steppe, Aydarkul-Arnasay Lakes systems (AALS) and north-western part of Kyzylkum desert

Climate:

The climate in this region is characterized by a dry continental with hot summer and severe winter. Average air temperature in summer varies from +16 - +19 °C with an absolute maximum of +43 °C during summer season. The first frosts occur at the end of October. The annual amount of precipitation received as snow and rain on the lowland of south part of Samarkand region varies between 210-380 mm with mean annual precipitation (MAP) value of 362 mm. About 160 mm rainfall occurs when the air temperature is less than 10 °C. Annual numbers of days with when the air temperature does not exceed 0 °C is 170.

Soil chemistry

Soil in the descriebed above agroecologiczone is meadow light sierozem and moderate clay loam with medium mechanical composition. Soil field capacity at 80-100 cm soil profile ranges from 17.2-19.3%, whereas, soil bulk density from 1.30-1.50 g/cm. Organic matter content in top soil is less than 1%. Depth of ground water varies with season. Usually ground water is at 1.5 -2.0 m depth with total dissolve salts (TDS) ranging 3000-7190 mg/l. Chemical analyses of soil samples collected from two different sites in the Karnabchuli steppe taken in March-April 2007 showed moderately salinity and high sodicity levels in the soil (Fig.12).

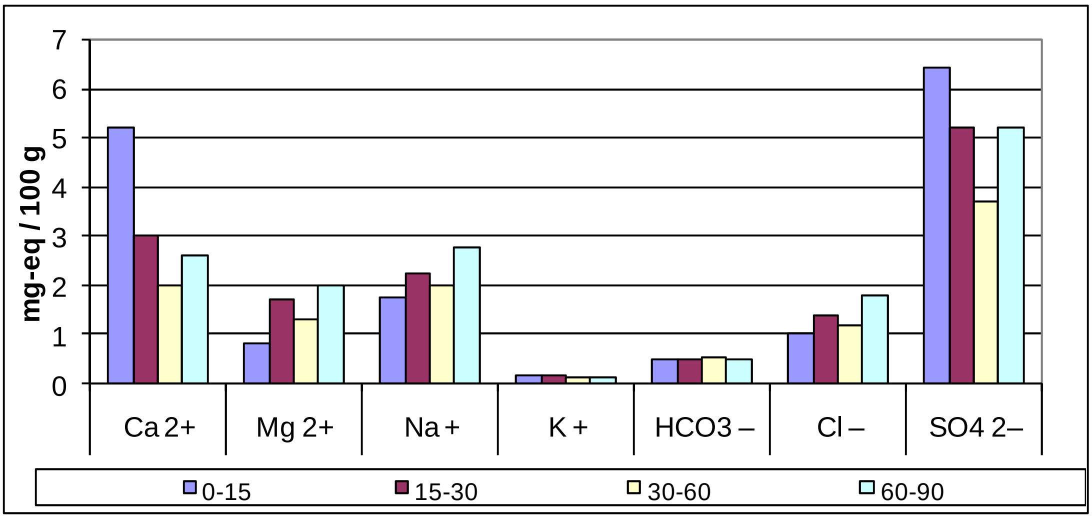


Figure 12. Chemistry of soil profile at the Mirzachuli steppe investigated in 2007

Sulfate remained the dominant ion in the tested plots followed by Cl^- and HCO_3^{-} Chemical analyses of soil showed higher concentration of Ca^{2+} followed by Na^+ among cations.

Salinity of irrigation water was at 3190 mg/l in early spring vegetation season and Ca^{2+} was the dominating cation. The anionic concentration in saline groundwater sampled revealed SO_4^{2-} as the dominant anion. High pH values exceeding 8 might serve as an indicator for possible rise of alkalinity in the top soil (Table 1).

Table. 1. Variation in chemical composition of soil at Karnabchuli site and neighbor territories

pH	TDS mg/l*	Soluble cations (mmol$_c$/L)			Soluble anions (mmol$_c$/L)			
		Ca^{2+}	Mg^{2+}	Na^{+}+K^{+}	CO_3^{2-}	HCO_3^{-}	Cl^{-}	SO_4^{2-}
7,6	1010	4.00	4.00	6.00	-	8.00	2.4	3.6
7.95	4420	2.00	5.00	57.00	9.6	14.40	6.40	33,6
8,4	8760	2.00	4.00	120.0	14.40	15.60	6	90
7.95	7360	3.75	5.00	28.10	trace	5.60	2.16	88,4

***- Total Soluble Salts**

The soil at Karnabchuli site is loamy type, varying from medium to heavy textured at soil depths from 0-100 cm. Soil samples collected from three different points throughout areas of Tutli district did not show any significant differences. Soil moisture and Field capacity did not show any variation of soil collected from two different sites, however, soil infiltration rate differed significantly. Bulk density varied from 1.37-1.58 g/cm3 at both the sites and at different depths Soil salinity and sodicity remained low with high concentration of Ca^{2+} and low of K^{+}

Organic matter varied between 0.50-0.84% with low nitrogen content in soil as compared to phosphorus and potassium. According to the particle-size distribution of the USDA classification system, the soil is silt loam in texture throughout the profile up to the depth of 0.90 m. Field capacity in the upper 0.15 m depth was 24.18%; for the 0.15-0.30 m depth, its value was 23.45%. At the 0.30-0.60 m and 0.60-0.90 m depths, the values of field capacity were estimated at 23.34% and 20.96%, respectively. Infiltration rate was relatively low (18.40 mm h^{-1}), this being a consequence of the high levels of Mg^{2+} on the cation exchange complex, which effectively results in these soils and exhibits similar properties to Na^{+} dominated soils, i.e. sodic soils that are easily dispersed when wet. Soil bulk density increased with depth and ranged from 1.52 to 1.67 g cm^{-3}.

The pre-experiment soil salinity levels in terms of total soluble salts (TDS) at different soil depths extending up to 0.9 m were in the range of 1010 mg/l to 8760 mg/l with the highest values being observed in the surface of 0-0.15 m, possibly reflecting salt accumulation at the crop root zone due to capillary rise. Among the anions, HCO_3^{-} was dominant having maximum concentration of mmol$_c$ L^{-1} at the upper 0.15 m depth. The concentration of HCO_3^{-} had an increasing trend from top to deeper layers,while the concentration of SO_4^{2-} was highest than that of HCO_3^{-} and had a slightly increasing trend from top to deeper horizons. The concentration of Cl^{-} was much less than that of SO_4^{2-} and ranged from 2.40 to 6.40 mmol$_c$ L^{-1} at different soils depths. Its concentration had small variations at different soil depths. The determinations of CO_3^{2-} did not find the anion in detectable concentrations in the soil. Among the cations, Mg^{2+} was dominant at the soil surface followed by Na^{+} and Ca^{2+} . The concentration of Mg^{2+} in the upper 0.15 m depth was determined to be 4.00 to 5.00 $mmol_c$ L^{-1}. It also followed a pattern similar to the dominant anion (HCO_3^{2-}) as its concentration had a decreasing trend from top to deeper horizons. The concentration of Ca^{2+} was almost equal or less to the Mg^{2+} concentration at the different soil depths and ranged from 2.0 to 4.0 $mmol_c$ L^{-1}. The soil has an alkaline reactivity with soil pH in water ranging from 8.03 to 8.25. The SAR levels had a slight increasing trend from top to deeper horizons.

Soil characteristics

Soil has silt loam texture in all the sub-plots where different plant species were grown. Field capacity of the soil varied from 18-23% at 0-90 cm soil profile depth. Soil N, P and K content showed low amount of N as compared to P and K in top and sub-surface profile depth (Fig. 13)

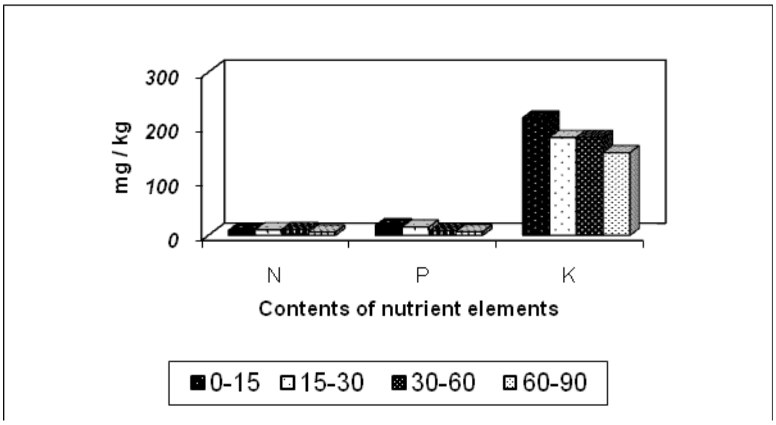


Figure 13. Contents of nutrient elements in the soil of Karnabchuli steppe

Top soil layer (0-30cm) was characterized by poor soil-nutrient stocks (humus varied 0,4-0,68% and 0,45-0,56 at the 60-90 cm depth) and severe secondary soil salinization. Over the two growing seasons, the ground water table (GWT) averaged 2.5 m and 0.5 m below the soil surface, respectively. The mean electrical conductivity of the groundwater was 3300 and 7900 mg/l. Chemical analyses of soil done at transplantation of plants showed moderate salinity and sodicity levels. Sulfate remained the dominant ion in all sub-plots followed by Cl^{-}. Studied sites at the Mirzachuli and Karnabchuli steppes could be characterized as sodium-calcium (as for content of cations) and sulfate–chloride (based on anions distribution throughout the soil profiles). The amount of salts at the end of growing season (September 2005-2006) had increased trend throughout the soil profile up to 60-90 cm. The maximum soil salinity increasing up to 32.30 % under tree plantation might be associated with higher ground water salinity. Another reason of the highest soil salinity under cotton might be explained by shallow ground water table (2.27 m) at the end of September 2006 which has impacted to increasing of the soil salinity at the 30-90 cm soil depth.

Thus, the mobilization and introduction of phytogenetic resources both native and very-carefully-trialed, domesticated, salt-tolerant plants in combination with studies of their ecological, morphological and structural-functional properties, seed and biomass production; cultivation with testing of alternative low-cost advantage technologies will optimize not only the selection of halophytic wild arid plants and reveal the novel models for prediction of desert rangelands productivity, but will also provide a sustainable development of saline/sandy deserts ecosystems. In some cases remediation requires application of sodium-displacing amendments followed by vegetative opening of the soil via the rhizocanicular effect permitting the leaching of excessive soluble salts. The use of metallohalophytes from the Uzbek floras to reclaim soils could represent both a practical and economically viable strategy (Toderich et al., 2003, 2006b, 2007). Accumulation, extraction and practical use of biologically active substances of metallohalophytes are crucial needed. Today there is much hope that plants can be transformed to remove specific pollutants for land cleaning and a host of other soil-plant improvements. Even though the scientific technology for molecular transforming plants is very well established, unfortunately plants that are well adapted to desert environments have not yet been investigated.

2.2. Ecological and botanical characteristics of Asiatic genus Salsola

2.2.1. Botanical and economic significance of Central Asian Salsola representatives

The ecological and botanical characteristics of the Central Asian representatives of genus *Salsola*, growing mostly under conditions of Kyzylkum desert is given in the Table 2.

Table 2. Characteristics of Asiatic genus *Salsola* of different growing origins

N	***Nomenclature of species***	Life form	Type of mesophyll	
	I Mountaineous species from West and Central Tyan-Shan, Pamir-Alay		Cotyledons	Leaf
1.	*Salsola dzungarica* Iljin	semishrub	Kranz-dorsiventral with hypodermis	Kranz-centrical with with hypodermis
2	*S. roshevitzii* Iljin	semishrublets	*no studied yet*	Kranz-centrical with with hypodermis
3.	*S. titovii* Botsch. Endemic for CA	Semishrub	no studied yet	no studied yet
4	*S. Drobovii* Botsch. Endemic for CA	Semishrub	no studied yet	no studied yet

5.	*S. montana* Litv. Endemic for CA	Semishrub	Isolateral-palisadic -	Centrical
6.	*S. pachyphylla* Botsch	Semishrub		Centrical
	II. Species of Pamir-Alay			
7.	*S. baranovii* Iljin	Semishrub	no data	no data
8.	*S. pulvinata* Botsch.	Semishrub	No data	No data
9.	*S. forcipitata* Botsch. Endemic for CA	Annual	No data	No data
.	**III. Species with wide Arial of distribution (Caspian, Aral-Tyan-Shan-Pamir-Alay)**			
10.	*S. dendroides* Pall.	semishrublet	Kranz-dorsiventral with hypodermis	Kranz-centrical with hypodermis
11.	*S. micranthera* Pall. Endemic for CA	annual	dorsiventral	Kranz-centrical with hypodermis
12.	*S. nitraria*	annual	No data	No data
13.	*S. orientalis* S.G.Gmell	semishrub	Kranz-dorsiventral	Kranz-centrical with hypodermis
14.	*S. gemmascens* Pall	semishrublet	dorsiventral	Kranz-centrical
15.	*S. leptoclada* Land.	annual	No data	No data
16.	*S. sclerantha* C.A. Mey	annual	dorsiventral	Kranz-centrical with hypodermis
17.	*S. turkestanica* Litv.	annual	No data	Kranz-centrical with hypodermis
18.	*S. arbuscula* Pall	shrub	Kranz-centrical with hypodermis	Kranz-centrical with hypodermis
19.	*S. arbusculiformis* Drob.	Shrub	isolateral-pallisadic	Centrical
20.	*S. collina* Pall	annual	No data	No data

21	*S. iberica* Sennet. Et Rau.	annual	Isolateral-pallisadic	Kranz-centrical
22.	*S. paulsenii* Litv.	annual	Kranz-centrical	Kranz-centrical
23	*S. praecox* Litv.	annual	Kranz-centrical	Kranz-centrical
24.	*S. rosaceae* L.	annual	No data	No data
25.	*S. tamaricina* Pall.	annual	No data	No data
.	**Deserts species (northern and southern deserts)**			
26.	*S. incanecens* C.A. Mey	annual	No data	No data
27.	*S. laricina* Pall	semishrub	No data	No data
28.	*S. implicata* Botcsh. Endemic for CA	annual	dorsiventral	Kranz-centrical
29.	*S. ausheri* (Mog.) Bge.	shrub	No data	Kranz-centrical with hypodermis
30.	*S. gossypina* Bge.	semishrub	No data	No data
31.	*S. tomentosa* (Mog.) Spach.	semishrub	No data	No data
32.	*S. wedenskyi* Iljin Endemic for CA	annual	No data	Kranz-centrical
33.	*S. chiwensis* M.Pop. Endemic for Uzbekistan	semishrub	No data	Kranz-centrical with hypodermis
34.	*S. europhylla* Botcsh.	semishrub	No data	Plastichatyy-Kranz-centrical with hypodermis
35.	*S. paletzkiana* Litv.	shrub	Kranz-centrical with hypodermis	Kranz-centrical with hypodermis
36.	*S. transhyranica* Iljin	shrub	No data	No data
37.	*S. foliosa* (L.) Schrad	annual	Kranz-centrical with hypodermis	Kranz-centrical
38.	*S. richteri* Kar. Et Litv.	shrub	Kranz-centrical with hypodermis	Kranz-centrical with

				hypodermis
39.	*S. androssovii* Litv.	annual	No data	No data
40.	*S. angusta* Botsch.	annual	No data	No data
41.	*S.aperta* Pauls.	annual	Isolateral-pallisadic	Kranz-centrica with hypoderm
42.	*S. laricifolia* Turcz.	semishrub	No data	No data
43.	*S. deserticola* Ilijin Endemic for CA			
44.	*S. sogdiana* Bge	annual	No data	No data
45.	*S. tragus* L.	annual	No data	No data
46.	*S. mutica* C.A. Mey	annual	No data	No data
47.	*S. soda* L.	annual	No data	No data

2.2.2. Plant material (examined in the present study)

Perennial, drought/salt-tolerant woody-shrubs/shrublets (*S. arbuscula, S. richteri, S. subaphylla, S.orientalis, S. laricina, S. dendroides, S. arbusculiformis)* and tree-like (*S. paletzkiana*) are morphologically closely related species within the sections *Caroxylon* and *Coccosalsola,* subsection *Arbuscula*, in the flora of Uzbekistan. They are considered to be characteristic species of psammohalophytic plant communities in the sandy/arid environments. These species find a wide application for fixation of shifting sands and/or improvement of degraded rangelands, as well as being an excellent component for the creation of pastoral-protected belts. Stems, fruits, leaves are considered a good palatable, year-round feed for camels; sheep and goats prefer it in summer, and to a lesser degree in the autumn-winter vegetation period. Fruits of the plants are of great importance as fattening feed for karakul sheep, camels, and goats, and may be used as partial substitute for concentrates, especially in autumn and winter. In addition to their biomass production, *S. richteri* and *S. paletzkiana* can be used for medicinal, industrial and commercial purposes. These perennial species are usually woody at the base with a lifespan of 7-12 years. Plant surfaces are glabrous or with a minutely hirtellous indumentum. They have a pivotal (5-10 m deep) and superficial (8-12 m radial) root system.

Annual *Salsola* species, known in practice of pasture economy of Uzbekistan as “solyanki” are drought /salt-tolerant, short and/or long-lived succulent plants and form a dominant group in the flora and vegetation of saline /arid environments and are very promising ecologically for rehabilitation of degraded and saline/affected lands of Kyzylkum. Some of the species are locally common on ruderal sites or as weeds. The early seed germination gives them an advantage in winter/spring rangeland cropping system. Many among them are considered useful for rehabilitation of degraded and salt/affected lands. Most of them have good forage value for livestock and can be used for biomass production on arid sandy/saline lands of Kyzylkum Desert. Fruits of these plants are of great importance as fattening feed for karakul sheep, camels, and goats and may be used as partial substitute for concentrates, especially in autumn and winter. In addition to their high reproduction potential and biomass production, many species of Asiatic *Salsola* spp. can be used as a material for medicinal, industrial and commercial purposes.

A brief botanical decription of Asiatic *Salsola* species taken for present investigation.

***Salsola lanata* Pall.** - Habitat: Solonchaks and solonetz soils, clay and gypsiferous deserts, on takir-like, sandy salted soils, on margins of salt-marshes (solonchak-alkaline soils). Occurs on the territory of Central Asia: Aral-Caspian regions, Amudarya and Syrdarya valleys, Kyzylkum, Karakum; very rare in Tyan-Shan, Pamiro-Alai. It is also frequently found in Afganistan, Iran, China and Mongolia, and very rarely in Europe. Life form: annual, 10-60 cm high, erect, branching from base, covered with long spreading subsequently felling hairs; leaves alternate, except the lowermost, fleshy, semiterete; brads somewhat shorter than to equaling the bracteoles; flowers solitary in spiciform inflorescence; perianth segments lanceolate, acuminate, hairy, winged in fruit below the middle; wings relatively large 10-17 mm in diameter reniform, red overlapping; anthers with bladdery roseate short-stipulate appendage; stigmas thick, style many times as long as stigmas. Flowering: July-September.

S. subaphyla* (recently *Halothamnus subaphyla): Habitat sands, agrillaceous and gravelly solonetz slopes and solonchaks. Found in Central Asia, Mongolia and China. This species is a shrub 30-120 cm high, stem covered with light gray longitudinally fissured bark, profusely branched, glabrous; leaves alternate, linear terete, sessile, acute; bracts short, the upper broadly ovate or orbicular; flowers solitary in spiciform inflorescence disposed in a panicle; perianth glabrous, oblong-ovate, obtuse, wings overlapping, coloress or roseate; fruiting perianth including wings -10-20 cm; tepal lobes connive and forming a gently sloping cone; filaments liniar, slightly dilated toward base; anthers unappendage, fused in a circle, divergent up to the middle; stygmas flat, broad, enlarged at the end. Flowers: May-July.

S. arbuscula* Pall:* Habitat - forms desert plant communities on sands and solonetz soils, shallow hummock sands, gravelly and chalky slopes and more rarely on rocks. Occupies considerable areas - EuropeCentral Asia: Aral-Caspian, Balkhash, Kyzylkum, Karakum, Iran, Mongolia, China. Life form: shrublet 20-100 cm high, divaricately much branched, with light gray bark; young branches milky-white and smooth like the leaves; leaves alternate, narrowly liniar, constricted just above the base, bracts surpassing the bracteoles; flowers solitary; perianth segments membranous, obtuse, winged in fruit below the middle; wings semiorbicular or narrower, scarious , slightly yellowish with a faint rosy flush, often slightly hairy; the tepal lobes gradually dilated toward apex, near the wings closely adherent to the fruit, in upper side expanded and sometimes reflexed; anthers with an oblong-ovate or lanceolate appendage; stigma subulate, enlarged below and flat. Flowering: July-September.

***S. arbusculiformis* Drob. in Tray.** Habitat: gravelly debris cones, gravelly and stony slopes of coniform hills and mountains. Grows in Central Asia. Described from foothills of the Ala y montaneous Range. Life form: Shrublet 20-50 cm high, much branched with light gray bark; shoots white, glabrous and smooth; leaves alternate, narrowly linear, 10-35 mm long, terete dull and commonly glaucous bracts shorter than leaves, surpassing the broad, often suborbicular; flowers solitary in a spiciform inflorescence, perianth segments glabrous, pale yellowish, obtuse scarious margined, wing in fruit at the middle. Tepals in the mature fruit are connivent in a steep cone, in lower part adherent, lo fruit as in *S. arbuscula*; anthers separated to the middle or the deeper, terminatig in a sessile oblong to subovate appendage; stigmas broad, flat, gradually attenuate toward apex. Flowering: August-September.

***S. orientalis* S.G. Gmell**.- Habitat: The plants can either be grown alone for grazing pastoral system) or in association with other tree-like and semisrub species (silvi-pastoral system). Species grows on foothill semi desert area on gray-brown takyrs, takyr-like, clay higher gypseferous soils, as well as on low-hillock sands. Areal: Middle Asia, Caspian region, Caucasus, Iran, Afganistan, China. Form: Xerohalophyte. Perennial, polymorphic, widely branches, friable semishrub (15-70 cm). Life longevity is 7-25 years. Root system of a universal type penetrates on depth 1.5-7 m. Stem: gray-green colour, rigid, crooked. Leaves: alternate, linear, juicy, blunt at the basis extended with covering hair layer. Perianth: egg-shaped, hulled-bordering with lanceolate leaflet. Inflorescence: wide panicle. Flowers: single, bisexual, calyx-shaped, dark-yellow, proterogeneous. Anther lengthening -oblong form with a small orbicular appendage, open introrse by longitudinal cracks. Pollen grains three-cellular multiporous. Stigmas is two-lobed, pubescent up to two times shorter than style. Ovary: superior with one anacampilatropous, crassinucellate bitegmic ovule. Typical anemophilous plant, but geitonogamy is admitted too. Flowering: May-August. Fruit maturation: end of October-November.

***S. richteri* Karel in Shed.** Habitat: steppe plant communities in sands and sandhills on the desert areas of Central Asia and Iran. Life form: tree or tall shrub with light gray bark, ultimate branches milky-white, smooth, glabrous, leaves alternate, terete, subfiliform, bracts - semiorbicular, flowers solitary; perianth segments broadly lanceolate, acute or micronulate from an obtuse apix, narrowly scarious marginated, stiffish, wings in fruit below at the middle; tepal lobes above the wings vauted and connivent into a rather loose beak; anther divergent to beyond the middle, terminating into sessile oblong or oblong-ovate appendage; stigmas flat, acuminate. Flowering: June-

September.

***S. paletzkiania* Litv.** - Habitat: Psammophyte. Occurs on the sandy desert of Central Asia. Endemic. Life form: tree to 3-4 m high, many stemmed, profusely branched, ultimate branches very slender and long, milky white, glabrous, smooth; leaves alternate, semiterete, thin, linear, 30-70cm long; bracts leaf-like, perianth segments lanceolate, acuminate, dark narrowly scarious margined in fruit clustered in center and winged below the middle; wings large, light colored, subpellucid; anther strongly divergent beyond the middle, borne on flat linear fillaments, terminating in a narrowly lanceolate pale appendage to 1 mm long; stigmas fat and glabrous. Flowering June-August.

***S.dendroides* Pall.** Habitat: Solonchaks, especially puffy, gypseferous clays, argillaceous saline sierozems , in river valleys, and as a weed of irrigated crops.Grows in the Europe, Caucasus, Ural, and Central Asia. Life form: shrub, 75-150 cm with a stout stem, 5-10 cm in height, branches long, densely covered with crisp hairs; leaves alternate, small, linear, fleshy, obtuse, very slightly dilated at the base; bracts ovate-triangular, keeled: flowers numerous, solitary forming a dense widely paniculate inflorescence; perianth segments ovate, obtuse, membranous, wings semiorbicular or obtuse, tepal lobes of fruiting perianth connivent; anther appendiculate, stigmas flat. Flowers July-September.

Two species from drylands of Western Europe were used for comparative study.

Salsola ruthenica- habitat: Sands sandy steppes, shore bluffs, cultivated fields, vineyards, gardens and ruderal sites; grow in groups or scattered, also solitary. Occurs in Europe, Caucasus, Central Asia, Mongolia, China.Life form: annual, 5-100 cm high branching from the base, rather rigid, glabrous or roughned with very short papilliform bristle; leaves alternate, filiform terete, spinescent, mostly slender. Flowers are solitary in a spiciform inflorescence. Anthers with locules fused in upper part, unappendaged; seeds horizontal; fruit flat (cupola-shaped). Flowing: July-September.

Salsola kali - Habitat: Sandy seashore-Europe; coasts of Western Europe Life form: annual, 5-40cm high with long prostrate or ascending branches from base, densely covered with short scarious bristles; leaves alternate, spinascent, somewhat thick, flat; bracteoles spinascent, longer than flower, deflexed in fruit. Flower solitary, segments of fruiting perianth mostly wingless or with wings reduced to pectinate or roseate winglike appendages. Stigma is longer than style. Seed horizontal. Flowering July-August. Material for last species has been kindly collected and determined by prof Karol Lotowski, Department of Plant Taxonomy, A.M. University, Poznan, Poland.

2.3. Methods of investigation

The quantitative assessment of environmental impact by salinization and industrial mining pollution in the Kyzylkum desert was conducted using geoecological aerial photographs at the scale 1:500 000 (Goltstein, 1997).

The study area encloses a heterogeneous landscape comprised of sand dunes, gypsum flats, clay and many solontchak depressions. The species studied undergo extreme, continental, arid conditions that have a limited and unreliable precipitation and a minimal annual precipitation (MAP) = 100-180 mm. The region is dominated by sandy soils with poor vegetation cover. Most of the selected sites are located inside or close to gold-uranium and gas industry complexes. At each site three cylindrical soil cores (depth 5-10 cm) were taken from within squares measuring 100 by 100m. Plant samples were taken from sites that were within an area of 20 by 20 km. Each plant sample was cut into small pieces, dried at 105 ^{0}C, ached at 500^{0} C for at least 24 hours, mixed thoroughly, and transferred into plastic containers. After that, the various spectrometric measurements for metal content in the plant-dried materials were done using ICP-MS (Perpcin Elmer-Sciex. ELAN 6000).

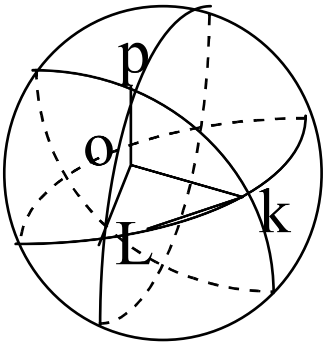
Samples of plant examined in this paper cover the full range of plant life forms. Many are herbs or small woody-based shrubs, although some are large shrubs 1-3m in height and a few tree-like species.

Cytoembryological and palinological methodology

Generative organs of 22 both annual and perennial shrubby *Salsola* species, at different developmental stages were studied using light and electron microscopy analyses. Embryological sections of reproductive organs were prepared according Z.P. Pausheva, 1970 and selectively stained by safranin in combination with fast green, haematoxylin or toluidine blue. Anthers were collected at the anthesis.

Diversity statistics and canonical discriminant analysis of pallonological traits were used to determine the relationship between different sections of genus *Salsola*. As far as the pollen grain of Chenopodiaceae family has more or less spherical shape it was difficult to count the number of pores on exine surface. There are many contradictory opinions concerning the measurement of this palynological parameter. Therefore we decided to apply the spherical geometry theory to calculate the biometric value of the number of pores on the surface of a pollen grain, if we take the pollen grain as a sphere and centers of pores as points on it.

The shortest distance between adjacent points on the surface of a sphere is measured along the great-circle arcs, along the edge of a plane that passes through the center of the sphere. Since pores are distributed approximately equally on pollen grain surface, tops of equilateral spherical triangles can represent their centers. These tops (for example, p. O, p. K, p. L)are points of crossing of three beams that pass through the center of the sphere and through the surface (fig.



14).

Figure 14. geometrical scheme of the pollen grain as mathematical unit

There are 4 possible versions of pore positioning: around each pore could be allocated 5, 6 or several numbers of pores.

If we take into consideration the second case and, defining the equilateral spherical triangle as LKP, it becomes easy to define the following:

- *a,b,c (KOL, OKP, OLP)- the sides of LKP* Each of them is less than 180^0
- *A,B,D (LPK, PKL, KLP)- the internal angles of LKP*
- *r(C)- the length of the chord joining two adjacent point*
- *R(D/2) the radius of the sphere*
- E- *the spherical excess of spherical LPK* E=*(A+B+C-π)*

Therefore, by extending arches to each pore we form 6 equilateral spherical triangles, so that each pore on the surface of pollen grain is surrounded by 6 more or less equal parts (fig.15) .

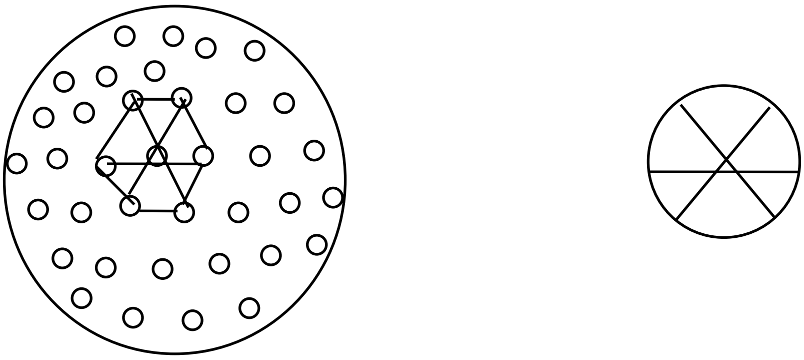


Figure 15. Spatial distribution of pores on the surface of sphere

Thus, its corresponding 3 1/6 parts from each pore to each triangle, which forming this triangle, i.e. each triangle contains 1/2 of pore. Therefore for account of amount of pore it is enough to find the relation between the surface of pollen grain (S_S) and 2 surfaces of spherical triangle (S_R).

Diameter D is covered with N equally distant points corresponding to the centers of the pore areas such that the great-circle arches joining each point to its nearest neighbors partition the surface into 2N equilateral triangles of equal area -S_R).

The great- circle arch on the sphere surface corresponds to each side of a spherical triangle. The spherical triangle angles A (LPK), B (PKL) and C (KLP), which are allocated accordingly in front of the side a, b, c, represents angles between the great- circles arches appropriating to the side of triangle, or angles between planes determined by the given beams. By definition, these angles are also less than 180^0.

The geometry of sphere surface is not Euclidean, therefore in each spherical triangle the sum of the sides varies from 0 up to 360^0, when sum of angles ranges between 180^0 - 540^0.

If R- radius of the sphere (half of average diameter D/2), the area of a spherical triangle S_R is expressed by the formula:

$$S_R=R^2 (A+B+C - \pi), \quad (1)$$

$\varepsilon= A+B+C- \pi$ is a spherical excess

as A=B=C we have:

$$S_R=R^2 (3A - \pi) \qquad (1').$$

Applying the sine and cosine theorems for spherical triangles, we obtain:

$$\frac{\sin a}{\sin A} = \frac{\sin b}{\sin B} = \frac{\sin c}{\sin C} \qquad (2),$$

$$\cos a = \cos b \cos c - \sin b \sin c \cos A \qquad (3).$$

As we have the equilateral spherical triangle, i.e. à=b=c and A= B= C, the formula (3) transforms into the following equation:

$$\cos a = \cos^2 a + \sin^2 a \cos A \qquad (4).$$

Hence,

$$\cos A = \frac{\cos a - \cos^2 a}{\sin^2 a} \qquad (5).$$

For definition of the angle let’s consider triangle OKL according to the theorem of cos for the flat triangle:

$$r^2 = 2R^2 - 2R^2 \cos a$$

Hence, (6),

$$\cos a = \frac{2R^2 - r^2}{2R^2}$$

r = KL - interpore distance calculated on striate line can be measured easy (it is possible to use average distance).

From trigonometrical identity:

$$\sin^2 a + \cos^2 a = 1$$

We have:

$$\sin a = \sqrt{1 - \left(\frac{2R^2 - r^2}{2R^2} \right)^2} \quad \textit{(7).}$$

From (5), (6), (7) we find:

$$A = \arccos \frac{2 - \kappa^2}{4 - \kappa^2} \quad \textit{(8),}$$

where

$$\kappa = \frac{r}{R} = \frac{2C}{D}.$$

Therefore, the area of a spherical triangle is equal:

$$S_R = (3\arccos \frac{2 - k^2}{4 - k^2} - \pi) R^2 \quad \textit{(9).}$$

Finally we find:

$$N = \frac{S_S}{2S_R} = \frac{2\pi}{\left(3\arccos \frac{2 - k^2}{4 - k^2} - \pi \right)} \quad \textit{(10).}$$

The formula (10) defines number of pores on the surface of the pollen grain.

(10) $\sin^2 a + \cos^2 a = 1$

If radius of the pollen grain is larger than interpore distance , it is possible to use the simplified formula:

$$N = \frac{2\pi R^2}{\sqrt{3}r^2} \quad (11).$$

In case when there are 5 pores distributed around of each pore, the formula for the number of pores on the surface of pollen grain is similar, with a difference only in the multiplicator, since in this case 5/3 of triangles contain one pore:

$$N = \frac{3S_S}{5S_R} = \frac{12\pi}{5\left(3\arccos\frac{2-k^2}{4-k^2} - \pi\right)} \qquad (12).$$

However, when pores are located unequally: around of analyzed pore are dislocated 5, 6 or 7 pores on the surface of pollen grain, the above described formula can also be used.
The calculation of pore numbers on the pollen grain exine surface gets difficult, when pollen grain has an ellipsoid shape. In such a case it is needed to take an average diameter in combination with interpore distance (mean value) and calculate spherical triangle area.

Two methods of sample preparation were used for SEM, i.e. chemical fixation and freeze-drying. For chemical fixation, material was fixed, post-fixed and dehydrated as described for TEM, critical point dried, putter-coated with gold and observed with the JEOL JSM-T330 scanning electron microscope (Bozolla and Russell, 1998). All slides were deposited at the Laboratory of Electron Microscopy of A.M. University in Poznan (Poland), as well as at the laboratory of Tree Cell Biology, Kyoto University (Japan). Plant samples (leaves, flowers and fruits) for isotope studies were collected from natural Kyzylkum Desert Environments Different floral organs of all examined species were immersed in 3% glutaraldehyde in sodium cacodylate phosphate buffer (PH 7.2) for 3 hours prior to mounting on stubs. The material was then placed in an Edward freeze-dryer for 24h-55 ^{0} C. Specimens were coated with carbon. The salt secretions on freeze-dried leaf-like organs (bract/bracteoles and perianth segments) were analyzed by energy disperse X-ray microanalysis (EDX) with a JEOL JSM –T330A SEM. The elemental composition of crystalline deposits associated with salt glands with various ecological types of arid plants was determined. Experiments were conducted at the laboratory of plant cells structure at the Kyoto University and Laboratory of Electron Microscopy at the Georgia University of United State of America.

Morphology of fruits and seeds was investigated according to the N.N. Kaden et al., 1971 and N.M. Dudik, 1971. Anatomical sections of bracts, perianth segments, anthers, embryo and fruits were selective stained with safranin in combination with fast green, haematoxylin or toluidine blue. Samples for anatomical studies of fruit covers were fixed in alcohol: glycerin: water (1:1:1). Sections were stained with methylene blue.

The description of plant material characteristics used for palynological investigation is given in Table 3.

Table 3. Characteristics of *Salsola* species used for palynological studies

n/r	Nomenclature of species	Life form Genome	Habitats and distribution	Note of collection
1.	**I. Section Coccosalsola (Ulbrich) Botcs., subsection Arbuscula** *Salsola arbuscula* Pall. Synonim: *S. arbuscula* Pall.; *S. arborescens* L.	Shrub,Perennial N = 9 (Grant 1982a, Turner 1994)	Fixed saline sands; stony gravely or gypsum containing sites	Coll. by K. Toderich in 1997 in Cen/Kyzylkum, Buchara oasis, Aral region (near Myinak),
2.	*S. arbusculiformis* Drob.	Shrub.Perennial	On slopes, rocks, skeletal calcareous or gypsum gravely soils	Coll. by K. Toderich and T. Matyuninna in 1999 in Kul'djuktau, S/W Kyzylkum
3.	*S. Richteri* Kar. et Litv. *Salsola richteri (*Moq.) Kar. ex Litv. *(S. arborescens* L.γ *richteri* Moq.)	Shrub., tree-like 2n = 18, 36, 72 (Japakova, unpubl. Data)	Grey-brown weakly salted sands; on semifixed sandy dunes	Coll. by U. Japakova in 2000 and 1998 by K. Toderich in Nurata foothills, Karakul forest station; Southern Kyzylkum and near Nukus(Karakalpakstan)
4.	*S. paletzkiana* Litv. Synonims: *S. paletzkiana* Litv.	Small tree 2n = 18 (Japakova, unpubl. results)	On semifixed sandy dunes.	Coll. by U. Japakova and in 2000 and Toderich in 1999, Karakul Forest stati Kyzylkum Reserve;
5.	*S. montana* Litv.	Shrublet	Endem for CA.	Coll. by Tsukervanik, in 1974, Tyan-Shan

6.	*S. pachyphylla* Botsch.	Shrub/shrublet		Coll. in 1974 by Tsukervanik, Tyan-Shan mountains
	***II . Section* Malpigipila**			
7.	*S. gemmascens* Pall. Synonoms: *Salsola gemmascens* Pall. Subsp. *oreina* Botsch. *Subsp. subglabra* Botsch. *subs. nodulosa* (Moq.) Botsch. = *S. nodulosa* (Moq.) Iljin	Semishrublet, Perennial	Edificator on takyrs and clay loamy gypseferous soils; occurs also on compacted saline sands; conglomerates and more rarely rocks. Distr. Central Asia, Iran, Mongolia	Coll. by K. Toderich in Central Kyzylkum, Buchara oasis
	III. Cardiandra			
8.	*S. sclerantha* C.A. Mey Synonims: *S. sclerantha* C.A. Mey.	Herb,annual	Compacted grey-brown weakly saline sands or on loam-sands; sandy – argillaceous saline expanses, and rarely stony places. Distribution: Central Asia, Usturt plateau, Iran	Coll. by K.Toderich in 1999 in Kul'djuktau, Buchara oasis and Central Kyzylkum
9.	*S. leptoclada* Land	Herb, annual		Central Kyzylkum
10	*S.carinata* C.A. Mey Synonims: *S. sclerantha var carinata* Minkw. *S.*	Herb. annual	Solonchaks depressions among sands, margins of	Coll. by K. Toderich in 1999 in Central Kyzylkum

	leptoclada Gandog.		takyrs, saline meadows, loess slopes and more rarely old fields. Distr. Central Asia and Iran	
	IY Belanthera Iljin			
11	*S. aucheri* (Mog.) Bge Synonims: *Noaea cana* Litw. ; *Noaea aucheri* Moq	Shrub, perennial	Gravelly slopes. Distr. : Central Asia and Iran	Coll. by U. Pratov in 1979, Kungrad, Karakalpakstan
12	*S. gossypina* Bge. in Boiss. Synonims: *S. crassa var tomentosa*	Semishrub, annual	Saline, gypsiferous clays and chalk outcrops. Distr. : Central Asia and Iran	Coll. by U.Pratov in 1974, Kopetdag
	Y. Caroxylon (Thunb.) Iljin			
13	*S. dendroides* Pall. *S.verrucosa* M.B.; *S. ericoides* C. A. Mey*;* *S. foetida* Pauls*; S. georgica* Bge*.; S. ericaefolia* Adams.; *Halogeton georgicus* Moq.	Semishrublet, perennial	Solonchaks, especially puffy, gypseferous clays, argillaceous saline sierosems, in rivers valleys, as weed of irrigated crops. Grows in groups. Distribution: Caspian Sea, European part, southern Russia, Central Asia,	Collected in 2000 by U. Japakova, Karakalpakstan.

			Caucasus, Iran	
14	*S. micranthera* Pall.	Herb, annual	Endem for CA	Coll. by Nabiev in 1974, Sands of Central Fergana.
15	*S. orientalis* S.G.Gmell. Synonims: *Salsola rigida* Pall. = *S. orientalis* S. G.Gmel.	Shrub., perennial 2n = 18, 36, 72 (Zahar'eva 1968, Fedorov 1969)	Grey-rown, takyr-like soils and sands with high gypsum content	Several fixation by K.Toderich, Nurata-Papanay Station, Buchara oasis, Karnab Experimental Station
16	*S. laricina* Pall. Synonims: *S. vermiculata* Bge.	Semishrub, perennia	Grey-rown, takyr-like soils and sands with high gypsum content	Nurata –Papanay Experimental station, P'yankov collection
17	*S. incanecens* C.A. Mey Synonims: *S. spissa* Boiss.	Herb, annual	Argillaceous and sandy – argillaceous saline wasteland habitats	Coll. in Gulistan, Syrdarya Valley in 2000 by A.A. Butnik and H. Freitag. Distribution: Caucasus, Central Asia , Iran
	YI. Section *Kali (Salsola)*			
18	*S. iberica* Senet et Rau.	Herb, annual		Kul'juktau, Central Kyzylkum
19	*S. praecox* Litv. Synonims: *Salsola praecox* Litv., *S.kali var. praecox* Litv., *S. elegantissima* Iljin *praecox; S. nodiflora*	Herb, annual 2n = 18 (Toderich, unpubl.data)	Grey-brown weakly saline sands; sandy dunes (barchanes)	Coll. by Toderich several years in Buchara oasis, Aral region, Central Kyzylkum
20	*S.ruthenica* Iljin.	Herb, annual	Sands, sandy steppes, shore	Collected by Prof. Karol Lotowski,

	Synonims: S. *kali, var. angustifolia* Fenzl. *; S. pseudotragus;* *S. pestifera* A. Nilson*; S. collina* Pal*l; S. paulsenii* Litw.*; S. aperta* Iljin		bluffs, cultivated fields, vineyards, gardens and ruderal sites; in groups or scattered. Distribution: Central Europe, Central Asia, Caucasus, Mongolia, North China, America recently naturalized	several years Wielkopolski lowlands, Poland
21	*S. kali* L. *S. kali var. baltica* Zapalow.	Herb, annual	Sandy seashores. Distribution: costs of W. Europe	Collected by Prof Lotowski , several years Wielkopolski lowlands, Poland
22	*S. aperta* Iljin. Synonims: *S. sogdiana* Litv.	Herb, annual	Solonchak sands, Haloxylon associations, loamy saline soils. Endem for Central Asian deserts.	Collected in Southwestern Kyzylkum, June, 1972 by Uktam Pratov
23	*S. paulsenii* Litv. Synonims: *Salsola paulsenii* Litv., *S. pellucida* Litv.	Herb, annual	Solonetz sands, sandy-clay areas, more rarely blown sands and sandhills. European part, Caucasus, Central Asia	Sands, Central Fergana deserts, July , 1974 by Nabiev and in Central Kyzylkum in 1999 by Toderich K.N.
24	*S. pestifer* A. Nelson	Herb, annual	Sands, sandy steppes, shore	Coll. by K. Toderich in 1999 in

			bluffs, cultivated fields, vineyards, gardens and ruderal sites; in groups or scattered	Samarkand region and Buchara oasis
	YII Physurus Iljin.			
25	*S. lanata* Pall Synonims: *Climacoptera lanata* (Botsch.); *Salsola lanata* Pall.	Herb, annual 2n = 18, 36 (Turner 1994)	Saline compacted sands, saline alkaline and sodic soils; on margins of salt-marshes, coast of salty lakes. Distribution: Central Asia, China, Mongolia, very rarely European part.	Coll. by K. Toderich , several years in Buchara oasis, Aral region; and by A. Butnik in 2000 in Syrdarya Valley
26	*S. crassa ,* Synonims: *S. frutescens* Pall.; *S. rosacea* M.B. Beschr. *Climacoptera crassa* (by Botschantzev,1969)	herb, annual	Solonchaks and crustose or lumpy solonetzes; sometimes in large groups. Distribution: Caucasus and Central Asia	Coll. by K.Toderich in Aral region in 1997.
27	*S. ferganica* *Climacoptera ferganica* (Pratov.)	herb, annual		
28	*S. subaphylla* S. A. Mey Synonims: *Aellenia subaphylla* (C. A. Mey.) Aell.	Shrub, perennial 2n = 18, 36 (Turner	Gypseferous tertiary clays, takyrs, and gravelly gypseferous slopes; usually	Coll. by K. Toderich , several years in Nurata-Papanay Station, Buchara

	(Salsola subaphylla C. A. Mey., *Aellenia subaphylla subsp. Eusubaphylla* Aell. nom. illegit., *Salsola subaphylla var. typica* Drop. Nom. Illegt., *S. subaphylla subsp. Typica* (Drob.) Iljin, nom. illegt.)- subsp. *eusubaphylla* Aell. = *A. subaphylla- subsp. turcomanica* Aell. = *A. turcomanica* *S. subaphylla* C.A. Mey. (Flora USSR); *Caroxylon subaphyllum* Moq.	1994)	growing in groups. Dist.: Caucasus and Central Asia.	oasis, Kul'juktau.

Isoenzymatic analysis and biochemistry. Seeds were collected from 10-15 mother plants of each species and mixed together to make the seed pool. A sample of 100 seeds from each species was randomly chosen for germination and then used for electrophoresis and cytological analysis. On the basis of starch gel electrophoresis of isoenzymes from randomly chosen embryos, variability of the following enzimatic systems was studied: phosphoglucanate dehydrogenase (6PGD, E.C. 1.1.1.44), malate dehydrogenase (MDH, E.C. 1.1.1.37), glutamate dehydrogenase (GDH, E.C. 1.4.1.2), glucose-6-phosphate dehydrogenase (G6PD, E.C. 1.1.1.49), phosphoglucomutase (PGM, E.C. 5.4.2.2), phosphoglucoisomerase (PGI, E.C. 5.3.1.9), glutamate oxaloacetate transaminase (GOT, E.C. 2.6.1.1), NADH diaphorase (DIA, E.C. 1.6.99). Enzymes were extracted by homogenization of a single embrio in 80 µl of extraction buffer: EDTA, KCl, $MgCl_2$, TRITON, PVP, TRIS-HCl. Izoenzymes were separated on 10% starch gel using two buffer systems (Muona et al. 1987; Odrzikoski and Stazak, unpub.): (1) TC: electrode buffer of Tris and citric acid, pH 8.0 with 2M Tris; gel buffer of 10 ml of electrode buffer diluted with 90 ml H_2O, pH 8.0 with 2M Tris; and (2) PK: electrode buffer of boric acid and NaOH, pH 8.2 with 4M NaOH; gel buffer of Tris and citric acid, pH 8.7 with 2M Tris. Electrophoresis was carried out for about 6-7 hours under the following conditions: TC buffer system, 90V, 40-50 mA; PK buffer system, 210 V, 70-80 mA at 5^0C. Staining of particular enzymes as well as genetic interpretation of results followed standard techniques (Rudin and Ekberg 1978; Szmidt and Yazdani 1984; Muona and Szmidt 1985). On the basis of electrophoretic data the following parameters were calculated to describe genetic structure of the population: frequencies of alleles and genotypes, mean number of alleles and genotypes per locus (A/L, G/L), expected and observed heterozygosity (He, Ho), Wright's fixation index (F), genotype polymorphism index (Pg), genetic distance and similarity based on alleles (Nei) and genotypes (Hedrick) frequencies (according to procedures described by Nei and Roychoudhury 1978; Nei 1972; Hedrick 1974; Sneath and Sokal 1973; Wright 1969).

The carbon izotope ratios (^{13} C values relative to the PDB standard) were determined according to Schulze et al. (1996) using a Heraeus CHN rapid elemental analyzer coupled on-line to a trapping-box-gas-isotope-mass spectrometer system (Finnigan MAT Delta S).

Cytogenetical analysis. At least three root apexes were examined from each population. The chromosomes were counted exclusively on mitotic plates (three to five plates for each species) at metaphase or anaphase. The samples were handled according to following schedule: a) fixation in freshly mixed 3:1 absolute alcohol: glacial acetic acid, for at least 24 h in a refrigerator; b) transfer to 45% of acetic acid for a 24 h; c) root apices were cut and then macerated; d) meristem fragments were carefully heated to boiling in a drop of haematoxylin for 5-7 min; staining solution was removed with blotting paper; e) permanent preparations were made by mounting stained tissues in Euparal or in Hoyer's medium.

CHAPTER 3. Floral micromorphology, peculiarities of micro-and macrosporogenesis and micro-and macrogametophytogenesis

3.1. Biology of and sexual polymorphism of flower organs at the species and population levels

Self-reproduction of many native species of genus *Salsola* under the conditions of the Kyzylkum is going badly because of lower quality of seeds and attack of seedlings at approach of summer heat. Seed productivity and its quality in *Salsola* species depends mostly on meteorological environmental conditions of the year (Bochantseva, 1948; Bespalova, 1960, 1961; Shatskaya and Konycheva, 1965; Shirinskaya, 1970; Konycheva, 1963, 1977; Konycheva et al, 198; Semenova, 1986; Toderich et al 1992). It was determined that wet years promote good seed maturation for desert plants. In the droughty years seed formation sharply falls and many plants do not produce seeds at all. According to the data of Shatskaya and Konycheva,1965 the viability of seed under Kyzylkum desert conditions for different years varies from 4-51% at *S. orientalis,* 4.0-50% at *S. arbuscula* and 6.0-65% in *S. gemmascens.*

The sterility of male and/or female organs, widely widespread among wild-growing desert plants is considered one of the main causes in falling down of buds, flowers and for the formation of empty seeds (usually without a well developed embryo). Therefore the purpose of the present chapter is the description of flower organs and some reproductive process of some desert *Salsola* species valuable as forage species. It was also hoped that with the help of embryological studies it will be possible to reveal differences and characteristic (diagnostic) embryological patterns in view of their use for establishment of taxonomic and phylogenetic relationships within various groups of genus *Salsola.*

In the present chapter we examine the applicability of floral micromorphology techniques to test generic and infrageneric classification of some representatives of genus *Salsola,* and its relatives We also try to determine if there is a link between the floral micromorphology diversity and adaptive evolutionary trends of sexual reproduction system within species of genus *Salsola*, growing under harsh desert conditions.

Another unanswered question is to what extend great morphological variability of flower generative organs represents developmental or environmental variability (Konycheva, 1977; Rilke and Reimann 1996; Toderich et al, 2001 and Wojnicka-Poltorak et al 2002).

The description of floral organs diversity for investigated species was summarised by us and given as follows:

Salsola arbuscula. Flowers: green inconspicuous, bisexual, protogynous, pentamerous, solitary on axillary or rarely in clusters forming loose spike. Bracts: leaf-like but shorter, at the base auriculate with wide hyaline, often ciliate margins, always longer than bracteoles and tepals. Bracteoles are similar to upper bracts. Perianth segments: ovate-ligulate, m glabrous, membranous, winged in fruit below the middle. Anthers: 2.2-3.5mm long, divided up to 1/2; appendage minute, ovoid 0.4-0.5 long. Pollen grain: 3-nucleate, high fertile (85-92 %). Ovary: conical, superior with 1 ana-campilotropous, crassi-nucellate, bitegmic ovule; style 0.7-1.0mm long; stigmas- 1.5-2.0 mm long, flat at base ca 0.4mm wide, at apex almost subulate, deeply red Stigmas subulate, enlarged bellow and flat, 2-4 times as long as more rarely equalling the style. Fruiting maturation: end of September - October.

Reproduction: Sexual. Heterocarpy, polyembryony, apomixis are peculiar. Flowering: end of May till September. This species is mostly anemophilous, occasionally entomophilous.

S. richteri. Flowers: solitary, bisexual, protogynous. Bracts: lef-like but shorter at base with hyaline, sometimes ciliate margins, always much longer than bracteoles and tepals. Bracteoles: cuculate, ovate or circular in outline, usually apiculate and obtuselly keeled in upper part with wide hyaline and ciliate wing-like margins embracing the flower. Tepals are triangular to ovate, in upper part often ligulate; apex rounded or apiculate, back without distinct green blotch, glabrous. Anthers 2.0-2.5 mm long, divided up to 1/2; appendage 0.2-0.5 mm long; filaments linear; disc with short, broad, densely papilose lobes. Ovary conical; style thick, short, 1.0-1.5 mm long; stygmas 2.1-1.5mm long, flat up to the apex 0.3-0.4 mm wide, red.

S. Paletzkiana. This species is very similar and closely related to S. richteri, but differing in the following: Bracts are often recuvered. Bracteoles with a subulate recovered and at the upper part terminated by c. 0.5 mm long mucro, at base wide. Tepals are 4.5-5.0 mm long, apiculate with a shortly excerted middle vein. Anthers 3.0-3.5 mm long, divided for 1/2-2/5; appendage 0.8-1.0mm long, acute. Stigmas: 0.2-0.3 mm wide.

Self-pollination is much characteristics for *S. richteri* and *S. Paletzkiana* . A significant amount of sterile or undeveloped anthers has been found for these species. Sterile specimens are readily confounded. Some characters, in particular the distinct mucros on bracteoles and tepals (at fruit maturation stage) point to a hybrid origin between *S. richteri* and a species of section *Salsola,* perhaps with *S. paulsenii.*

Sexual vegetative (cuttings) reproduction is very common for these two woody species. Flowers: June – August.

S. arbusculiformis. Flowers are solitary, bisexual, although the different sexual types are also described. It is frequently found the degeneration of separate pollen sac, rarely whole anther as well. Often we marked the dehiscence of pollen sac inside of the closed flower (kleistogamous plant). Bracts: leaf-like, but shorter, incurved, at base widened and sheathing with narrow hyaline margins, inside with hairs longer than bracteoles and tepals. Bracteoles with wide wing-like hyaline margins forming a collar-like structure around the lower half of the flower; ovate or circular in outline, at the apex with broad hyaline margin, slightly keeled. Tepals ovate to ligulate, stiff, 3-5 veined with broad hyaline margins, apex obtuse, ofyen apiculate, back with diffuse triangular to semi-circular green blotch. Anthers 2.5-3.5 mm long, red or yellow, linear divided up to 1/2; appendag minute, 0.2-0.4 mm long and wide, obtuse; disc with small interstaminal and epistaminal lobes, glabrous.

This species resembles *S. arbuscula*, but highly distinctive are the papery white collars around the lower half of the flowers, the large, usually bright red anthers with a minute appendage and the fruits with the upper parts of the tepals forming a truncate cone instead of a funnel.

S. montana. Flower: bisexual, small, solitary and very rearly in clusters forming a narrow or wide, ocassionally diffuse paniculate onflorescence. Bracts: leaf-like, but shorter, wooder, semi-terete, the lower longer than bracteoles and tepals; at base with hyaline margins sheathing, incurved. Bracteoles: cuculate, c 1.0mm shorter than tepals, ovate or almost circular in outline. Tepals ovate, firm 5-veined with wide hyaline margins, apex broadly obtuse, crenulate, green blotch narrow triangular, glabrous. An original morphology of anther's appendage is found. Anthers: 1.5-2.0mm long, narrow triangularor sagitate, divided up to 1/2; appendage minute, 0.2-0.3mm long and wide, obtuse; disc subglobular; style 0.3-0.6mm long. Ovary: subglobular; style 0.3-0.6mm long; stygmas 2(3), 0.8-1.3mm long. Protoandrous type of flower is mostly peculiar for this species. Sexual polymorphism, which is expressed in sex differentiation of male and female reproductive organs, morphology of stygmas etc. of organs, are common as well. Pollen productivity of some anthers is very low.

Thus, the examined species of section *Coccosalsola* (subsection *Arbuscula)* have five stamens, usually incurved in bud, with the filaments free (connate, wide to the base), arising from receptacle or saucer-shaped with ovoid lobes, covered by short papillae (*S. richteri, S. arbuscula*) or glabrous, rarely with short hairs (*S. paletzkiana*) hypoginous disk. The anthers are large (2.9-3.8 mm –*S. paletzkiana*; 1,7-2.8 *S. richteri*; 2,4-2.8 mm *S. arbuscula, S.*

arbusculiformis), usually 4 sporangiate and 2 locular at anthesis, basifixed or dorsifixed almost at the middle, opening usually introrse, by 2 longitudinal slits, sometimes with a large appendage (0.2-0.5 mm *S. richteri, S. arbuscula*, 0.4-0.8 *S. arbusculiformis* and 0.7-0.9 mm *S. paletzkiana*), narrowly lanceolate or oblong ovate, sharp pointed (*S. paletzkiana*, *S. richteri*) or blunted at the apex.

Common evolutionary tendency in flower' morphology and biology of woody species of section *Coccosalsola*, subsection *Arbuscula* is to support protoandry in the bisexual flowers at a case for *S. richteri, S. Paletzkiana, S. arbuscula* and *S. montana.* This feature is co-ordinated with the well-developed nectarious disk and large and, sometimes coloured anther's appendages.

***S. gemmascens* (Section *Malpigila*).** Flowers small, bisexual, solitary. A strong tendency to protogyny is observed. Leaves covered with a dense indumentum of adpressed, smooth, thick- or thin-walled, 2-3 armed (malpighian) hairs. Bracts: ovate to triangular, the lowermost as long as bracteoles. Bracteoles are scale-like, cuculate, circular, transversely ovate or obovate, keeled, shorter than tepals. Tepals: narrow to broad ovate, 3-4_ veined, transverse lines at 1/4-1/3, green blotch at least in some tepals deeply divided. Anthers divided up to the appendage; appendage 0.5-0.7mm long, ovate-ligulate with broad obtuse apex, slightly separated from thecae. Ovary: subglobular; style long, thin. Stigmas: flat, inside very shortly papillose, reddish. Nectarious disc is thick cup-shaped, smooth with undulate margin. Flowers: August-September;

S. orientalis. (section *Caroxylon*) Flowers: solitary, ovoid, bisexual (different sexual types also occurred), dark yellow, assembled in a friable panicule. Lower bracts are leaf-like, longer than bracteoles, the upper scale-like, only 2.5-1.5 long, ovate to almost circular in outline, keeled. Tepals are narrow ovate, 1-veined, transverse line at 1/4-1/3, green blotch triangular, margins and apex usually ciliate with denticulate or flexuose hairs, the back glabrous or hairy in various extent and density. Anthers: distinctly excerted on 2.9-3.0mm long long flaments; appendage with obtuse or flattened apices, semicircular to trapezoid. Ovary: superior with one ana-campylotropous, crassinucellate, bitegmic ovule. Size of style with stygma is about 3mm long. Stigmas: short, thick, flat, inside long papillose. Disk is (nectariferous) very small. Flowers: June-September.

S. dendroides. Flowers solitary or in clusters, small, ovoid, bisexual. A peculiarity of micromorphology of flower is the development of small anthers on enlarges stamen filaments. Disc absent or very small; anther' fillaments narrow triangular with ca 2mm wide base fused at ovary base. . Ovary: ovoid, tapering into the 0.5-0.7 mm long and thick styles; stygmas 2, flat, widened with very long papillae. This species can be characterized as typical protogynous plant. Self-pollination is also admitted. Flowers: July-September.

S. incanescens. Flowers are bisexual, small. Bracts: tringular sparsely pilose with semi-adpressed hairs. Bracteoles are with wider hyaline margins, enclosing the perianth or slightly surpassed by it. Tepals ovate, 1-veined, transverse line at 1/2, green blotch small triangular; back pilose with stiff ascending hairs. Anthers 0.6-1.2 mm long, including the 0.1-0.15 mm long, obtuse appendage, divided for 3/4.; disc absent. Ovary is globular, style thin; stygmas large, inside papilose. Flowers: July-October.

Summarizing the data we concluded that species of section *Caroxylon* have an evolutionary tendency to cross-pollination despite the lack of pronounced, specialized flower organs. This is mainly expressed in a simultaneous development of different sexual types of flowers and a difference in the longevity of pollen grain and embryo sac maturation within individual bushes. For instance, bisexual flowers at *S. orientalis s*trongly keep their tendency to protogyny and development of female functioning flowers. These two sexual types of flowers couple with weak development (*S. orientalis)* or completely absence (*S. dendroides)* of nectar disk and anther appendages.

S. sclerantha* (section *Cardiandra*)*: large-flowered; flowers: bisexual, pink or violet. Bracts alternate, obtuse, semi-terete, succulent, and glabrous at base and with farinose ('mealy') indumentum of bladder-like hairs in upper part. Bracteoles are succulent, usually short, trullate. Tepals: lanceolate, densely covered by vesicular hairs. 1-veined with 1 or 2 green blotches. Anthers 1.3-1.8mm long, divided for two 3/5 to close to appendage; appendage 1/4-1/2 length of thecae quadrangular to broadly rectangular; fil.laments arising from outer side of disc; disc thick, rim-like with broadly triangular to semiglobular lobes, glandular without papillae. Ovary ovoid to almost conical; style 0.5-1.2 mm long; stygmas narrow linear. Perianth leaflets at flowering stage are much longer than bracteoles, heavily clothed with bladdery scales and usually with some simple hairs. All species of Section Cardiandra *a*nd *S. sclerantha* in particular have a well-pronounced nectarious saucer-shaped disk. Stamens are oblong with narrowly linear filaments, anthers strongly divergent beyond the middle, terminating in a sessile ovate obtuse appendage several times shorter than anthers. Species has daily (morning) type of blooming. Period of flowering of one flower: from 6-30 until 12-00 p.m. Longevity of pollen grain: 30 min, rarely 60 min. Protogyny mostly occurs. Cross-pollinated (by insect, rarely wind) or autogamous (self-pollination within one flower) are noted.

S. turkestanica, S. forcipitata and ***S.implicata*** identify the same characters as *S. sclerantha.* In habit and ecology all these species are similar, and sometimes are mixed in the same collection. It differs in the large, broadly overlapping fruit wings, the longer anther appendages and the extraordinary shape of the stygmas. The widened lateral and apical parts of the stygmas are devoid of the normal glandular surface. It seems that they function only in gathering the pollen grains and forwarding them to the papillose tissue restricted to an inner central line at the base of a longitudinal furrow. Remarkable variation has been observed in length of style and stygma of *S. forcipitata* and in the absence of hairs on the lower tepal backs.

Salsola micranthera. This species is characterized by a very small size of anthers. Stygmas: glabrous from outside. Protoandrous plant.

***S. gossypina* (section *Belanthera*).** Flowers are solitary, bisexual. Bracts: leaf-like, at base wide with sheathing hyaline margins, longer than bracteoles. Bracteoles are similar to bracts with shorter blade, 6.0-3.0mm long. Tepals narrow lanceolate, 3-5 veined, apex obtuse or slightly lobed, hidden by dense and long semi-adpressed curled hairs, transverse line at 1/3-2/5. Anthers with appendages in cleistogamous flowers divided to the appendage; appendage separated narrow triangular, acute. Disc is thick with short densely papillose lobes. Ovary: subglobular to obovoid; style 0.4-0.5mm; stygmas 2, 1.2-1.5mm long from the 0.2mm wide base gradually tapering. . A self- pollinated plant. Protoandry is also common.

S. aucheri. Flowers bisexual, small. Bracts are leaf-like, lower longer than bracteoles and flowers. Bracteoles with a very broad sheathing base, slightly cuculate, the blade recurved; the lower much longer than tepals. Tepals narrow ovate, 5 (-6) veined, apex acutish, obtuse or 2-3 lobed. Transverse line at 1/4, above densely hairy; hairs semi-adpressed, persistent. Anthers with appendage 1.9-2.5 mm long divided almost up to the appendage; appendage separated from thecae; at base 0.35-0.45 mm wide, narrow triangular, obtuse. Disc is thick, slightly lobed, glandular papillose. Ovary subglobular; style 0.8-1.0mm long, erect, flat, up to 0.4 mm wide, apex subdentate. Anthers are linear, divergent almost to the middle, terminating in a sessile lanceolate acute pale appendage covered with acute papillae and slightly shorter than anther. Stygmas is glabrous from outside. Protoandrous plant.

S. aperta (Section *Salsola,* sub. *Kali*). Flowers are small, bisexual, arranged singularly at the axis of spinacent bracts and assembled in a spike-shaped panicule. Bracts and bracteoles are with prominent spines. Bracts are oblong to ovate. Bracteoles shortly acuminate from an ovate base, Tepals narrow ovate to lanceolate, 3-veined, midrib finely visible, transverse line at 1/4-1/5. Anthers oblong-elongated 1.3-1.9 mm long, divided up to 2/3 with a small (0.1-0.2mm long) , knob-like appendage. Nectars disk is slightly differentiated, usually with rounded, ciliate lobes. Ovary is subglobular, style 0.4-0.7mm long. Distinct differences from many other species of section Kali are shorter stygmas and slightly larger fruits. It is a self-pollinated plant.

Ovule is ana-campylotropous with slightly curved nucellus. Micropile part consists of 8-12 rowed-cells, chalazal, more massive than embryo sac is dislocated at 1/3 of ovule. Integuments have 4 *layers that afterwards are differentiated into seed coat.*

S. paulsenii. Flowers are bisexual with spinascent bracteoles. Anthers: oblong, small (0.5-0.7mm) with inconspicuous .appendage. Flowers are solitary. Bracts and bracteoles are spreading to recurve. Bracts abruptly narrowed into a long spine. Bracteoles are 8-4mm long, exceeding the flower. Tepals narrow-ovate, 3-veined, transverse line at 1/6-1/3, without a green blotch, densely papillose on back, acuminate, midrib of 3-5 tepals, protruding and becoming hardened. Anthers oblong, sometimes slightly triangular, 0.5-0.8 mm long including minute appendage. Stygmas filiform, 0.7-1.3mm long, up to 2 times style length. Ovary greatly compressed with a unusually long and curved funiculus that is deeply inserted into receptacle towards vascular bundle. Mature ovule is ana-campilotropous, crassinicelate, bitegmic with endostomic micropile. Embryo sac is distributed at the middle part of nucellus. Flowers we characterised as protoandrous. Sex expression and sex polymorfism are very characteristic for this species. Frequently the degeneration of anthers at well developed stygmas has been observed. So, the simultaneous function of bisexual and functionally female flowers is common. Flowers: May-September.

S. paulsenii can be easily confused with closely alied species of section Kali. In fruit, it differs in the large wings, distinctly veined from the base, and the lower narrow spine-like upper tepals.

S. praecox. Flowers are solitary remote; perianth much longer than bracteoles 3-5mm long at anthesis, heavily clothed with bladdery scales and usually with some simple hairs; Anthers divergent well beyond the middle, terminating in a sessile ovate obtuse appendage; style as long as mostly several times as long as stigmas; stygmas obtuse, often slightly enlarged at tips with papillae. Flowers: April-June. Anemophylous.

S. praecox shows a close relation to *S. paulsenii.* In typical specimens, the differences from S.paulsenii in the dimensions of the vegetative parts and the resulting habitat are striking, but intermediates have been seen. Both taxa are separated by their flowering and fruiting time. Due to occurrence of many morphologically transitional forms these species were collected in late summer, in between the fruiting times of both taxa. , the differences may only represent seasonal dimorphism.

S. ruthenica. Flower solitary, sometimes in addition assembled into more or less condensed lateral spikes. Bracts and bracteoles are spreading. Bracts up to 3 times length of bracteoles, apically abruptly narrowed into prominent, pungent 1.0-2.5mm long spine, base in fruit often inflated, sometimes adnate to the bracteoles. Bracteoles are longer than flower, tapering into 1.5-3.0 mm long spine. Tapals narrow ovate, 2.0-3.6mm long, 3-veined, acuminate, acute or obtuse and erose-dentate, transverse line at 1/4-1/3, without a green blotch, midrib distinct to 3/4 of the tepals. Anthers oblong, 0.6-1.4mm including the minute, triangular apendage, divided for 1/3 to 1/2. Flowers: July-October.

S. pestifer **.** Morphologically, it approaches S. *kali subs. iberica* and *S. ruthenica,* in Europe, but differs in smaller tepals, smaller anthers and most obviously, by the densest and longest indumentum occurring on bracts and bracteoles surface. This species is highly polimorphic, especially with regard to growth form, shape of inflorescence and undumentum. This led to the recogniction of several species and a wealth of infraspecific taxa. Many of them can be reduced to synonymy, which has been done by early authors. However, some of them still remain to be checked.

This species up to fruiting stage has more succulent bracts and bracteoles and, seemingly most significantly wingless fruits with the bracteoles adnate to base. Surface of bracts and bracteoles are leee covered by hairs. The last flowers produced from serial buds in the lower part of plant remain enclosed in the enlarged sheathing base of bracts and bracteoles. Flowers: July-September.

A weakly pronounced protoandroecy and a tendency to protogyny are very common features for investigated species of Section *Salsola*. These floral patterns correlate with not well developed nectariferous disk, large, papillate stygma and small, glabrous and compact anthers appendages. The developments of different sexual types of flowers are described.

Salsola lanata **(section *Physurus*).** Flowers: solitary, bisexual, sepaloïd (five–lobed perianth), violet-coloured, or rarely in clusters forming loose spikes. Bracts leaf-like, 12-5mm long with 4-5mm wide sheathing base. Bracteoles 8-5mm long, at base 3.5-1.5mm wide. Tepals 1-5 veined narrow ovate with ascending stiff, 0.5-1.5mm long hairs, after anthesis in upper part brown without green blotches. Anthers: pink/violet, tetrathecas, linear divided up to 1/3, partly excerted; appendage large, vesicular ellipsoid, ovoid or subovoid, 0.7-2x0.5-1.1mm, yellow, distinctly stalked; filaments narrow triangular; nectariferous disc weakly developed. Ovary: apically distinctly narrowed; style 2.5-0.1-0.2 mm included or to 3mm exserted; stygmas 0.3-0.7mm long. Ovule: ana-campylotropous, crassinucellate, bitegmic.

S. subaphylla (recently described as *Halothamnus subaphyllus*) Flowers are bisexual, protogynous, occasionally unisexual, and single in spikes assembled in a friable panicle. Anthers lengthened with small ovoid appendage. Ovule is usually ana-campilotropous, bitegmic, crassinucellate.

3.2 Anther wall development, microsporogametophytogenesis and pollen grain formation

As a part of ongoing study on reproductive biology of Asiatic genus *Salsola* this paragraph describes and correlates the formation of anther wall, microsporogenesis, as well as structure and development of parietal tapetum and pollen wall of several representatives of desert species of *Salsola,* growing in Uzbekistan. Very few reports are available concerning detailed development of anther wall, especially tapetum (Konycheva, 1983; Toderich et al. 1995; Toderich unbublished data), none of which makes a detailed correlation with pollen wall development. Our supervision on wall development of anther and pollen grain in different *Salsola* species belonging to the section *Caroxylon (S. orientalis*); section *Malpigila* (*S. gemmascens*); subsection *Arbuscula (S. richteri, S. arbuscula and S. arbusculiformis*) and section *Salsola* sub. *Kali* (*S. praecox, S. sclerantha and S. aperta*) has been taken from developing flowers ranging in size from 0.4-1,2 mm buds to anthesis.

It was determined that the development of stamen in all examined representatives of genus *Salsola* starts with the initiation of stamen's primordia that consists of several not differentiated meristematic cells. For the representatives of genus *Salsola* in comparing with other flowering plants (as a case of *Gossypium*) the formation of anther is going before development of stamen's filaments.

The anther of *S. orientalis* is tetrasporangiate, and each lobe is made up of two layers of morphologically differentiated groups of cells, i.e. epidermis, and initial archaesporial cells. Later as results of mitotic division of these cells the secondary archaesporial cells and primary parietal layer are formed. The male sporangium tissue represents a group of large isodiametric cells that differ by degree of differentiation of their internal content (dense cytoplasm and greater on size and condensation of nuclei) and stain more intensely than the parietal cells. During the formation of an external wall of the sporangium archaesporial tissue rather actively divides mitoticaly. The division of archaesporial cells, however, is not focused. Cells of parietal layer are more vacuolate and as in contrast with archaesporial tissue the mitotic divisions in cells of initial parietal layer are strictly focused. So, the anticlinal divisions lead to the increasing of number of cells, while the periclinal division of parietal cells gives the formation of new layers: inside to the tapetum and to the secondary parietal layer outside from archaesporial tissues. Pictures of cell division and formation of the specified layers of anther's wall can be observed in developing flowers in size of 1, 0-2.8 mm buds. Sooner the periclinal divisions in the secondary pariental cells derived to the formation of endothecium and middle layer.

Gradually the differentiation of secondary archaesporial tissue into microspore mother cells (MMCs) is visible. After the mitotic division prior to meiosis, the MMCs enlarge and their cytoplasm becomes denser. The MMCs form a loosely arranged central group of isodiametric cells that stain more intensely than the tapetal cells.

Thus, for examined here *Salsola* species a centrifugal type of anther wall formation is characterised. As far as the tapetum represents a derivative of secondary parietal layer the anther wall development of Salsolas can be attributed to the first type (Solanaceae-type), following the system offered by Batygina et al (1963). In conformity with their classification the morphologically differentiated anther wall of Salsolas species is made by several layers of groups of cells: epidermis, endothecium, a single middle layer, tapetum and microspore mother cells.

The tapetum cell layer of the anther represents a specialised and unique tissue that provides developing pollen grains with various materials for growth and development (Fernando and Cass, 1994). There is a direct relationship between tapetum and developing pollen grains in anthers, where the tapetum becomes secretory as in *Salsola* species. At the early stage of anther wall development the tapetum in the examined *Salsola* species is a variably thick and loosely arranged layer of uninucleate cells surrounding the MMCs. The tapetal cell walls are thin and less dense than those of the MMCs. Soon at the beginning of meiosis in MMCs the majority of the cells of the tapetum greatly increase their size and the dividing of its nucleus is observed. However, there is no strict synchronism in the development of tapetum cells and male archaesporial tissue. So, it is marked, that at the start of prophase in MMCs we can sometimes see already binucleate cells. At the same time sometimes at later stages of prophase we observed uninucleate cells of tapetum. Frequently the same morphological condition of tapetum cells is observed at different late stages of development of male sporogenic tissue. The poliploidization of the nucleus of the tapetum cells and its transformation in a typical cenocytic state is noted since stage of synapsis in MMCs. As the MMCs undergo meiosis, the uni-binucleate tapetal cells become highly vacuolate and then enlarge, attaining maximum size at the early tetrad stage. The tapetal cells remain to keep the outline of their cell walls at late tetrad stage. Some of the vesicules of electron-dense materials can be observed into the locular space through the tapetal plasma membrane. These exudates accumulate to form electron–dense aggregates that can be found outside the tapetal plasma membrane around the callosic walls of tetrads of microspores and later on the newly released microspores.

The investing callosic walls start to desintegrate at late tetrad stage. It seems inside the tetrad each microspore has started the synthesis of its exteexine. The tectum with its punctate patterns is initiated at this stage as well. However the microspores remain in tetrads even after the callosic walls have completely disintegrated. At late microspore stage the tapetum loses its nuclei and gradually begins to degenerate. The content of tapetum gradually disperses into electron-dense debris and rectangular or elongated structures. These structures posses dark outlines and hollow centres.

During microspore mitosis the pollen walls are completely formed. At this stage, the tapetal cells have completely disappeared. The locular space is filled with tapetal products containing electron dense particles. Starting with the release of microspores from callose walls to mature pollen grain stage, a marked change in the thickness of the pollen wall layers occurs. This phenomenon occurs mostly due to contribution from the tapetum desintegration. At the early stage of pollen grain development the electron dense bodies that form aggregates outside the tapetal plasma membrane remain mostly around the pollen grain or rarely attached to the outer membrane of endothecium cells. We report these structures as sporopolelenin bodies (orbicules or Ubisch bodies that are very common features of parietal secretory tapetum in different groups of flowering plants (Pacini, 1990; Fernando and Cass, 1994). This probably indicates efficient transport mechanisms to the developing extexine of newly formed pollen grains. According to Pacini, 1990 the intimate contact between parietal tapetum and pollen grains is the first step toward a more active nutritional role of the tapetum. The limiting membranes of tapetum and the rectangular structures associated with the baculla have been recognised as a source of ektexine formation (Rowler and Dunbar, 1964). At the same time H.T. Horner et al, 1978; N.I. Gabaraeva, 1986 considered that the foot layer is tapetally derived. Polymerization of the primeexine and sporopolenin bodies from the tapetum probably brings about the development of the foot layer. Although the pollen grain is also involved in foot layer formation, the foot layer remains similar to the baculla and tectum in staining density and texture. However there is still a contradictory opinion concerning the role of sporopolenin (tapetal origin structures) in the formation of endexine. Blackmore and Barnes, 1987 consider that the endexine of angiosperms can be interpreted as terminal sporopolenin accretions. Since the endexine is well developed in the representatives of genus Salsola, its detailed study could provide a link to the evolutionary development of pollen wall structures in different mono-and dicotyledons groups of plants.

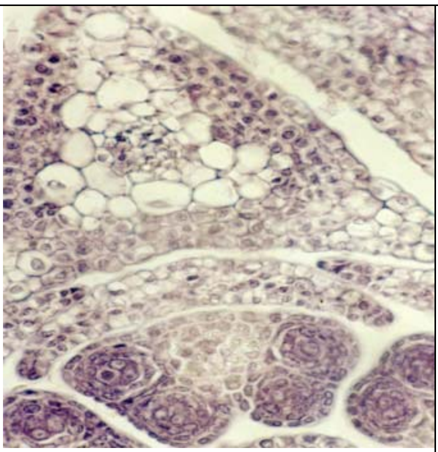
Besides that the end-products of the dissolution of the tapetum that are dispersed as lipid bodies, rectangular or ovate-elongate structures and/or electron dense debris could be responsible for the yellow/orange coloration of the pollen grains. They also enable pollen to grains to stick together, to stygmas and to the bodies of insect pollinators, which is very rarely found within *Salsola* species. Although sporopollenin bodies are not universal, their presence in the secretory parietal tapetum of *Salsola* species strengthens our view of the role of tapetum in pollen wall development, particularly extexine formation.

Middle layer of the anther wall for examined taxons of *Salsola,* as we noted before arise as a results of periclinal divisions of secondary parietal cells. Functionally this is a temporary layer in the anther's wall structure of all examined species of *Salsola*, despite this described cell layer is formed by one of the last at formation of anther wall sporangium. Beginning at the meosis (synapsis) stage in MMCs its cells assume the characteristic elongated form. Gradually the nuclei of middle layer' cells show features of disintegration and remain attached to the peripheral cell membrane. The first signs of degeneration of cells of middle layer in all examined *Salsola* species occurred at the late prophase stage in MMCs. Starting from free uninucleate microspores and consequently toward pollen grain formation the middle layer has completely disappeared.

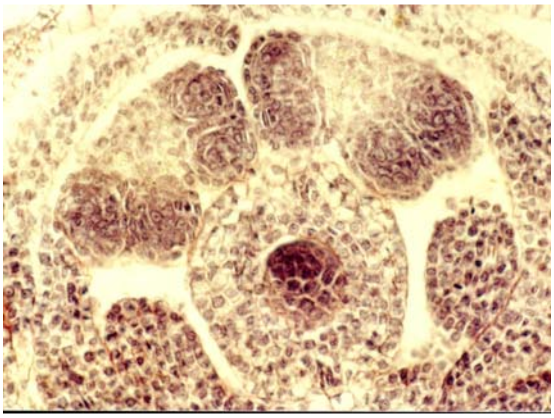
Endothecium, as well as the middle layer, is an end-product of the formation of the wall of sporangium from secondary pariental cell layers. Endothecium like epidermis cells after formation of sporangium wall, usually in the beginning of prophase in MMCs intensively start to expand. This is brightly expressed in the vacuolization of cells. To time of end of meiosis in microspore mother cells cytoplasm settles down streamlet along cell walls. At this time the characteristic thickening of endothecium cell walls is observed. The period, during which cells of the fibrous layer very strongly expand and get size of mature cells, is very short. At disintegration of tetrads and formation of young pollen grains in the size 5-7 microns, the endothecium is without thickenings; in a very short time when pollen reaches the size of 10-12 microns, these thickenings already are well distinguishable. Very important characteristics of *Salsola* species is that these fibrous thickenings could be also found in the connective cells. Owing to the development of fibrous thickenings both in endothecium and connective cells, the explosive portioned release of pollen took place. The presence of thick layer of cuticule on the epidermis probably defends pollen grains from the influence of high temperatures.

In the present work we were described microsporogenesis and pollen grain development for *S. arbuscula* and *S. orientalis.* The same regularities were observed for almost other species. As we noted the differentiation of secondary male archaesporial cells into microspore mother cells occurs approximately at the end of formation of anther wall, i.e when each lobe of microsporangium consists of epidermis, endothecium, middle layer and binucleate tapetum.

The stage of synapsis is the longest in all period of prophase of meiosis of microspore mother cells. Following meiosis, daughter cells derived from each microsporocyte are separated by an infurrowing type of cytokinesis. Darkened areas indicate the sites along which cell division will occur. Newly formed walls appear to be composed of callose, which is indistinguishable from callose that surrounds the microsporocyte. Completion of cytokinensis marks the onset of the tetrad period of microspore development. Reduction division in *Salsola* species passes on simultaneously type. Spindles are focused differently therefore the tetraedral and izobilateral tetrad types are formed. Callose wall breakdown marks the end of the tetrad period and the beginning of the free microspore stage. Microspores are released from tetrads and sparsely distributed in the cavity of pollen sac. The initial wall formed around the young uninucleate pollen grain (the primexine matrix) is laid down unevenly so that wall material appears in discrete regions between the spore protoplast and the callose wall. Gradually the primexine matrix becomes continuous around the microspore except at aperture sites. Soon the microspore nucleus, which remained in a central position during the tetrad stage, migrates to the cell periphery and, usually is positioned adjacent to the plasma membrane between apertures. Being in this position the spore nucleus undergoes the first mitotic division resulting in a bicelled pollen grain with a smaller generative cell within the cytoplasm of a larger vegetative cell. Vacuoles formed during the free microspore period are re-sorbed and the vegetative nucleus migrates to the centre of the cell. Generative cell is appressed to the plasma membrane, assuming a spindle shape and undergoes the second mitotic division. The mature pollen grain in *Salsola* species is tricelled. The mature wall patterns of pollen grain are well distinguishable at this stage. At this moment the mature anther wall consists of only two layers: epidermis and endothecium with well developed fibrous thickenings. Results are summarized and shown in the Fig.16 (a-e).



S. *sclerantha* (a)



S.orientalis (b)

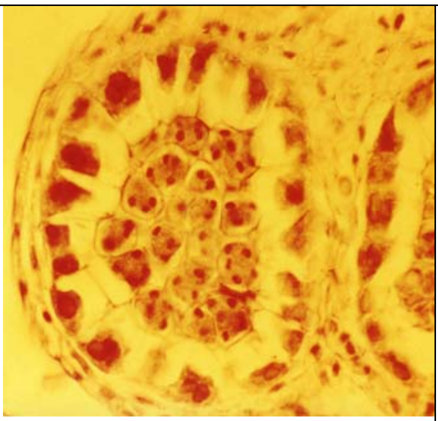
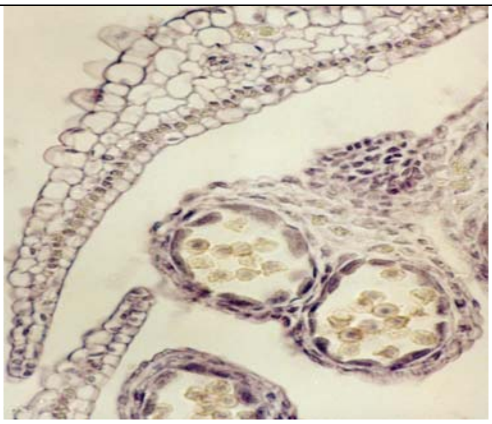
 *S.orientalis* (c)	 *S.sclerantha* (d)
 S.arbusculae (e)	a) tetrasporangiate anther; differentiation of secondary archaesporial tissue into microspore mother cells (MMCs) and wall anther's formation. b) Meosis in the MMCs, differentiation of tapetum cells; c) microsporogenesis and tetrads formation; d) release of microspores from callose walls; degeneration of tapetum and middle layer e) mature pollen grains and anther wall; epidermis and endothecium with fibrous thickenings are markedly visible; pollen grains are freely disperese inside of pollen sac.

Figure 16. Anther wall development, microsporogenesis and pollen grain formation

Thus, our embryological studies on the development of male generative organs for different species of Salsola during ontogenesis allowed concluding the following:

- all examined species are characterised by identical structure of microsporangium that indicates the lacking of any distinguishable taxonomic traits within genus *Salsola*;
- four layer structure of microsporangium (by the presence of single middle layer) is a diagnostic parameter of *Salsola* tribe, and this peculiarity would be regarded as a progressive feature in the evolutionary development of *Salsola* with Chenopodiaceae;

- annomalies during microsporogenesis are considered the main reason in formation of heterogenous both in size and quality pollen grains that lead to the development of great numbers of not potential ovaries on plants, consequently on formation of seeds with various germination ability.

3.3. Morphology, ultrastructure, interspecies variability and quantitative indexes of pollen grain

Many authors indicate the difficulty to distinguish the pollen grains of Chenopodiaceae even from those of some very closely related families of order Centrospermae, like Amaranthaceae, Caryophyllaceae, Dysphanaceae and Phytolacaceae. This is because a strong similarity in their floral and pollen morphology is marked.

Chenopodiaceae have a long history of pollen morphological study. A. Moquin –Tandon (1849) has been the first to describe pollen grains of the family. The general description of the pollen morphology of some representatives of Chenopodiaceae we found in the classic work of Moore et al. 1926; Averdieck, 1958 and G. Erdtman (1966), who described Chenopodiaceae as a stenopalynous family with (oligo-) polyporate pollen grains. M.H. Monoszon, 1951, 1952, 1973 presented a more detailed morphological survey of the family, drawing attention to the taxonomical significance of pollen characters and basing mainly on sizes of pollen grains and aperture configurations. He described the pollens of some genera of Chenopodiaceae from the USSR, comparing those of main groups of Chenopodiaceae (Cyclolobeae and Spirolobeae) with Alismataceae, Amaranthaceae and Caryophylaceae that are morphologically similar. M.N. Monoszon gave the description of pollen grains for more than 117 species belonging to 50 genera of Chenopodiaceae family. Among them *Salsola* species, such as S. *kali, S. lanata, S. laricina, S. longistylosa, S. ruthenica, S. soda, S. dendroides and S. rigida* have been investigated by the author. In her paper she is corresponding an artificial keys for distinguishing species based on palinological characters is also described. Palynological studies conducted by Monoszon,1951 however, were conducted mainly on fossil pollen or on restricted numbers of individuals per species using light microscopy analysis that cannot fully exploit the morphological characteristics of the male gametophyte if we take into consideration the conservative and stability associated with reproductive structures and reproduction processes. M. Tsukada,1967 firstly intended to delimitate Chenopodiaceae from Amaranthaceae by means of electron microscopy identification by such essential palynological parameters as apertures and specificity of exine sculpture. Later using variability on the number of pores, perforations on the surface of exine, form, sizes and number of spinules and others sculptural parameters of exine Nowicke, 1968, 1975; Nowicke and Skvarla, 1976; 1979, made conciliation to allied Chenopodiaceae to the Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Halophytaceae, Nyctaginaceae, Phytolaccaceae, Portulacaceae and Caryophylaceae. Although differences in internal morphology were observed at inter-and intra-familial level authors interpreted them as reflecting variations rather than major differences. The conclusion is that ultrastructure of pollen exine in Centrospermous families is very similar and all families have close pollen morphological relationships. The ultrastructure of pollen grain of Chenopodiaceae resembles Amaranthaceae in several aspects by similarly thickened tecta, the aperture structure, which consists of reduced pointed flecks of exine underlain by lamellar plates, and a thickened amorphous endexine (Skvarla et al., 1979). The high homogeneity of morphological parameters of pollen grains of Chenopodiaceae, however, may be the result of restricted numbers of genera (*Aellenia, Anabasis*, *Haloharis*, *Beta*, *Chenopodium*, and *Nitrophila*) and some species examined by Nowicke and Skvarla , 1979.

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 (Monoszon, 1952; McAndrews and Swanson, 1967; Uotila, 1974; Gomez Ferreras and Pedrol, 1987; Chung Youngjae, 1995; Helena Silva, 1999 and Toderich et al, 2000).

Summarizing previous work, we concluded that the pollen morphology of Chenopodiaceae, and *Salsola* representatives in particular, have not received considerable attention from research workers. Few studies for genus *Salsola* pollen morphology have been completed, and those that are available provide descriptions of a very few species. The pollen morphology in genus *Salsola* was discussed only briefly in the previous publications of Monoszon, 1973; Nowicke and Skvarla 1979, Toderich et al. 2000. General description of pollen grain of *S. tragus* is given in the classical work of G. Erdtman, 1966. Some palynological data of Salsola is also included in the monograph of L.A. Kupriyanova and L.A. Alyoshina, 1972 concerned pollen flora of Russia. Some palynological data is also given for *Salsola komarovii* of Korean Flora from the taxonomical point of view (Chung, 1995).

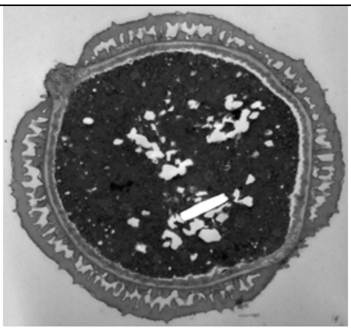
Pollen morphological analysis of Central Asian *Salsola* species, however, is not yet investigated in the literature. It seems that the paucity of detail in pollen grain morphology, added to the taxonomic difficulties within the family, has discouraged palynological studies. There are no worldwide monographs on this genus, and in some species, owing to the high degree of polymorphism and expansive, even transcontinental dispersal as in the case of *Salsola kali,* identification of species with the aid of local floras is inadmissible.

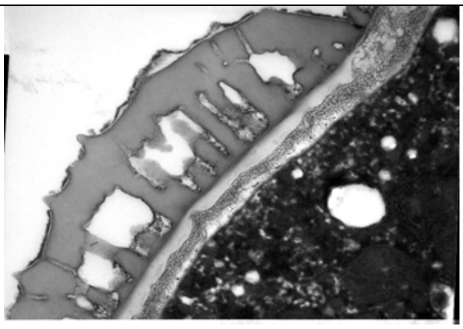
The present contribution provides the first comprehensive survey at the light and electron microscope level of Asiatic *Salsola* pollen grain analysis with the specific objectives of detecting possible evolutionary trends in pollen-morphology and providing additional data to further clarify the intraspecies and intrageneric systematics and phylogenetic relationships of this chenopods group. Attention has been focused primarily at the species level. It was hoped that pollen morphology might supplement a taxonomical revision of the genera *Salsola*, tribe Salsoleae (Chenopodiaceae), since, in spite of different geographical distribution, important macromorphological characters for the distinction of many species within this genera cannot be found.

The analysis of our data obtained for different Asiatic species of *Salsola* has shown insignificant interspecies differentiation at the level of pollen ultrastructure (Fig. 17 a-h).

Examined taxa of *Salsola* manifests a range of variation in the aperture types and their morphology,with a lesser extent to the surface of tectum and exine ultrastructure. A thick tectum supported by stout columellae on a thin foot layer underlain by a fragmented lamelar endexine is common for all the examined species. The structure of the tectum is described in relation to the underlying pattern of columellae. The size, shape and distribution of the columellae form an important characteristic. They are mostly small (>1mk in diameter) and relatively short, but in the larger grains as in the case of species of section *Physurus (S. lanata, S. crassa*) may become much larger. Their height is generally equal on poles, but they always decrease more or less gradually near the apertures. The columellae of the majority species of *Salsola* are arranged in a reticulate character in a single row, conforming to the tectal patterns. The combined reticulate pattern of columellae and tectum may be rather uniform. Equatorial view showing the irregular reticulation of the exine in the pore's membrane and the gradual decrease in reticulum dimensions along the pore borders.

There is nearly a complete uniformity of the internal morphology of pollen grains of genus *Salsola* with exception of *S. lanata and S.* crassa (revised recently as *Climacoptera* complex). The genus has been divided into two types on the basis of above-mentioned characters of pollen grain ultrastructure.





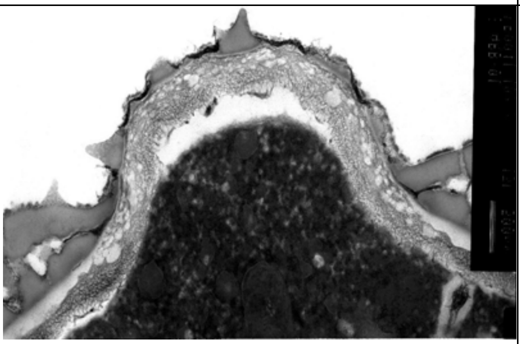
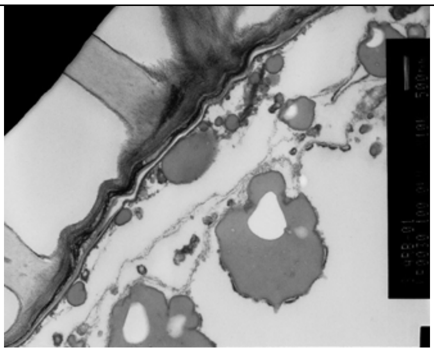
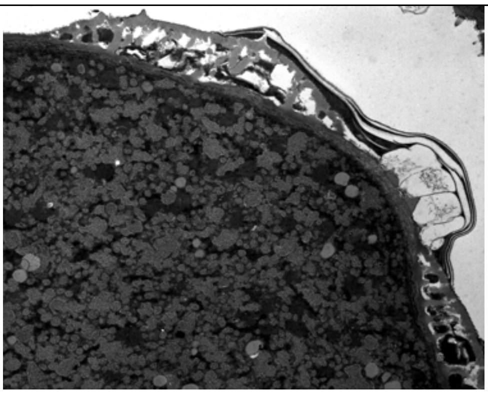
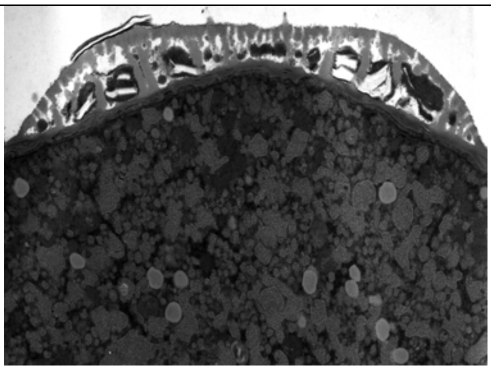
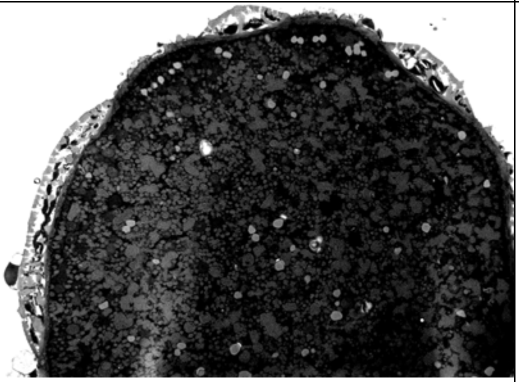
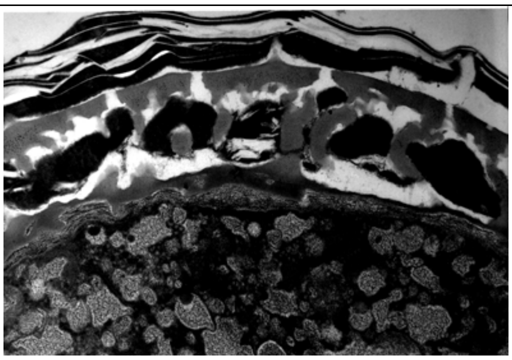
a) radial section through whole grain	b) radial section through mesocolpus; the tectum is much thicker than foot layer
 c) Section through pore area; note electron dense endexine under colpus; uniform spinules are well seen on the tectum	 d) Electron micrograph of the endexine and thin intine of *S. arbuscula.* The small tapetum's bodies are well distinguishable
 *e) S. lanata:* radial section across mesocorpus and adjacent pore.	 f) Short sparse columellae are irregular in shape and surface of the same species
 g) Somewhat oblique section through pollen grain of *Climacoptera crassa;* pores are observed in proximal walls	 h) Radial section of partially acetolized grain of C. *lanata* note thick intine and irregular collumellae with sculptured surface; none of the sections show columellae continuous with foot layer.

Figure 17. Transmission Electron Micrographs for two phylogenetically remote species

***S.arbuscula* (a-d) and *S. lanata* (e-h)**

Type 1. Grains are small to medium large, wall thick. As it is demonstrated on the *S. arbuscula* the morphology of this pollen type consists of a thick perforate tectum with short spines and prominent columellae terminating basally in a thin foot layer, which is underlain by a thicker, irregular endexine. For this morphological pollen type the small aperture region is present between several of columellae, i.e. columellae partially outlining aperture regions.

Type 2. Grains are large, wall thin to medium thick. This type posses a thin, slightly perforate tectum, with numerous short spines, unprominent and unbranched columellae that are irregularly distributed; foot layer approximately same thickness as tectum ; endexine extremely thin , except in the aperture regions. The aperture region of *S. lanata* and *S. crassa* as is shown in the micrographs consists of flecks of reduced, angular enktexine underlain by lamellar plates of more and less distinctive endexine (similar to many species of Amaranthaceae). An interesting feature is the presence of thin plate-like lamellae underlining the aperture (colpus) region. The origin of these lamellae is uncertain, they appear to be derived either from the lower part of the foot layer or they are endexine.

In thin section the exine surrounding the aperture of the last two taxa consists of short columellae that are slightly bifurcate at proximal and distal extremities. Random fusion of adjacent distal portions of collumellae forms a sporadic tectum. In the aperture region the columellae are greatly reduced and are caped by a continuous tectum. The irregular nature of columellae is reflected in a “stalaktite” or srates appearance commonly seen in the electron micrographs (Fig. 17h). Columellae are fewer in number than noted in other taxa of the family and taper somewhat where they attach with the foot layer; where columellae form the tectum they are expanded. Both taxa in comparison with other *Salsola* species posses minute perforations in the collumellae and tectum. The foot layer is more reduced than in previously described *Salsola* species. Markedly acute and thick spines project from the tectum surface in these last two taxa showing also the irregular shape of the lumina of the tectum. of special interest is the uneven intralumina proturbances, which form regular geometric patterns each of which encloses a pore area. And only finer columellae are noted along the borders of the pore.

The morphology of pollen grain (by SEM analysis) of investigated *Salsola* species has been described by using the following quantitative and qualitative pollen characters:

- Pollen diameter (D_{1}- maximum diameter, μm); Polar axis (D_2- diameter perpendicular to D_1, 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})
- Sinking of pore (++, prominent; +, weak; - none{flat}.

The pallynological data obtained by means of light, SEM and TEM analyses showed that all species have the 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; echinus number on pore, interpore distance and C/D ratio value. Data for examined species is given in Table 4.

Table 4. Interspecific variation of pallynological traits of some Asiatic species of *Salsola*

Salsola species	diameter of pollen (μm)	polar axis (μm)	Distance of interpore (C) (μm)	C/D ratio	Number of pores	Size of pore[1] (μm)	diameter of pore (μm)	pore area (μm)	Thickness of exine	form index	number of spinules /per 100μm^2	*Sinking of pore*[2]	*convexness of mesoporial exine*[3]
Section *Coccosalsola* (Ulbrich) Botcs., subsection *Aarbuscula*													
S.arbuscula	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	+	+
S. arbusculiformis	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	+	+
S.richteri	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	+	+
S. pachyphylla	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	+	+
S.paletzkiana	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	+	++
S. montana	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 *Malpigila*													
S.gemmascens	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 *Cardiandra*													
S. carinata	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	-	+
S.leptoclada	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	++	+
S.sclerantha	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 *Belanthera*													
S. aucheri	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	-	-
S. gossypina	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 *Caroxylon* (Thunb) Iljin

S.dendroides	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	-	+
S.micranthera	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	+	-
S. orientalis	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	+	-
S. laricina	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	++	+
S.incanescens	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 Salsola subsection Kali

S. iberica	14.70±0.09	13.72±0.13	3.54±0.04	0.249	37	.57±0.09	1.36±0.03	1.51	1.05±0.05	0.930	250±11	+	+
S.praecox	17.39±0.35	16.87±0.47	2.55±0.15	0.330	34	.95±0.18	2.07±0.05	3.37	1.17±0.14	0.969	140±6	++	+
S.ruthenica	21.76±0.38	20.78±0.23	2.73±0.09	0.215	49	.71±0.11	1.85±0.10	2.68	0.89±0.03	0.955	134±6	+	+
S. kali	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	++	+
S. aperta	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	+	+
S. paulsenii	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	-	-
S.pestifer	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 *Physurus* Iljin

S. lanata	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	++	-
S. crassa	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	++	++
S.subaphylla	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 hollow around it

[2] - level of sunking of pore; ++ prominent, + weak, - smooth

[3] - degree of convexnes of mesoporial exine; ++ prominent, + weak, - smooth

Based on this data we comprised the pallynological characteristics of Asiatic Salsola species as follows:

I. Species of section *Salsola* subs. *Kali* Ulbrich.

S. praecox - anthers are large, 4 sporangiate and 2 locular at anthesis, basifixed and opened usually introrsely by 2 longitudinal slits. Anther is free in lower one-third and sometimes with a small lingulate appendage. Pollen grains as is shown on Fig. 3. d nest into depression of the locular surface of bilocular walls of the longitudinally split anther. Pollen grain: radial symmetrical, isopolar, polypantoporate, spheroidal or nearly so; pollen size: polar axis 14.86-18.42μm in diameter with a polar axis of 13.42- 18.21μm. The exine is 0.25-2.27 μm. Ornamentation 123-160 spinules per 100μm^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 mk thick; tectum subtectate 0,56 mk thick, collumellae foot layer continuous, endexine irregular.

S. paulsenii - has palinological characters almost indistinguishable from S. praecox. Size of pollen grain: polar axis: 17.37, diameter of pollen: 17.73; number of pore 24-32; interpore distance 1.51-2.32; pore area 3.20-5.31; size of pore 2.02-2.60; 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: 0.48-0.77μm; number of spinules per 100 μm^2: 232-284.

S. iberica - this species differs from two previously described species by its smaller anthers that are divergent in lower part at least to the middle. Each anther terminates in a minute dot-like or ovate, flatish, sessile appendage. Size of pollen grain: polar axis: 13.01-14.28 μm, diameter of pollen: 14.29-15.20 μm; number of pore: 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; number of spinules per 100 μm^2: 234-258.

S. ruthenica - this species is characterized by unusual linear, basifixed and long stamen filaments. Anthers are oblong-ovate, with locules free in lower one-third, where connected by the rather small firm semioval, sessile appendage, which merges imperceptibly with the locules. Size of pollen grain: 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; pore numerous 40-58, circular, small 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 - this species is very similar with S.ruthenica in morphology of anthers and apppendage. Both species have pores which are numerous, small, semi-sunken and regularly placed on the spinulose punctate exine surface. Size of pollen grain: polar axis 18.54-20.24 μm; diameter 18.71-20.61 μm; number of pores 48-56; thickness of exine 0.92-1.16 μm; interpore distance 1.57-2.06 μm μm; diameter of pore 1.61-2.51; pore area: 2.99 μm^2; size of pore: 2.30-3.44 μm; spinulus on operculum 25-32; nanospinules on extexine 18-24; C/D value 0.163-0.212; number of spinules per 100 μm^2: 222-259.

***S. aperta* -** having in common some pallinological features with all above described species of section *Salsola* this species 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, where connected by the 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 in number and symmetrically placed on the scarcely perforated, punctate tectum. The most notable features are that *S.aperta* by number of pores 22-33 and C/D ratio value 0.452 is more related to the woody species of subsection *Arbusculae,* section *Coccosalsola* than to species of section *Salsola*. Size of pollen grain: 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* Botsch., subsection *Arbuscula*:

***S. arbuscula* Pall**.- the anthers are large (2.4-.2.6 mm) with an oblong-ovate uor lanceolate appendage (0.5 mm long) and short, linear, broad at the base stamen filaments.

Pollen grain of *S. arbuscula* is spherical or nearly so, 11.77-14.11μm in polar axis and 12.01-14.41 μm in diameters. The exine is 0.72-1.41 thick. The C/D ratio ranges from 0.304-0.392 that corresponding to 18-24 pores. Pore diameter varies by 1.36-2.54 μm, which is about two thirds of the diameter obtained from the light microscope measurements. Evidently the pores are wider inwards, which explain the difference. 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 densities make 274-307 spinules per 100 µm^2.

S. arbusculiformis - filaments broadly linear, pointed to the conective, basifixed to the saucer-shaped glabrous with ovoid lobes hypoginous disk. 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). Size of pollen grain: 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; size of pore: 2.34-3.96 µm; number of spinules per 100 µm^2: 186-193.

S. richteri - filaments broadly linear throughout their length; anthers 1.7-2.8 mm long oblong, divergent in lower one-third to one-half with a firm yellowish or whitish oblong-ovate to broadly lanceolate appendage 0.2-0.5 mm long. Size of pollen grain 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. Paletzkiana - 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 to 1mm long. Size of pollen grain: diameter of pollen: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 - anthers separated beyond the middle to two-thirds of their length, terminating in a small sessile obtuse ovate appendage. Size of pollen grain: polar axis 11.93-13.56 µm; diameter: 12.94-13.67 µm; number of pores: 20-28; pore area: 3.26-6.61; 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 - size of pollen : polar axis:17.10 µm; diameter 17.97 µm; number of pores 16-24; diameter of pore 2.50-2.79; 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 - This species has anthers with linear locules divergent up to the summit; terminating in a yellowish oblong-ovate to broadly lanceolate, acute appendage, one-third to one half the length of the anther. Nanospinulus on operculum ranges 36-48. Size of pollen grain: polar axis: 12.15 µm; diameter: 13.17 µm; number of pores: 24; interpore distance: 2.16-2.77 µm; thickness of exine: 0.677; pore area: 2.99-3.41 µm^2; diameter of pore: 2.036; 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 evident among species of Section *Belanthera*.

S. aucheri - anthers are linear, divergent almost to the middle, terminating in a sessile lanceolate acute pale appendage covered with acute papillae and slightly shorter than anther. Size of pollen grain: 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; 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, accuminate, white, about as long as anther Size of pollen grain: 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* show only punctate spinulose ektexine.

S. sclerantha - stamens with narrowly linear flaments, anthers strongly divergent beyond the middle, terminating in a sessile ovate obtuse appendage. Size of pollen grain: 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 - anthers divergent beyond the middle, terminating in a small ovate obtuse 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 grain: 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 homogeneous group and have a very similar, sometimes indistinguishable pollen morpholoy with the exception of S. micranthera, whose anthers are extremely small.

S. orientalis - stamen filaments long, linear; anthers large divergent to one-third their length. Size of pollen grain varies: 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 ration: 0.09; number of spinules per 100 µm^2: 406-469.

S. laricina – size of pollen grain 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; 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 - size of pollen grain: 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 - size of pollen grain: 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* -** size of pollen grain: 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; C/D value: 0.358, number of spinules per 100 µm^2: 161-238.

YII. Section *Physurus*

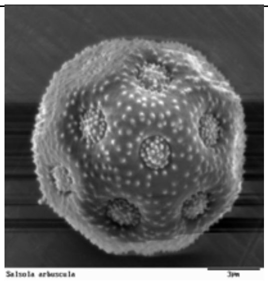
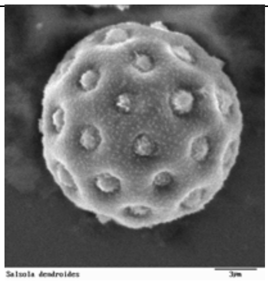
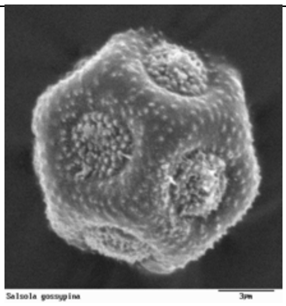
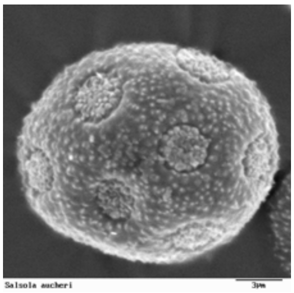
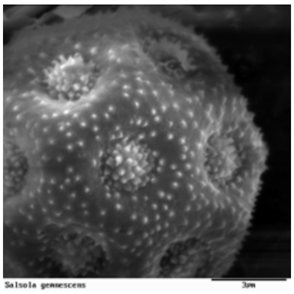
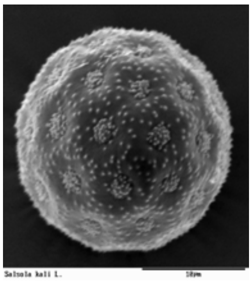
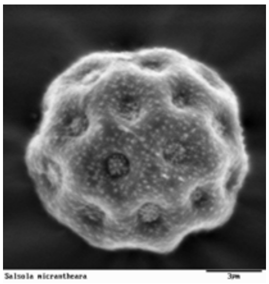
Species of this section are clearly distinguishable from all examined *Salsola* sections by their specific structure and morphology of appendage, very large, almost spherical pollen grains, ca –28-30 µm in diameter, numerous large pores, very thick walls and non-perforate tectum with short, sparsely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

S. lanata – anthers large 3.2-4.0mm oblong-lengthened, free in lower one third, terminating in a bladdery white or large globose or oblong-globular appendage, borne on a short stipe. Pollen size: polar axis: 21.08-25.90 µm; number of pore: 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 ratio 0.260; pore area: 9.26; number of spinules per 100 μm^2: 198-321.

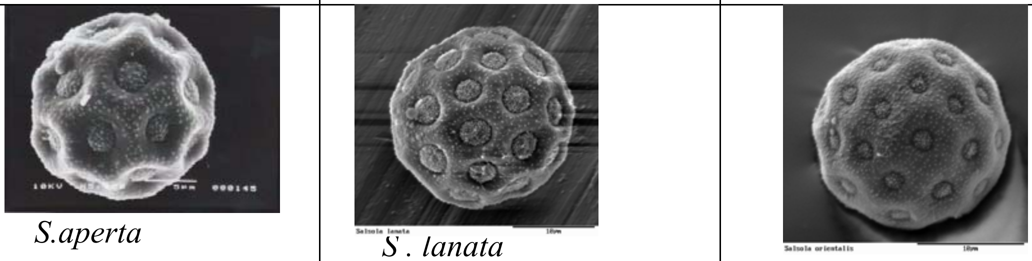
S. crassa – anthers free in lower one third, terminating in a bladdery white or roseate oval rounded appendage, borne on a very short stipe. Pollen size: polar axis 24.45-26.88 µm; diameter 26.72-30.21 µm; pores number: 36-48; interpore distance 2.78-3.13 µm; pore large: 3.13-3.65 µm; pore area: 9.45-13.65 μm^2; flat, prominent sunken with well defined circular outline; exine thickness 1.14-1.52 µm; C/D ratio: 0.233; index form: 0.95; number of spinules per 100 μm^2: 228-245.

***Salsola subaphylla* –** stamen filaments wide, linear, dilated toward base; anthers divergent below the middle, terminating in an absolenscent oblong obtuse, sessile appendage. The pollen of S. subaphylla 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 polyhedrallike shape of mesoporial exine is particular for this species. Operculum is protuberant and uniformly covered by short rounded ovate echinus. Number of pores varies 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 evidently circular are 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.

The palynological characteristics of genus *Salsola* have been analyzed, and values of each quantitative parameter of pollen grain are shown in the micrograph-plates (Figs. 18 and 19)

 *S. pestifer* (Bukhara)	 *S. pestifer* (Samarkand	 *S. arbusculaformis*
 *S .arbuscula*	 *S. dendroides*	 *S. gossypina*
 *S. aucheri*	 *S. gemmascens*	 *S. kali*
 *S. laricina*	 *S. micranthera*	 *S. montana*

S. pachyphylla *S. paletzkiania* *S. ruthenica*



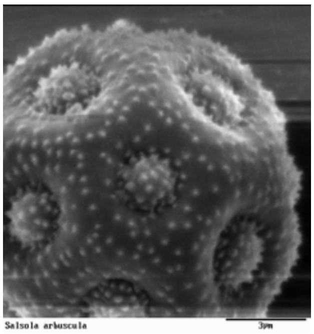
S.aperta *S . lanata* *S. orientalis*

S. carinata *S. crassa* *S. paulsenii*

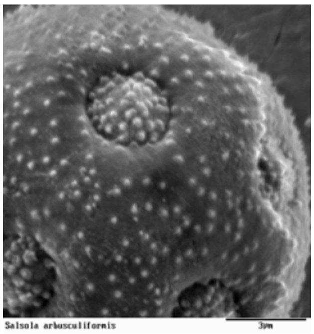
S. leptoclada *S. incanescens* *S. scleranta*

S. subaphyla *S. praecox* *S. richteri*

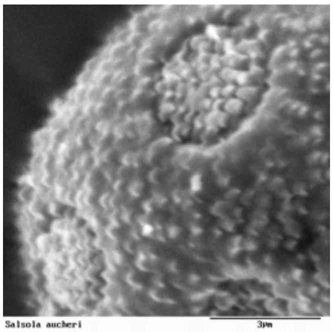
Figure 18. Scanning electron micrographs of pollen grain morphology for some Asiatic *Salsola* species (all magnifications x 5000)



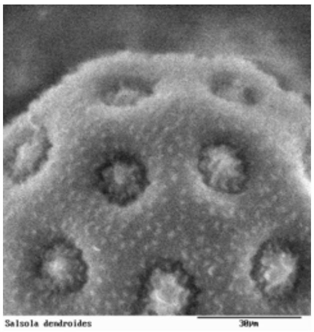
S. arbuscula



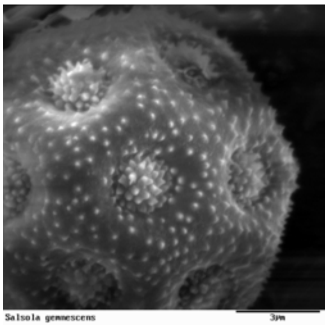
S. arbusculiformis



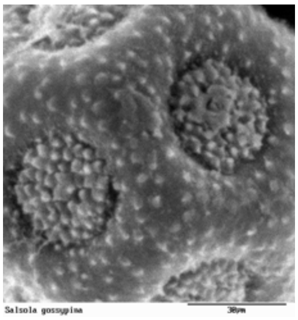
S. aucheri



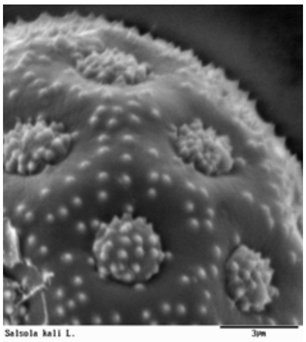
S. dendroides



S. gemmescens

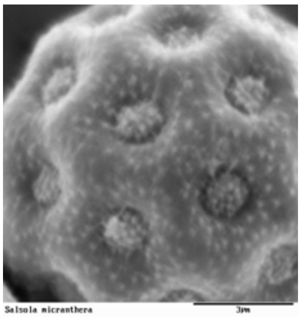


S. gossypina

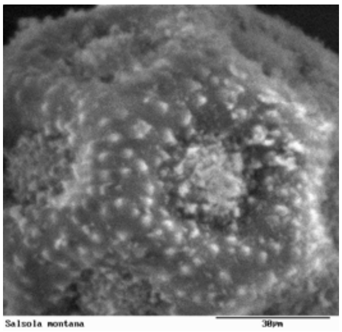


S. kali

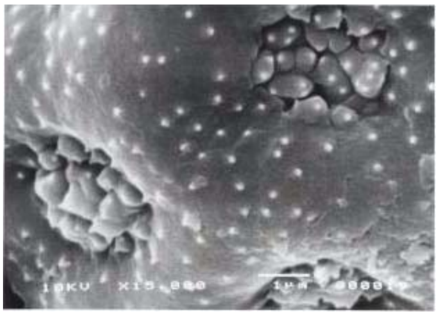
S. laricina



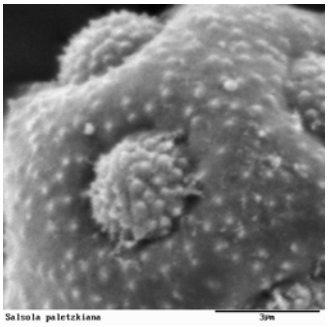
S. micranthera



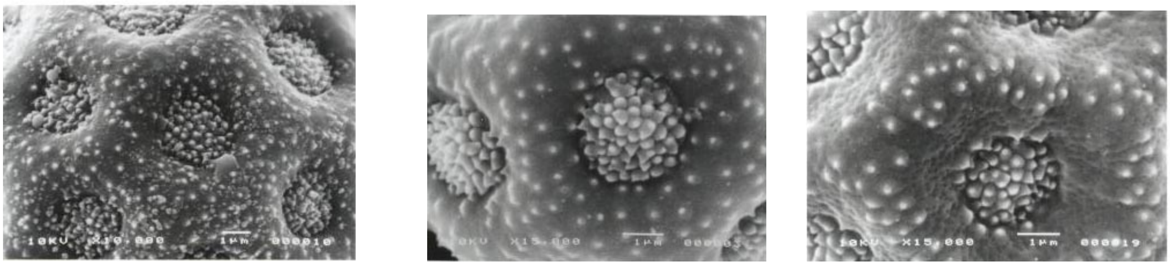
S. montana



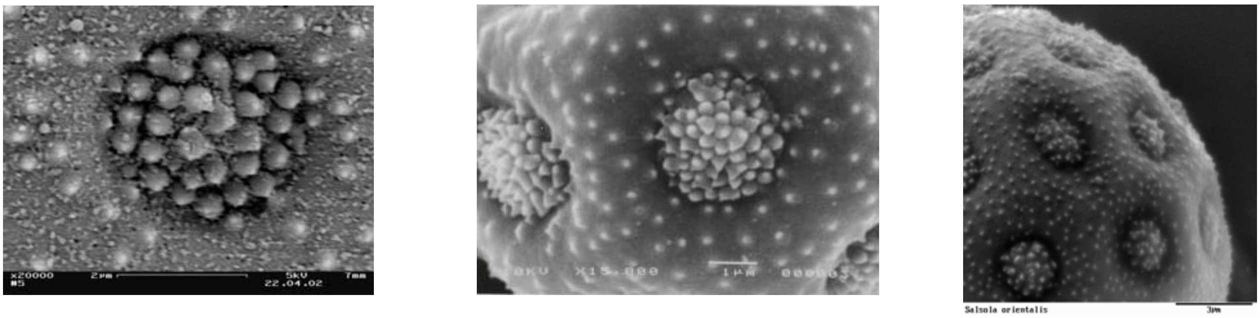
S. pachyphylla



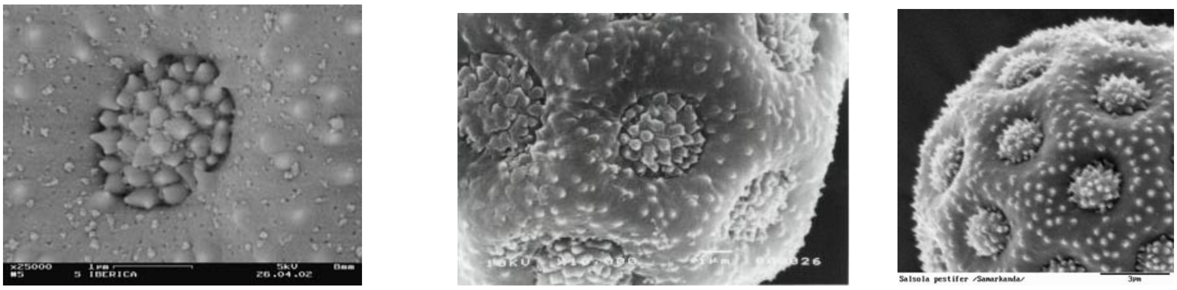
S. paletzkiania



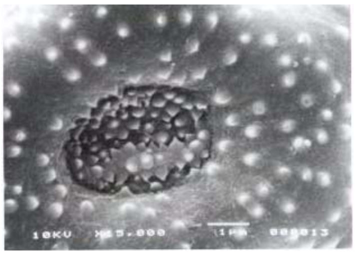
S. paulsenii *S. aperta* *S. carinata*



S. subaphylla *S. orientalis* *S. crassa*



S. iberica *S. richteri* *S. pestifer*



S. lanata

Figure 19. **Scanning microphographs of mesoporial structure in some species of *Salsola***

Diversity statistics and canonical discriminant analysis were used to determine the relationship between different sections of genus *Salsola*. As results, the pallynological study of 28 Asiatic and European *Salsola* taxa has shown that this genus is rather homogenous with a few exceptions.

It was revealed that 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 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. The genus has been divided into three types on the basis of above-mentioned characters. A group of species: *S. orientalis, S. leptoclada, S. ruthenica, S. pestifer, S. paulseni* have large (17.41-20.76 µm) grains with numerous pores (40-58) and lack the convex mezoporialexine; *S. arbuscula, S. arbusculiforms, S. Paletzkiana, less S. gemmascens* are characterized by small size of pollen grains (11.78-16.20 µm) with sunken pores (16-28) and distinctly convex mezoporial exine, while S. *praecox, S. sclerantha and S. leptoclada* are more intermediate in number of pores (30-38) and extexine spinule/punctate density. A less conspicuous link exist between *S. subaphylla* (recently named as *Halothamnus*) and species of section *Physurus*, such as *S. lanata* and *S, crassa* (recently genus *Climacoptera*) all of which have large (3.60-5.04 µm), sunken, well configured pores with densely spinulose aperture membrane. Its pollen morphology differs clearly from the 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 extexine perforations.

Remarkable examples of intraspecific variation in pollen grain morphology have been described for the C/D ratio. This parameter was discovered to be highly specialized supporting the evident delimitation of investigated by us *Salsola* species and appears to be more conservative than some flower and fruit characters (Fig. 20).

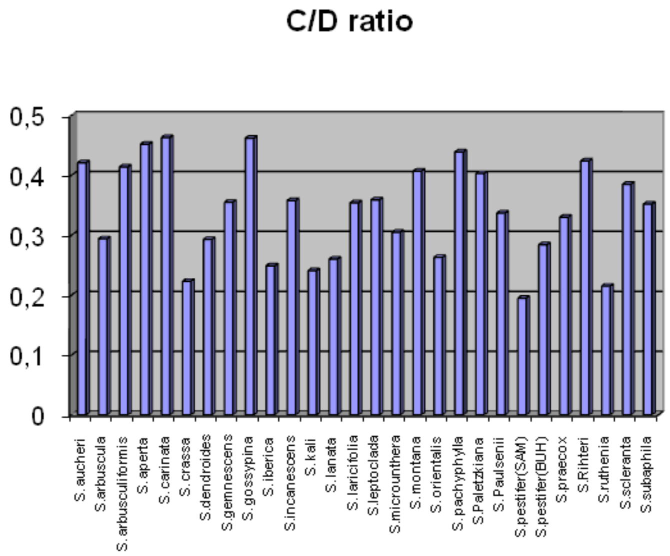


Figure 20. Variability of C/D ration within examined species of *Salsola*

C/D ratio and implied pore numbers as taxonomic traits rest upon their constancy within well-defined species and show a high similarity between closely related species. For instance *S. ruthenica, S. praecox, S. pestifer, S. paulseni* showed a high degree of variability of C/D value (0.065-0.15); the variations may be related with to the complexity and polymorphism of all these species. The similarity of palynological features of *S. ruthenica* with other species of this section supports the relatedness of the Asiatic and European species of Section *Salsola sub. kali. S. arbuscula, S. arbusculiformis, S. Paletzkiana* and *S. richteri* from section *Arbuscula* have high (0.197; 0.233; 0.217; 0.212) C/D values in contrast with other studied species. Thus, the C/D values support with evident grouping of species into separate Sections and appear to be more conservative than some leaf and seed characters.

It was suggested that species with many pores (low mean C/D ratio) tend to have larger pollen grains than species with a few pores, but this relationship does not hold for individual grains, especially for Asiatic desert species. It seems that size and configuration of grain is strongly depending on the influence of harsh desert climate conditions.

Representatives of genera *Salsola* like many others members of Chenopodiaceae have the spinulose and punctate tectum, but the perforations are very small and sparsely distributed. *S. laricina* and *S. dendroides* from section *Caroxylon* showed an evident number of spiniles on the mesoporia area of pollen grain (Fig.21)

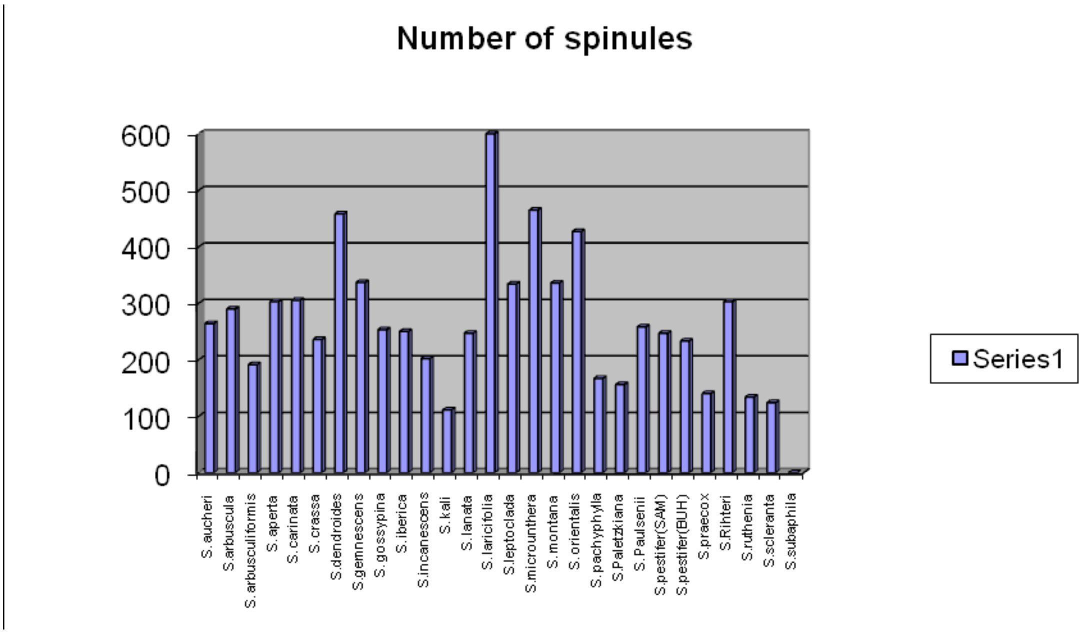


Figure 21. Variation of number of spinules on the exine surface of pollen grain

Within the taxa examined, the pollen grains from sections *Salsola* and *Caroxylon* have pores, which are small, numerous, not sunken. In addition species of Section *Salsola* and in particular *S. iberica, S. ruthenica, S. kali subs. tragus, S. pestifer and S. paulseni* are characterized by the very similar, sometimes indistinguishable pollen grain morphology**.**

Based on above mentioned pallynological characters and as is shown in Figs. 22 and 23 two pollen groups are distinguished within genus *Salsola*:

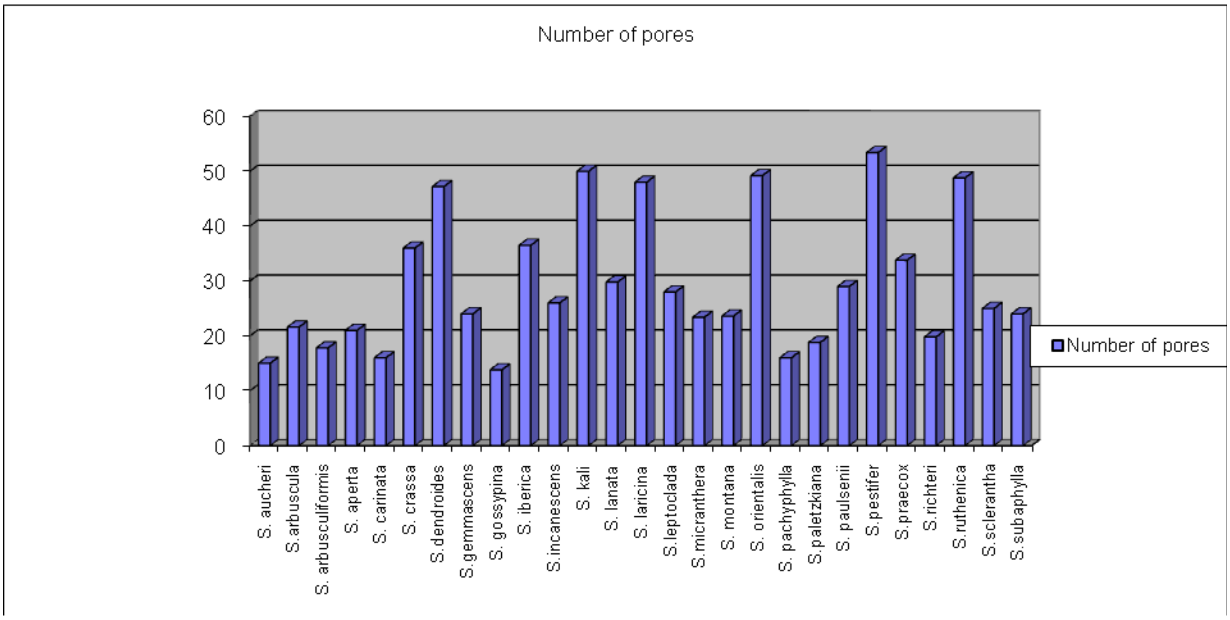


Figure 22. Variation of number of pores in *Salsola* genus

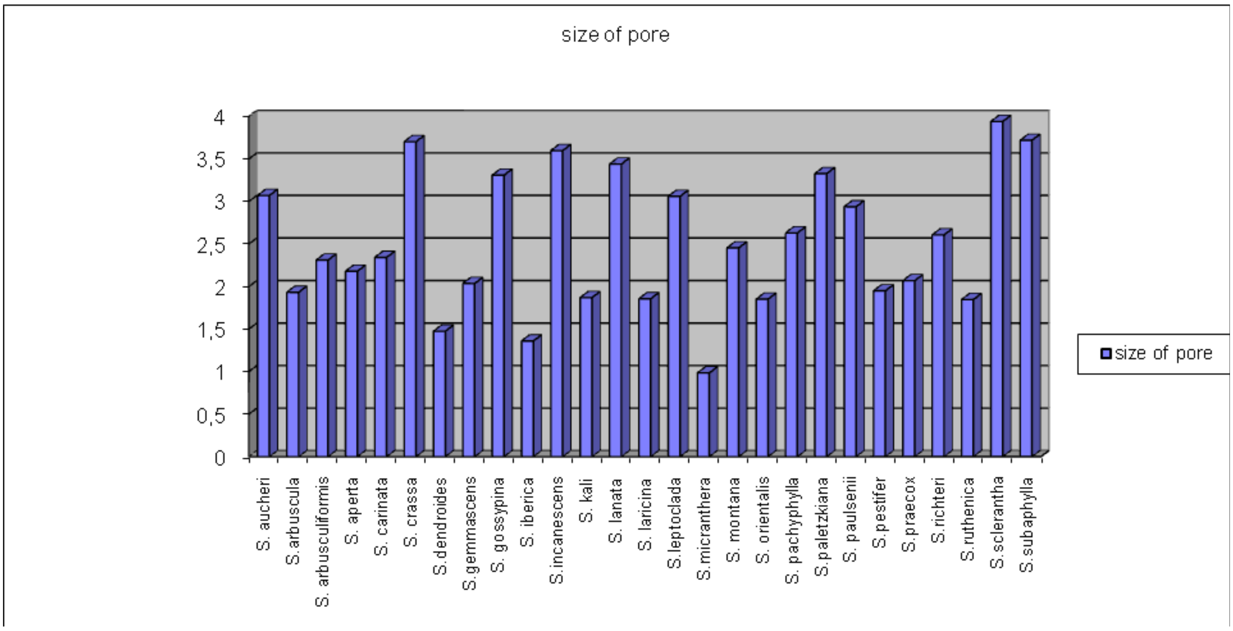


Figure 23. Range of variation of size of pore in some species of *Salsola*

I – species with numerous small pores *(S. pestifer, S.dendroides, S.kali, S.laricina, S.ruthenica, S. orientalis, S.praecox ., S.paulsenii, S. ruthenica, S. kali)*

II – species with a few larger, slightly sunken pores, which in combination produce a polyhedrallike shape *(S. aucheri, S. crassa, S. gossypina, S. incanescens, S. lanata,* and lesser *S. Paletzkian* and *S. aperta).*

The following species like *S. arbuscula*, *S. arbusculiformis, S. carinata, S. gemmascens, S. iberica, S. leptoclada, S. micranthera, S. montana, S. pachyphylla, S. rihteri, S. scleranta* and *S. subaphylla* takes an intermediate position. The informative quantitative parameter of pollen grain, which indicates shape variability, is the index form that comprises the numerical value by the ratio between the length of polar axis and diameter (P/E). The palynological results represented in this study show that the pollen grains of examined species are radial symmetrical, isopolar, pantopolyporate, spherical or subspheroid. Although such definition is rather arbitrarily based on quantitative characters, clustering groups and ordination (data not shown) analyses of species from different Sections/subsections within genus *Salsola* indicate that overall pollen traits (features) almost reflect current taxonomic boundaries. So, most species that belong to the same section are grouped together. This is the case for woody-shrubby species of subsection *Arbuscula* of section *Coccosalsola,* which form a taxonomically separate monotypic subsection Arbuscula, section *Coccosalsola* and species of section

Physurus, recently separated as *Climacoptera*. The cluster analysis illustrated in Fig.24 defines two subgroups, in which annual herbaceous Asiatic species and European taxa from section *Salsola sub. Kali* (Ulbrich) are predominantly grouped together. However other species of section *Salsola* are partitioned in both clusters, and S.aperta and S. paulsenii, which typically belong to taxa of section *Salsola.*subs. *Kali* are included with species of section *Arbuscula* and *Belanthera*.

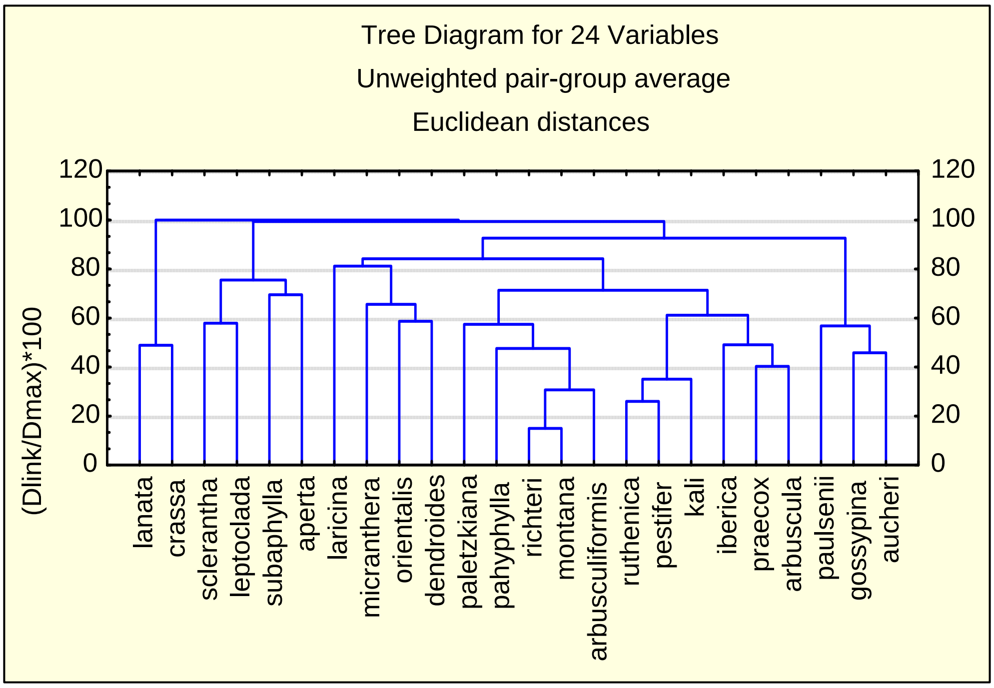


Figure 24. The dendrogram based on palynological distance data showing the relationship among 21 Asiatic species of genus *Salsola*

Euclidean distance was used to compute the disimilarity matrix, and the tree was made. Discriminate analysis based on pollen characters variations has shown an evident delimitation of species of section *Physurus* into the separate genus *Climacoptera.* Our pallinological and ultrastructural studies of pollen grain for various groups of *Salsola* confirmed that the identification of genus *Climacoptera* from *Salsola* done by Botschantzev, 1969 and Pratov, 1986 is well founded. Discriminate analysis based on pollen characters variations has provided convincing separation of species of section *Physurus.*

The genus Salsola comprises species with either punctuate, perforate or smooth non-perforate tectum pollen type as a case of *S. subaphylla*; 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* (Caryophylaceae) done by Ghazanfar, 1984.

On the dendrogram examined above the tax are arranged according to the trends from finely to coarsely tubuliferous/punctate extexine sculpture: uniformity or differentiation of sculpture. The punctate type is most clearly defined. Examination of pollen exine from the various species of *Salsola* (Chenopodiaceae), although highly limited, provides a more comprehensive knowledge of the pollen morphology and its contribution to a better understanding of the reletionships within genus *Salsola* and different representatives of the order Centrospermae as well.

In a general sense**,** all of the 28 species examined have basically similar ultrastructural pollen morphology. And it would seem that they form a rather natural genus. Although the pollen morphology of the *Salsola* species tends to be of a rather uniform type, a number of general evolutionary trends are evident within the genus *Salsola*. Scanning electron micrographs from each investigated species from different sections 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/O ration, distance of interpores, and echinus number on pore membranes and verruca number on mesoporial exine appeared to play an important diagnostic significance.

As noted previously, evolutionary trends in masoporial exine and pore membrane sculpture condition is somewhat unclear. Within the genus *Salsola* this character range from absent (as a case of *Halothamnus subaphyllus* or weakly developed to structurally complex. The majority of species have well distinguished spinules and minute tectal perforations. The latter are rather poorly differentiated and can be observed only at high magnification (more x 10.000). The transformation in the sculptural patterns that are well developed for different *Salsola* sections appears to be a distinct specialization within genus *Salsola.* The pollen grains of *S. lanata* and *S. crassa* may represent a trend in reduction of number of collumellae and an increase in the size or number of pores.

The derivation of reticulate ektexine from punctate ektexine and the association of reticulate ektexines with sporophytically advanced taxa are suggested. Besides that the pollen morphology of *S. aperta* from the section *Salsola* subs. *Kali* suggests inclusion of this species, probably, into the section *Cardiandra.*

From this point of view *Salsola* species palynologically 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 to the type *Amaranthus* from Amaranthaceae (Tsukada, 1967; Uotila, 1974; Skvarla and Nowicke, 1976; Chung, 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 pecualirity is clearly evident in *Salsola* with the pollen of S. *lanata* and *S. crassa.* *Salsola* pollen, comparatively large for the family, tends to occasionally have thicker exine than any other centrospermous representatives. However, the exine of pollen grain in species of sect. *Physurus* has not significantly increased in thickness of tectum and foot layer despite a very conspicuous increase in grain size. Many authors noted that there is a correlation between length of the polar and equatorial axes and size of the flower; the largest grain being found along with most members of section *Physyrus*, *Cardiandra* and with separately delimited *S. subaphyllus* (regarding as *Halothamnus subaphyllus)* that have some of the largest flowers in the genus.

Trends related to sculpturing are all derived by modifications of the basic uniformly reticulate/tectate condition. By the profound analysis of 24 *Salsola* species we found that representatives of species *Salsola* section *Physurus* (recently *Climacoptera*) and *S. subaphyllus* (recently *Halothamnus*) are well distinctive in both the genus and family and clearly represents a unique specialization (Freitag et al. 1986 and Kothe-Heinrich, 1991). However, as prudently elucidated by Turner and Heywood (cited in Mabry, 1973), phyletic relationships rather than taxonomic are of major significance. In this respect we can briefly summarize our results by emphasizing that exine with the spinulose and tubuliferous/ punctate surface pattern were structurally very similar between all examined taxa and with other representatives of Centrospermae and indicate a close phylogenetic association. Obviously, 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 the majority of representatives of order Centrospermae contain pollen with reduced endexine.

A presumed reduction of the reticulum dimensions has resulted in very finely reticulate to tectate-perforate grains in species of *Salsola*. Pollen grain of *Salsola* is clearly the most distinct in the family and seemingly has evolved along a line of evolution removed from the rest of the family. The essentially spherical, moderately small, pantoporate is regarded as a primitive condition for the family. Not only is this much generalized pollen type widespread in Chenopodiaceae, it is a basic type in dicotyledons as a whole. The widespread occurrence, both taxonomically and geographically of the pantoporate pollen grain type through all families of Centrospermae, which is often characterized by a rather simple reticulate/or punctate exine sculpture suggests that this is the basic type in the order of Centrospermae.

Major evolutionary advancement within the family were observed in:

- changes in outline and shape from spherical or subspherical to oblate; reduction in number of pores; increase in grain size ; change in sculpturing to various modifications of tectum and presumed reduction to very finely reticulate and tectate perforate (this type in Salsola comprises an advancing character). Many of the above-indicated specializations can be correlated with advancements in other groups of flowering species of plants. Similar morphologic trends have been described in others families of dicotyledons (Van Campo, 1966), including also the closely related family Amaranthaceae (Riollet and Bonnefille, 1976; Ugrorogho and Oyelana., 1992) with Caryophyllaceae (Ghazanfar, 1984);

- the formation of well-developed and structurally more complex endoaperrtures 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 not related genera;
- change in pollen grain outline from circular to semiangular has occurred independently in a number of chenopods genera and other representatives of Centrospermae. For example many species of genera *Salsola* represent a concomitant change in grain shape from nearly spherical to slightly varying degrees of oblateness;

The evolution within the *Salsola* groups has probably started from the basic types, which are both characterized by a smooth to finely reticulate uniform sculpture. The main trends develop from this basic one, leading to increased differentiation that couple of species with increase in coarseness of the reticulate sculpture on the mesocolpia; the other leading trends lead to the uniform increasing in coarseness of the reticulate sculpture over the whole pollen grain surface. It is of interest that the basic core comprises most genera, while the specialized types are mostly restricted to *S. subaphyllus* (revised as *Aellenia* or *Halothamnus*), as well to one section (*Physurus*). It also obvious that the evolutionary trends in *Salsola* genus and Chenopodiaceae family related to other Centrospermae families have developed parallel. The evolutionary sequence of *Salsola* pollen types thus appears much more completely preserved in Chenopodiaceae limit than in Amaranthaceae and Caryophyllaceae families in which many isolated and strongly specialized types are found (Barthold , 1998).

3.4. Ovule morphology, peculiarities of megasporogametophytogenesis and development of embryo sac

As results of our investigation it was defined that for the all examined *Salsola* species the female floral structures and their ontogeny are similar to those of S. *orientalis* in all essential details. Therefore *S. orientalis* has been taken as a model species. Differences between species are marked only in form, size of mature ovule and embryo sac.

A single ana-campylotropous crasinucellate ovule is attached laterally to the ovary wall by a short (or long) funiculus resting against the micropile. The young ovule is straight (anathropous), but with the appearance of integuments it curves and becomes campylotropus. Finally, the ovule twists about its own funiculus and comes to lie horizontally in the cavity of the ovary. At this moment multiple archesporium (consisting mostly from 6-8 archaesporial cells) are well visible in the nucellus. Each integument consists initially of two cells layers, except near chalaza where they are more numerous; but in mature seed coat, only a few remain, since the outermost layer of the inner integument disintegrates during the development of the seed. The cells of the outer integument are at first undifferentiated, but later the outer wall becomes thickened and is covered with an extensive cuticle.

The layers of the inner integument are at first meristematic; but as maturation of the seeds proceeds, the outer layer remains small, the nuclei disintegrate and the cells are obliterated. A thick cuticle is laid down between the inner integument and the nucellus that according to Esau, 1966 may be recognized by microchemical test when the embryo consists of approximately nine cells. It was suggested that the cuticle is lacking in the chalazal region where the phloem approaches the embryo sac, so that a "passage region" is formed through which materials can move into the latter. When the seed has reached maturity, the walls of the cells in this zone also become cutinized or suberized, sealing the embryo. It was defined by our investigation that for the all examined *Salsola* species the female floral structures during ontogenesis are similar to those of *S. orientalis.* Therefore we will describe the regularity of megaspogametophytogenesis and embryo sac development for *S. orientalis,* and sometimes using data for *S. arbuscula* and *S. sclerantha* taken them as a model species. Results are shown in the Figs 25 and 26.

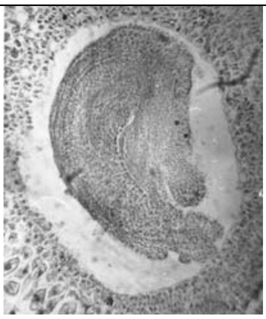
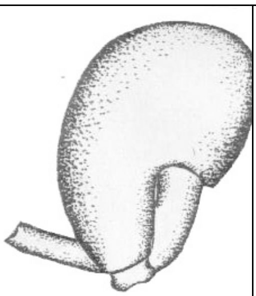
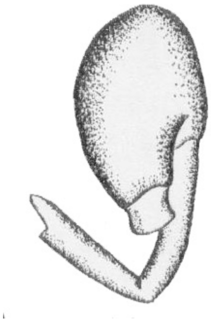
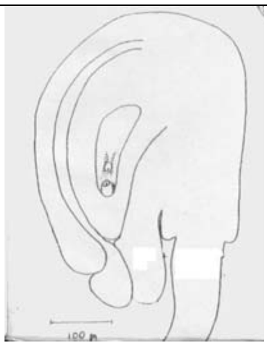
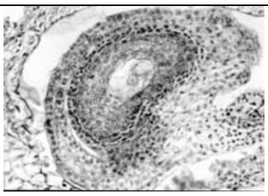
S. arbusculiformis		No data		
S. arbuscula				
S. richteri		No data	No data	
S. aperta		No data	No data	No data
S. sclerantha				No data

Figure 25. Diversity of ovary and ovule morphology for some *Salsola* species

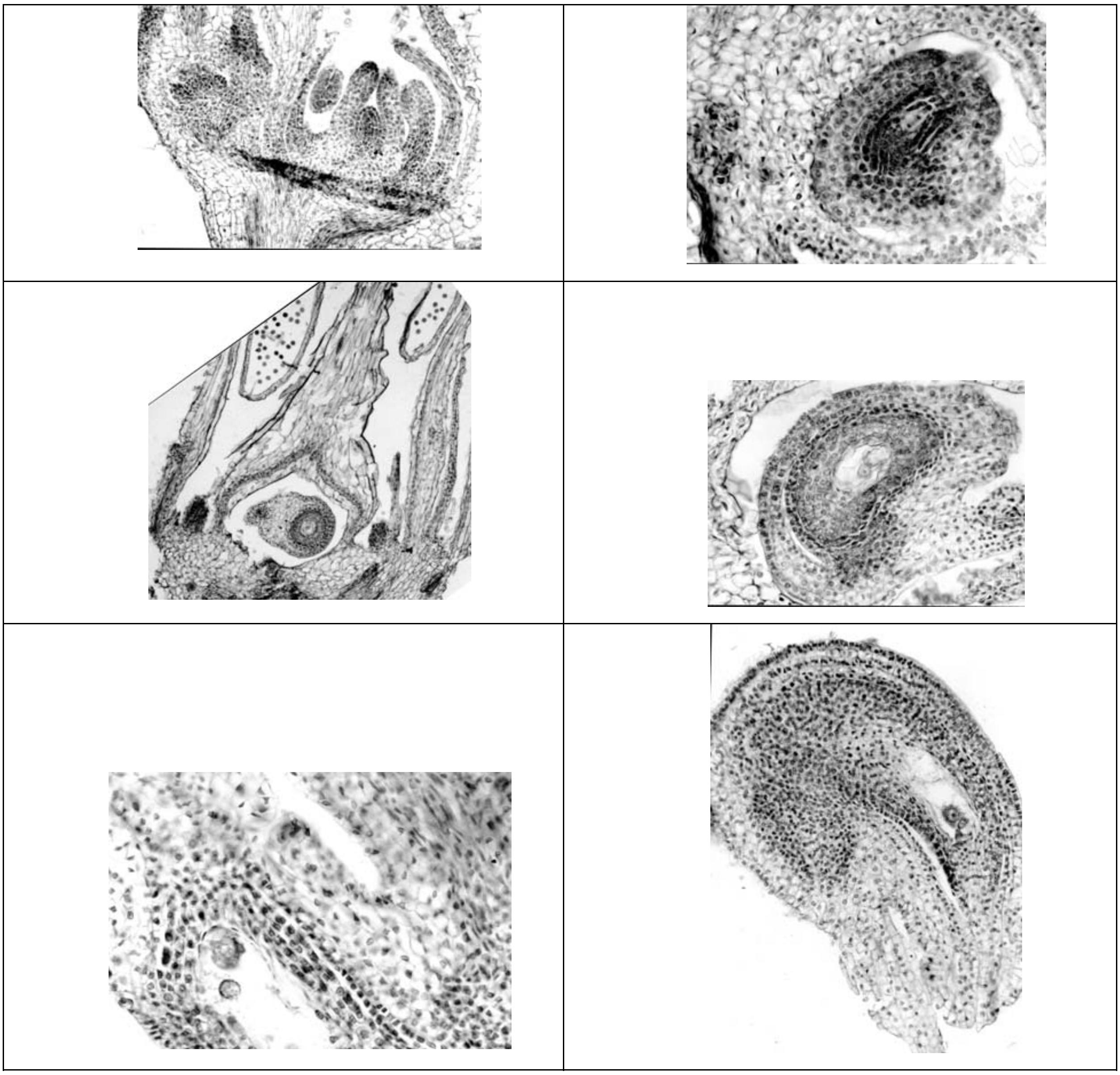


Figure 26. Regularities of megasporogenesis and embryo sac development for some Asiatic species of genus *Salsola (S.sclerantha* as particular case)

Features of high specialization have been noted in the structure of ovule of annual *Salsola* like *S. aperta, S. paulsenii, S. praecox, S. pestifer, S. iberica.* The ovary in all these species is greatly compressed with unusually long and curved funiculus that is deeply inserted into receptacle towards vascular bundle. Ovule is ana-campylotropous with slightly curved nucellus. A characteristic feature in ovule morphology of *Salsola* representatives is the presence to some extent of well developed nucellar cap of an epidermal origin and the parietal tissue.

Micropyle part consist of 8-12 rowed cells, chalazal is more massive that embryo sac is dislocated at 1/3 of ovule. Integuments have 4 layers that afterwards are differentiated into the seed coat. Embryo sac is narrow, elongated and allocated in the middle part of nucellus.

We found out that the development of archaesporial tissues in ovule and anther goes asynchronously. While in the ovule occurs the differentiation of mascosporangium, in anther meiosis already begins meiosis (bud of 2, 3 mm in size). Further in buds of 3, 3 mm we see already mature pollen, but its growth proceeds. At the same time the development of embryo sac is observed in the ovule. The development of embryo sac in the case of *S. richteri* goes quickly, and in buds 4mm in height, we have found a mature embryo sac, and in anthers - mature pollen.

Multiple archesporium cells function directly cells producing tetrads of megaspores. In most instances, only a single chalazal megaspore of the tetrads develops to form a mature megagametophyte; for *S. orientalis, S. arbusculiformis,* rarely *S. arbuscula* an ovule may content two well developed gametophytes (embryo sac). The development of embryo sac in all *Salsola* species goes according Polygonum type (Konycheva, 1983).

The mature embryo sac both in woody and annual species of *Salsola* consists of egg cell with characteristic vacuolization, two sinergids and two closely located to each other polar nuclei. Three T-shaped antipodes are localized in the lower part of the embryo sac. Already at this stage in antipodes traces of cell content degeneration are marked, and in day of flowering antipodes in the embryo sac are absent. The mature embryo sac is poor in cytoplasm that settles down around of polar nucleus, by thin stream is sometimes connected to the membrane of embryo sac.

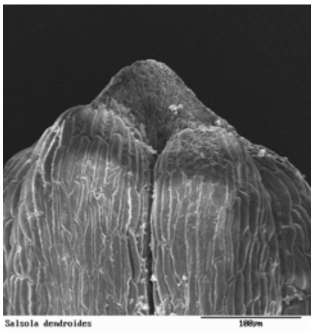
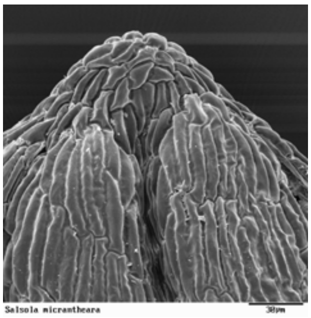
Our embryological studies of ovules from flowers before anther's anthesis usually showed the presence of egg and secondary nucleus of embryo sac or seldom two polar nuclei before its fusion. There were cases when two embryo sacs both containing well differentiated eggs and secondary nucleus are found. Thus, the lack of pictures of the double fertilization once again confirms by our and Bochantseva, 1969 hypothesis about double fertilization,which occurs after anther dehiscence and pollen dispersion from anthers of the flower on own stygmas. Polar nucleus fusion occurs before fertilisation, forming a secondary nucleus in the beginning with 2 nucleoles. In the mature embryo sac between egg and the secondary nucleus a distinct split is well visible.

In 70 % of the investigated ovules of *S. orientalis, S. arbusculiformis,* rarely in *S. arbuscula, S. paulsenii* the simultaneous development of two embryo sacs has been observed. For the first time we investigated the embryological features typically for apomixis (asexual type of reproduction) in genus *Salsola*. The distinctive apomictic features are: un- bi- or multi-nucleate aposporous embryo sac, the occurrence of several embryo sacs of the same or various age within the ovule, embryo sac with additional egg cells, embryo sac with nuclei of various sizes, presence of two or more embryo originating from different embryo sacs of an ovule, the development of adventitous embryo, especially from nucellar cells. Widely widespread within *Salsola* species nucellar embryony testifies to the higher variability of some parameters within the genus, and probably about its phylogenic youthfulness in comparison with other genus of the Chenopodiaceae family.

We consider that some representatives of genus *Salsola* can be considered as facultative apomictics, which would be strictly connected with the influence of extreme conditions of the desert, and might play an adaptative role for the reproduction and survival of plants under harsh environments.

3.5. Floral morphology and taxonomic relations among species of genera *Salsola*

The flowers are solitary on axillary bracts or in clusters of two-three in loose spikes. Unequal leaf-like bracts subtended bisexual, pentamerous, actinomorphic flowers. The sexual condition appears to be unstable for Asiatic *Salsola* complex. Frequently, flowers, which seem to be potentially bisexual when young, sometimes suppress the development of one of the sexes during subsequent development. Structural characters of androecium and gynoecium are fundamental in the recognition of genera *Salsola* within Chenopodiaceae family. The examined species have five, rarely 4 stamens, usually incurved in bud, with the filaments free (connate, wide to the base), arising from receptacle or saucer-shaped with ovoid lobes, covered by short papillae (*S. richteri, S. arbuscula)* or glabrous, rarely with short hairs (*S. Paletzkiana*) hypoginous disk. The anthers are large (2.9-3.8 mm –*S. paletzkiana*; 1,7-2.8 *S. richteri*; 2,4-2.8 mm *S. arbuscula, S. arbusculiformis, species of section* Cardiandra and Physurus) or small *(S. micranthera, S. aucheri, S. dendroides*), usually 4 sporangiate and 2 locular at anthesis, basifixed or dorsifixed almost at the middle, opening usually introrse, by 2 longitudinal slits, sometimes with a large appendage (0.2-0.5 mm *S. richteri, S. arbuscula*, 0.4-0.8 *S. arbusculiformis* and 0.7-0.9 mm *S. paletzkiana, S. lanata, S. sclerantha*), narrowly lanceolate or oblong ovate, sharp pointed (*S. Paletzkiana*, *S. richteri*), blunted at the apex (*S. aperta*), inflated short appendage (as for species of *Climacoptera*) or without appendage *(S. paulsenii)*. The springy-like mechanism of portioned dispersion of pollen, detected during the study, is owing to the well–developed fibrous thickening in the endothecium and connective cells. The development of fibrous thickening in the connective cells of anthers is an unusual feature for arid plants (Toderich, et al. 1995; Toderich et al. 2004). This adaptive floral mechanism in combination with the introrse anther's dehiscence by means of longitudinal slits greatly facilitates anemophily. However, in most flowers of *S. arbusculiformis, S. paulsenii, rarely S. sclerantha* anthers dehiscens synchronously promoting autogamy (selfing). There are differences in flowering periods: S. paulsenii (from May to June), *S. richteri*, *S. arbusculiformis, S. orientalis,* (from May to September), *S. Paletzkiana* (from June to September) and species of *Climacoptera* (former *Salsola*) which has a rapid daily (usually early morning time) flowering process and accelerated differentiation of pollen grains (from the base of the anthers to its tips), a faster germination on the stigma surface. But these differences were interpreted as reflecting variations rather than major differences of blooming/pollination systems. Flower morphology and diversity of stigma for examined Asiatic species of genus *Salsola* are shown in the Figs 27, 28.

 *S. dendroides*: a-c) small flower;	 b) stigma surface;	 c) appendage of anther
 *S. micranthera*: a-c) flower during blooming stage	 b) morphology of stigmas;	 c) anther's appendage

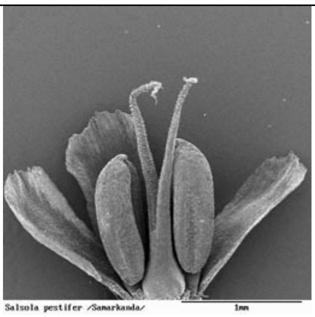
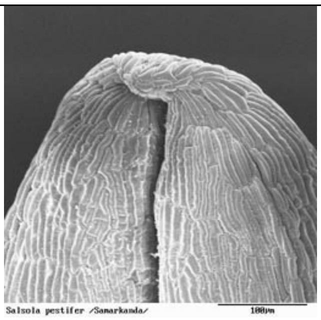
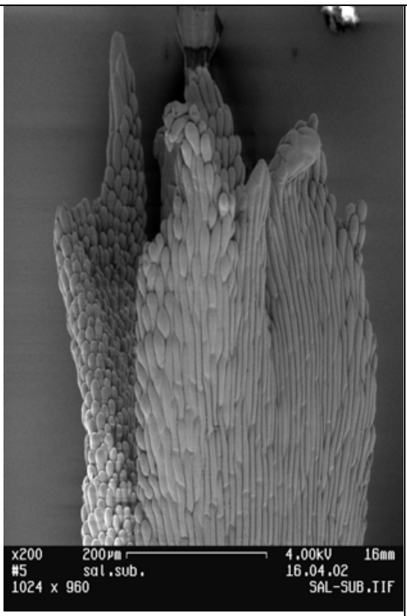
 *S. pestifer* (Kyzylkum desert ecotype): a-f - different stages of flower organs development; a) during blooming stage	 b) before anthers anthesis	 c) morphology of mature anther
 d-f – *S. pestifer* semidesert ecotype:d) papillae morphology of stygmas	 e) style and stigmas	 f) small appendage of anther;

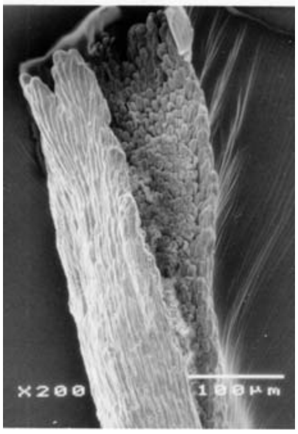
Figure 27. Polymorphism of flower organs for some species of *Salsola*

S.subaphyllus



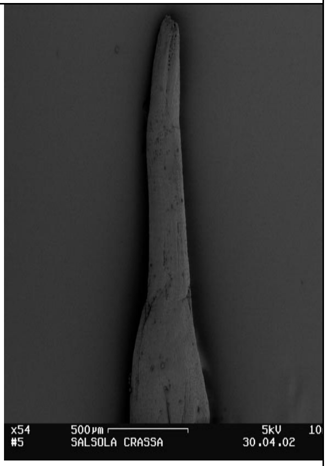
S.subaphyllus

S.arbusculiformis



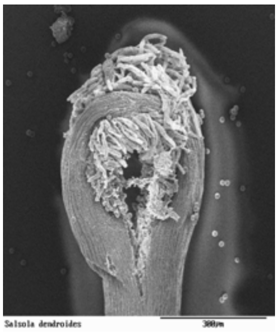
S.carinata

S. lanata



S.crassa

S. incanescens



S.dendroides

S. micranthera

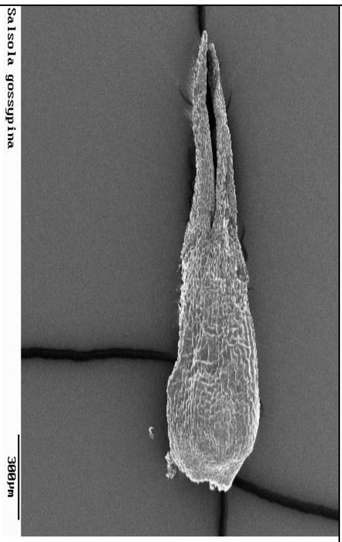
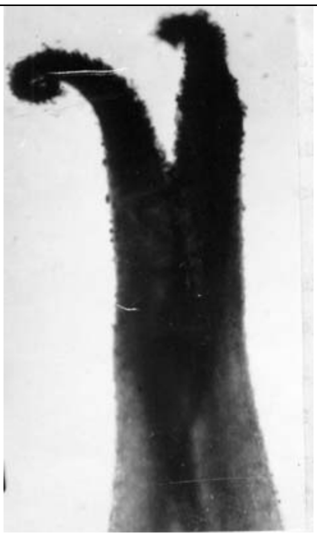
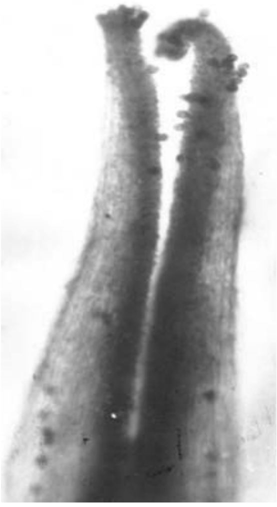
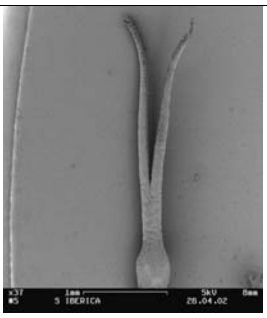
 *S.gossypina*	 *S.arbuscula*	 *S.aperta*
 *S.paulsenii:*a-c) stygma morphology on different stage of ontogenesis; a) before flowering process	 b) linear style with small papillae during blooming	 c) mature stygma with differentiated papillae

Figure 28. Diversity of stigma morphology at the stage of flower maturity for some *Salsola* species

Common adaptive traits of reproductive structures and processes directed to successful seed development are characterized for the majority of investigated species. This is evidently shown as distinct sex expression of floral organs (homogamous, ptoroandroecious and protogynoecious) within one individual bush, thus providing high plasticity of the pollination process that further ensure a potential possibility for seed formation. Our observation on pollination process of both shrubby perennial and annual *Salsola* species strongly support the concept of Knuth, 1909; Konycheva 1983; Blackwell et al., 1981 about that self-fertilization including both autogamy (within-flower), geitenogamy (between flower) and cleistogamy (fertilized in closed flower) which occurs as result of anemophily, is likely to provide reproductive success in the majority of desert chenopods. We found also that woody and a few annual *Salsola* species have an evolutionary tendency to cross-pollinate (xenogamy) despite the lack of pronounced, specialized flower organs. This is mainly expressed in a simultaneous development of different sexual types of flowers and a difference in the longevity of pollen grain and embryo sac maturation within individual bushes. For instance, for *S. richteri*, *S. Paletzkiana*, *S. orientalis, S. laricina, S dendroides* this is marked by the faster maturation of the male (dehiscence and anthesis of anthers takes only 30-60 minutes) compared to the female generative stage duration (stygmas stay viable for a day or more).

An evident morphological and structural similarity of reproductive organs is noted between *S. pestifer* (Kyzylkum desert environments), *S. pestifer* (semidesert ecotype) and *S. ruthenica (Iljin.),* the last of which is widespread in Western Europe. Glabrous stems and leaves separate these two species: linear, semi-terete to almost terete, at base dilated, sheathing, apex spine-tipped. Flowers of these species are solitary, bisexual, usually prothoandrous, sometimes at base of lower branches in addition and highly condensed lateral spikes. Flowering and fruiting stages: June-October. Anthers oblong, divided for 1/3-1/2, appendage minute or small, narrowed to the base. Ovary subglobular with ana-campylotropous, crassinucellate, bitegmic ovule, style thin, stigmas filiform. *S. ruthenica, S.praecox, S. pestifer, S. paulseni* showed high degree of variability or C/D (the distance between two pores to the diameter of pollen grain) value (0.065-0.15); the variations may relate the complexity and polymorphism of all these species. The similarity of palynological features of *S. ruthenica* with *S. pestifer*, and less *S. praecox* undertakes the relationship of the Asiatic and European species.

Common adaptive traits of reproductive structures and processes directed to successful seed development characterize all three of these species. This is evidently shown as distinct sex expression of floral organs (homogamous, ptoroandroecious and protogynoecious) within one individual bush, thus providing high plasticity of pollination process that further ensure a potential possibility for seed formation. Our observations of the pollination of shrubby *Salsola* species strongly support the conception of Knuth, 1909; Konycheva, 1983 and Blackwell et al., 1981 who suggested that self-fertilization, including both autogamy (within-flower), geitenogamy (between flower) and cleistogamy (fertilized in closed flower) that occurs as result of anemophily, is likely to provide reproductive success in the majority species of desert chenopods. Besides we found also that woody *Salsola* species have an evolutionary tendency to cross-pollination despite the lack of pronounced, specialized flower organs. This is mainly expressed in a simultaneous development of different sexual types of flowers and a difference in the longevity of pollen grain and embryo sac maturation within individual bushes. For instance, for *S. richteri* and *S. paletzkiana*, this is marked by the faster maturation of male (dehiscence and anthesis of anthers takes only 30-60 minutes) compared to female generative stage duration (stygmas stay viable for a day). This provides a good opportunity for cross-pollination and for an alternative way to develop normal seeds under harsh desert conditions. Protogyny (presenting receptive stigmas to receive outcross pollen before self-pollen is shed from anthers) is a very common adaptive floral trait for *Salsola* species that is viewed as self delayed mechanisms. A somewhat unusual feature may prove to be that relatively large, colorful anthers (bright yellow anthers, excerted from a small perianth as has marked for *S. paletzkiana* and S. *richteri*) serve as a primary (or sole) insect attractant. Insect visitations, especially bees from genera *Halictus* (Demyanova, 1974) have been observed in several instances, which also suggest that there is opportunity for cross-pollination in these perennial shrubby species. Some flowers of *S.arbuscula* contain a surprising amount of nectar that could furnish meaningful correlation with an apparent mode of ant pollination. However, the entomophyly is of very little importance. In *S. arbusculiformis* towards the end of flowering, autogamy becomes more significant owing to the timing of the development of homogamous flowers with subulate, flat densely papilloid stygmas. For *S. arbusculiformis* autogamy (self-fertilization) seems strongly advantageous to ensure the autonomous production of self-seed production. This kind of self-pollination strategy in this taxon is enforced by additional characters such as stamen filaments, short and gradually enlarged at the base relatively little pollen per flower, small number of open flowers per day, small sizes of anthers and their synchronous dehiscence inside of flowers.

According to Demyanova, 1974 and Konycheva, 1976 and our observations the flower of *S.orientalis* is strongly protogynous. The maturity of female generative organs happens 6-7 days earlier than the male. High stigma receptivity to pollen of neighbouring flowers occurs at 1-2 days before antesis. The well-developed nectarinous disk is marked at the basis of ovary. Mature ovule at *S. orientalis* is ana-campilotropous with micropile, oriented to the lateral side of ovary. Embryo sac elongated, slightly curved along nucellus. Antipods are absent in the mature embryo sac. In many ovules 2, rarely 3 embryo sacs at the different stage of development are revealed. Some of these embryo sacs subsequently are developed into the well-differentiated embryos. Seeds with 2 embryos at *S. orientalis* make about 5-8%.

CHAPTER 4. Processes of flowering, ecology of pollination, fertilization, embryo development and their adaptive significance

As the extensive literature on evolution of flowering plants showsed that under unfavorable/stressful environmental conditions the ksenogamy, the autogamy pollination are carried out separately or in combination. It is well known that autogamy is contributing to the preservation of the arising of new forms providing by providing their fast multiplication and recilience.. The flower, being a plastic organ, promotes survival of the fittest plants under harsh xerotermic conditions and determines the evolutionary development trends of the species. The most primitive way of pollination is considered enthomophyly (by insects); however other ways are progressive and have been developed as a result of changes of flower development and its adaptation to the harsh desert environments.

The ecology of flowering and pollination of the representatives of Chenopodiaceae family it is still the subject of special research because of the variety of ways, inconsistency and contradictory of the literature data (Romell, 1919; Iljin, 1937; Botszantzev, 1948; Bespalova, 1961; Demyanova, 1974; Konycheva, 1983 and Toderich, 2000) still exists. Different types of pollination, autogamy, xenogamy and geitenogamy, were described for the representatives of Chenopodiaceae . Flowering process of *Salsola* members occurs at the meso-and xerothermal periods of year. In the literature there are two points of view concerned biology and ecology of the flowering processes in the Chenopodiaceae. The majority of authors consider that the dispersion of pollen within the family representatives is carried out through the wind, and the pollination by insects is not characteristic for chenopods. Confirming this point of view is the presence of fine ordinary-looking flowers assembled in a spiky-paniculate inflorescence. These flowers are without nectar or smell. Other authors consider that enthomophyly is the prevailing factor during pollination of Chenopodiaceae. In confirmation of the suggested opinion we would like to note the following:

1. slightly free loose pollen grain
2. the absence of slender and flexible stamen filaments.
3. lacking of mass and simultaneous flower dehiscence.

Lastly there is an opinion that in *Beta vulgare* (Chenopodiaceae), for example, the pollination is carried out in a double means - by wind and insects. Iljin, 1937 by using *Anabasis aphylla* L. as an example, describes a cross pollination by insects in Chenopodiaceae. Based on his phenological observation, during mass flowering of *Anabasis aphylla*, there were a lot of insects on bushes, and the air was sated with a spicy smell produced by the flowers. This phenomena allowed him to conclude that in the Spirolobeae subfamily (Chenopodiaceae) all facts indicate only to the enthomophyly, while inside of Cyclolobeae there are events, testifying about dispersion of pollen by means of wind (species of *Atriplex*), although a number of cases of zoophyly is also known. In his later article Iljin, 1946 due to critically reconsidering the appropriate literature, he concluded that member of subfamily Spirolobeae (Chenopodiaceae) is peculiar extremely pollinated as enthomophyly. On the basis of own phenological data he states the assumption, that in limits of Chenopodiaceae the evolution went in a direction from anemophyly to enthomophyly. A cycle of works on the biology of flowering and ecology of pollination of some species of Chenopodiaceae was carried out by Botsantzeva, 1949. In this aspect she studied *Haloxylon aphyllum* and *Haloxylon persicum, Salsola subaphylla, Salsola richteri, Salsola Paletzkiana,* i.e. the most economically valuable rangelands desert species of Central Asian Flora. A very interesting feature has been described by her of the flowering process of woody *Salsola* species. In her opinion in the beginning of July up to the end of August this group of *Salsola* interrupts flowering, experiencing an original condition of anabiosis of reproductive sphere. M. Iljin, 1946 has established an ability of S.rihcteri to self-pollination. However, despite the morphological adaptability of S.richteri to reproduce by self-reprodction, there are also possibilities to reproduce as results of cross pollination (Botschantzeva, 1951b; Konycheva, 1963; 1976). She also noted that *Salsola Paletzkiana, which is taxonomic* closely related to *S.richteri* starts the blossoming at the beginning of August, which usually last up to middle of October. *S. richteri* in *Salsola Paletzkiana,* however, the development of pollen, embryo sac and ovaries goes parallel, i.e. on the generative sprouts of the last cited species simultaneously there are fruits of different age and size, blooming flowers and buds at various developing stages. Many authors suggest that in *S. Paletzkiana* seed development occurs mostly as a result of self-pollination.

It is necessary to specify, that as investigated by Konycheva, 1983 in S. rigida, *S. arbuscula, S. subaphyllus, S. gemmascens* compared with the above-described woody *Salsola* species, the analogous break (pause) in the development of embryo was not observed. Already at the end of July- August an almost morphological developed embryo is seen, though it is smaller than in a mature seed. Up to the end of September till October a gradual increase in its size is observed. Accordingly to the description done by Osmanova, 1969 flowers of *S. arbuscula* and *S. laricifolia* are proterogineous, the stamens in this case are seen only 2-3 days after appearing of stigma. She characterized *S. laricifolia* as anemophylous plant with the duration of blooming of a separate flower per 4-5 days. Bespalova,1961 studying flowering and pollination processes of many representatives of Chenopodiaceae divided them into 3 groups:

1. species pollinated by wind (anemophylous) (*Kochia prostrata, Camphorosma*

monspeliacum, Atriplex cana, A. verricifera, A. tatarica);

2. species (*Anabasis salsa, A. ramosissima, Halocnemum strobilaceum, Kalidium foliatum)*, at which the pollination occurs by means of wind and insects, and also by self-pollination (anemophylous – enthomophylous-autogamous complex)

3. species (*Nanophyton erinaceum, Anabasis truncata)* pollinated by insects, but the self-pollination could also be admitted (enthomophylous - autogamous).

Thus, at Chenopodiaceae there are some groups of plants, with differ in the way of pollination. However, as Z.G. Bespalova (1965) noted it is too early to summarize the flowering and pollination in the Chenopodiaceae family since many genera are not investigated yet in this respect. Further research would be necessary to came to the final conclusions. Antecology of some representatives of Chenopodiaceae of stony and solonchaks deserts of Southeast Kazakhstan were investigated by Demyanova, 1970_. In her opinion the process of pollination is carried out by different ways, however, the relative meaning of each of them is difficult to be established. We suppose that this might be because the morphology and biology of chenopodious flower, as well as its sex expression and adaptations to the pollination by insects, wind and/or self pollinated species are still insufficiently investigated. Besides that E.I. Demyanova, 1970 has studied species of Chenopodiaceae belonging to the subfamily Spirolobeae. These species, with the exception of *S. orientalis* and *S. pestifer* are willingly and in plenty visited by bees from the genus *Halictus*. She assumed that the basic way of pollination of chenopod from Spirolobeae subfamily is autogamy, while xenogamy (outcrossing) plays the subordinated role, though is also taking place. Hence, the antecology of these species is characterized by overlapping of autogamy and enthomophyly. On the contrary, *S. orientalis* and *S. pestifer* are typically anemophilous plants (linear, long with well developed pappillae stigma, linear, long stamen filaments and loose pollen). According to the observation of Demyanova, 1970 species of genus *Atriplex, Ceratoides, Suaeda* from Spirolobeae are strictly anemophilous. The cross pollination by wind is provided due to protogynous flowers, as well disexual flowers in the case of *Ceratoides* or gynononecious plants like *Suaeda.* Ponomarev and Lykova, 1960 for the first time have established cleistogamy at *Petrosimonia triandra* (Pall) Simonk. *Climacoptera blachiata* Pall, *Girgensohnia oppositiflora* (Pall). Fenzl. and *Halimocnemis villosa* Kar. Et Kir. Cleistogamous flowers in these species occur together with chasmogamous, the percentage ratio of which changes depending on ecological conditions. To these plants is particular a facultative ecological cleistogamy, that is caused by a lack of soil moisture and high temperature. For example, *Girgensohnia,* blossoming in opened desert in only cleistogamous, but in a wet place, mainly chasmogamous. At the other side

Demyanova, 1970 indicated the difference of hystochemistry and physiology of mature stygmas of self-pollinating and outcrossing plants within various desert chenopods.

Nevertheless, the formation of the representatives of genus *Salsola* occurrs in an arid climate and in these connection reproductive organs was developed by the certain features of functioning in adverse conditions of environment. The double fertilization of representatives of *Salsola* proceeds according to premitotic type as usual for flowering plants. Pollen tube, getting in the ovule through micropile, passes micropilar channel, formed by internal integument, and penetrates into the one of sinergids. As a result one sperm penetrates the eggcell and other merges with the secondary nucleus of embryo sac, which in all investigated by us *Salsola* species *is* very closely located to the egg in mature embryo sac. Endosperm is derived from the fusion of one sperm cell with the polar nuclei of the embryo sac. After double fertilization has taken place and when the zygote is already seen in the embryo sac synergids disappear (on slides are not visible).

In Chenopodiaceae, as in other flowering plants, after double fertilization the primary nucleus of endosperm divides first. Fertilized egg does not divide for some time. Accordingly to Yakovlev, 1950 the zygote is located in an active current of nutritious substances acting in embryo sac from chalaza through antipodes. Tzinger, 1958 has stated an idea about higher vital level of the primary nucleus of endosperm owing to threefold merge stimulating activity and fast division after double fertilization. Zygote in the investigated *Salsola* species represents a large, almost orbiculate shaped cell with a big nucleus that is often located in the center on longitudinal axis of embryo sac. Zygote, as a rule, has the precisely expressed morphological polarity: in its apical end the large nucleus is seen, and in the basal a large vacuole settles down. According to Wardlow, 1955 conception the division of zygote is caused by its metabolic activity. If the metabolic activity is identical in all parts zygote divides usually by cross partition (or seldom longitudinal) on two approximately identical parts. If the internal zygote state is not homogenous, as at the case of *Salsola,* division results in the formation of two unequal parts: largest- suspension brackets and smaller-embryo. In the majority of Chenopodiaceae, and *Salsola* representatives in particular, the first stage of zygote division coincides with an axis of symmetry, owing to what the first partition passes transversely. As a result of first zygote division a two-cellular embryo with largest basal cell -cb (in annual *Salsola* species) and smaller on the size apical (ca) cell is formed. In perennial *Salsola* species the two-cellular embryo consists of cells, equal in size, filled by dense granular cytoplasm.

Further the development of the embryo in representatives of Chenopodiaceae family, according to the classical works of Soueges, 1933; Schnarf, 1929, passes in conformity with

Chenopodium type, and the *Salsola* species examined by us are not an exception of this rule. According to this model given for the annual representatives of this genus, both formed embryos (ca-terminal and cв-basal) divide transversely and both cells participate in the formation of the basic parts of the embryo.

According to our data division of primary nucleus of endosperm at annual *Salsola* species appeared through 0, 5 - 1 hour after the pollination, while at perennial *Salsola* species in the evening of the first day of flowering or in the morning of the day after flowering. Besides that the division of the endosperm nucleus goes very actively on the first day of flowering: by evening there already are 8 or more endospermal nucleuses in the ovules, which clearly indicates that during 4-5 hours in the ovule up to three and more divisions taken place. At sixth day after flowering the embryo sac of annual species is completely filled by cellular endosperm, consisting of large vacuolated finely cells. Cellular endosperm against perennial species at annual is formed at the chalasal part of embryo sac as well.

On the 10th day after anthesis the endosperm is actively absorbed by the growing embryo and gets a character of very large degenerated and strong vacuolated cells. These cells are various under the shape and size or is more correct than a various configuration of cells, in slender amount around of strongly developed by its cotyledons embryo. The above-stated investigation testifies that ontogenesis of normal developing endosperm of annual species of genus *Salsola* is characterized by rather fast reduction of its vital level, which for 3-4 days after flowering is very high, and in the following 10th days sharply falls, when the embryo is almost completely generated. However, the zygote and primary nucleus of endosperm in perennial species in comparison with annual species can be observed only on the second day. At this time the primary nucleus of endosperm divides, forming 2 nuclei, from which one, as a rule, by stream of cytoplasm moves in the middle of embryo sac, while second remains near to the egg. Rate of endosperm nuclei division in perennial *Salsola* gradually decreases. For example at 3-4th days after flowering there are 6-8 nucleuses of endosperm in the embryo sac. First two are very large in size, but during next divisions nuclei of smaller size are formed.

At *S. orientalis* on 15th day after anthesis up to 20-30 of endosperm nuclei settle down in the stream of cytoplasm that is mainly distributed on the periphery of embryo sac. In 2 months after anthesis (blossoms in May) in ovaries fixed on July 30, nuclear endosperm still exists. By August 15th the endospermal tissue (cellular endosperm) as continuous brace fills the middle chalazal part of the embryo sac. At that time around the new formed embryo there is a zone of disintegrated cells of endospermal tissue that is actively consumed by developing embryo. Finally, on September 15 the embryo in the seed is completely generated (formed) and only a slender layer of deformed cells from former endospermal tissue could be seen.

Thus, in contrast to annual species the perennial species of *Salsola* the slowed down process of endosperm formation is described after anthesis. During two months an extreme‘s slow division of nuclear endosperm with farther between nucleoles of endosperm the cellular partitions are observed.

Embryo development. For the investigated species of *Salsola* the division of zygote is revealed at *S. orientalis, S. arbuscula* for the second day after flowering of flower and at annual *S. sclerantha, S. praecox* and *S. paulsenii* - in one hour after the beginning of flower opening. The first stages of embryo development are based on the *S. sclerantha.* The first partition divides pre-embryo into two cells located one above other: apical and basal. According to Soueges, 1935 after formation the first partition, pre-embryo has the precisely expressed physiological differentiation giving a completely different direction to the development of two these cells. In this case, in annual *Salsola* after occurrence of the first partition basal the cell increases at a rate of, whereas apical-smaller on the size and with more dense cytoplasma again divides by a cross partition on two new cells. Further basal cell does not divide, only increases at a rate of, whereas two cells which have turned out from apical divide by longitudinal partitions, and the turned out new cells divide again by cross partitions. Embryo, thus, is formed, which at this stage represents the lengthened multicellular formation with large basal cell. Later all cells, except basal are divided in various directions the spherical embryo is formed.

At *S. sclerantha* per the first day after flowering in embryo sac there are 6-8 nuclei of endosperm and 3-5 cells pre-embryo. Sometimes all 5 cells of pre-embryo can be located linearly. For the second day after flowering the number of cells increases up to 7 and the multicellular embryonic formation is formed. Embryo at the 5th day has spherical form on a suspensor- a stalk-like structure of the embryo from 5-6 cells or has a shape of the lengthened multicellular formation with large cell at its apex. At this time the embryo sac is filled by cytoplasm in which there are many nuclei of endosperm. For the sixth day after flowering endosperm of *S.sclerantha* becomes cellular. The 10-days embryo is already differentiated into well-developed cotyledons, embryonic sac between them, hypocotyl and root apex. Endosperm at this moment is almost all consumed by embryo and its remains (large empty destroyed cells) settle down on the edges of the embryo sac. At S. *sclerantha* on the 15th day the green (chlorophyll bearing) and spirally coiled embryo reaches its mature size. Thus, in annual Salsolas the cycle of embryo development has 15 days, where for the later 10 days the ripening of embryo is taking place, after that fruits are separated from the parent plant.

Almost the same rate of embryo development has been marked for S. *paulsenii S. aperta, S. praecox* and other representatives of section *Salsola*. It was found that mature fruits at *S.aperta* can be collected in 2-3 months after flowering plants, at *S. paulsenii* fruits at the stem's top usually fall down, although mostly are kept well, being in the axis of thorns.

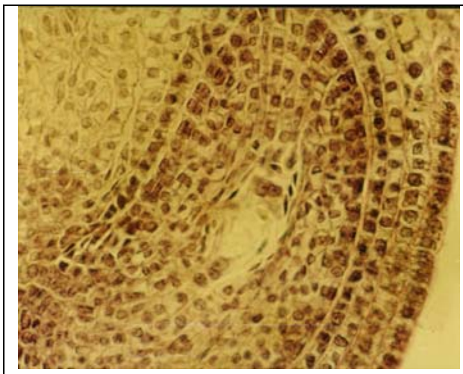
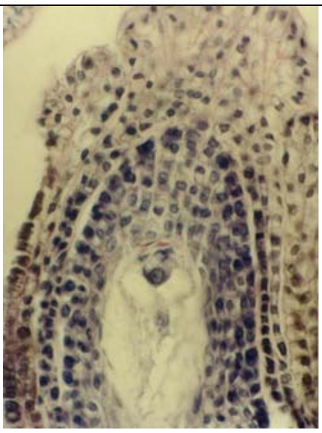
The development of embryo at perennial *Salsola* species as in the case of S. *orientalis* per the first day after pollination in the embryo sac the primary nucleus of endosperm divides, forming two nuclei that are arranged close to the zygote. Zygote is gradually increased in size and for the second day it is possible to observe 2-nd cellular pre-embryo, for the third day - 4-th cellular for the fifth day - 11-th cellular etc. Its cells always settle down linearly one above other. The suspensor at this time consists of 10-11 cells. In 10^{th} days the ovary does not undergoing appreciable changes and embryo sac has not increased its size. However, a small increasing of number of endosperm nucleuses is observed. In 15-th days the suspensor consists of one linear 11-12 cells arranged above each other with a large basal cell and 16-18 endosperms' nucleuses. At 20-day's embryo consists of 15-16 cells located one above other. At the 40-days embryo has the spherical shape on a large suspensor and small number of endosperm nuclei in embryo sac. The size of the ovule and whole ovary does not increase in 40 days after pollination, while the cavity of embryo sac insignificantly increases in connection with the formation of nuclear endosperm, as well as due to the degeneration of cells of surrounding embryo sac tissues.

Thus, if the blossoms of flower at *S. orientalis* occurred around 20-th of May, on July 30 in these ovaries a spherical embryo and cellular endosperm are noted. In middle of August the embryo assumes the heart shape with well-differentiated cotyledons and embryonal root. The endospermal tissue fills in the whole cavity of strongly increased embryo sac. Finally, to the middle of September the embryo in the majority ovaries of *S. orientalis* spirally is twisted and grows to full mature size. The embryo occupies the whole cavity of the seed and only some remains of endospermal tissue surround it. During October the seed passes a process of ripening, and as a result the endosperm is finally degenerated. Usually the seed dries up and at the end of October completely ripens and falls down or is kept at the parent plant.

In the ovule *S. arbuscula* for the second day after pollination still there is a primary nucleus of endosperm and zygote. There are no changes in growth both of ovule and embryo sac. And only in the evening of the second day after pollination the primary nucleus of endosperm divides into two nuclei. Sometimes and for 3-rd day after flowering we didn't observe out the division of primary nucleus of endosperm and zygote. Up to four pairs nuclei of endosperm and 4-th or 5-ти cellular pre-embryo could be observed in the embryo sac of ovules after 5-th days after pollination.

By 10th day after flowering two-lined suspensor, which in general consists of 14-16 cells is observed. Its two-lined form is appeared by many cells divided not only cross, but also by longitudinal partitions. The 20-day's suspensor consists of 17-19 cells located in one or two lines. Frequently in 40-48 day's ovaries we found out still multicellular (up to 22 cells) suspensor, but in some ovules there is a spherical embryo. The ovule, as well as embryo sac at this time shows an insignificant increase of its size. In the middle of August the embryo is morphologically completely differentiated and gradually in October the seed is ripe and ready for collection.

At *S. richteri* after flower pollination, the primary nucleus of endosperm divides firstly, however zygote does not divide even with a presence of 8 nuclei of endosperm. Late simultaneously with further division of endosperm nucleuses the first division of zygote in a cross direction is taking place. The division of apical cells passes transversely and as a result the one-lined suspensor is formed. In contrast to others *Salsola* like *S. richteri* the division of basal cell is going in longitudinal direction so that three celled pre-embryo sometimes gets a T-figurative structure. It was also marked that ovaries of *S. richteri* are developing slowly. So, if a flower bloomed at the end of June, in August in ovary still nuclear endosperm and one-lined consists from 10-12 cells. The fast development of embryo occurs in September, when cotyledons, embryonal bud between them, hypocotyl and rootlets are differentiated. The seeds ripen at the end of October. So, the period of formation of the embryo at *S. richteri* is shorter, than at others investigated perennial salsolas, namely 4 months (since July till October). The data on double fertilization, development of endosperm and embryo is summarized and given in Fig. 29.

 a) mature embryo sac before double fertilization	 b) the entering of pollen tube into the embryo sac of *S. arbuscula*

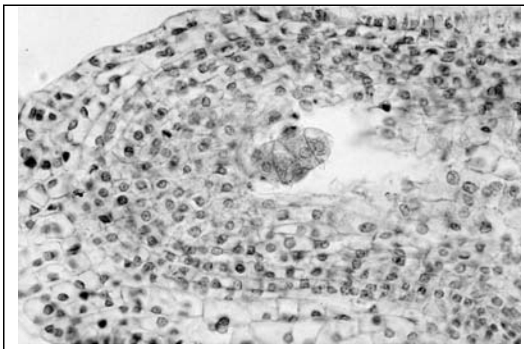
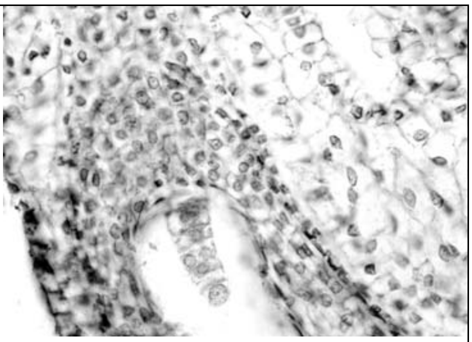
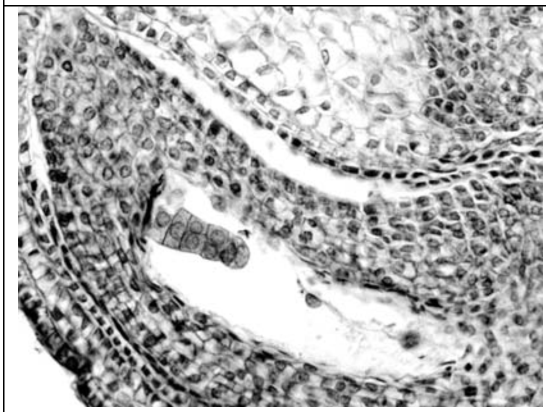
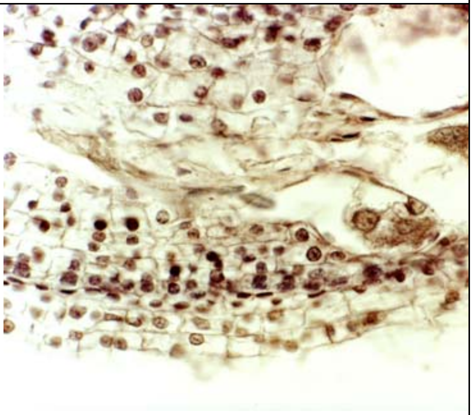
 c) the micropilar part of the ovule of *S.arbuscula;* proembryo is well differentiated	 d)first stage of embryo developme *of S. S. arbuscula*
 e) the embryo of *S. arbuscula* after 10th days aft pollination	 f) the development of two embryos in the ovule of *S. arbusculiformis*

Figure 29. Peculiarities of double fertilization and embryo development of *Salsola arbuscula*

Concerning *S. arbusculiformis* the formation of the embryo occurs in the same patterns as at *S. arbuscula.* For example, the mass flowering of this species lasts 2-3 weeks in May and further till October seeds ripen. Maturing of seeds is going also non-uniform. First flowers that bloomed in May form seed of high quality within 5 months, while flowers that bloomed at the end of June have limited time for ripening and among seed material in October a big quantity of fruits with underdeveloped embryo is found. Being located sparsely on the generative sprouts quality of well developed seeds significantly differs. Therefore it is recommended to collect seeds separately, i.e. only from the bottom and middle parts of generative sprout, where seeds are well developed and embryo organs completely differentiated.

CHAPTER 5. Morphology and anatomy of fruit

5.1. Species diversity and polymorphism of carpological characters

Fruit of 14 *Salsola* species of Flora of Uzbekistan were examined by light and scanning electron microscope (SEM) to evaluate the systematic significance of testa surface sculpturing and structural peculiarities of perianth segments during fruit stage development. It was determined that the campiloptropous seed with exotestal seed coat is characteristic for the genus *Salsola*. The external seed morphology, the peculiarities of the exotestal cells structure, including the diversity of macro- and micromorphology of the surface are more or less constant features of the species. Differences are mostly found between different sections than among species of each section. Micromorphological diversity of the thin microrelief of the seed cuticular covering has been shown. The revealed features of the ultrastructure of the seed surface can be used in the taxonomy of the genus. The preliminary conclusion about the connection between the structure of exotesta and its protecting function, as well as the plant's vital form has been suggested. The mature fruits of *Salsola*, frequently horizontally thickened, were characterized by the development of following cover elements: 5-lobed perianth, pericarp and spermoderma. As pericarp and spermoderma have primary thin parenhymatous structure, the seed dispersal and embryo protective functions are assigned to the perianth elements. In this case all 5 tepals (lobes) of perianth compactly envelop the fruit, but do not accrete together both among themselves and with the seed. Each lobes of perianth at the fruits stage maturity in the middle part is curved in such a manner that in an internal part the seed cavity is derivated. Also from this middle part of each perianth lobes fan-shaped wings are developed. Significant interspecies variation was found in the morphology of tepals that greatly enlarge and change their shape during fruit formation. To make them comparable, the respective data in the descriptions are given for the flowering stage, because in fruit they are more difficult to obtain. Of some value is observed in the position of wing formation that grows out along the so-called transverse line. The apexes of perianth lobes (tepals), closely approaching, frequently vertically up above the fruit and derivate into the various form of column. We found out that the pubescence features of perianth surface plays an important systematic significance. For example, fruits of species of Sections *Caroxylon, Cardiandra, Malpigila* and *Belanthera* belong to the evidently pubescent type, while representatives of Sections *Arbuscula* and *Salsola*, sub. *Kali* – to slightly or without pubescence perianth segments type. The wings of the fruit have an unequivalent degree of development, shape and size, as a rule, 3 rather broad and 2 narrow.

Although fruit morphology of *Salsola* species as for many representatives of

Chenopodiaceae is an utricle, it was revealed that a set of fruit structural features comprising sculpture of perianth surface, size, shape of fruit tepals and wings were useful to distinguish genus and even species within sections.

The fruit morphology and anatomy pecualirities ls for 14 Asiatic *Salsola* species is summarized as following:

Salsola arbuscula - fruiting perianth including wings is of 7,8 to 12 mm in diameter, pericarp fleshy to membranous, not adherent to seeds when dry. Tepals: ovoid-oblong 4-6 mm, gradually enlarged toward apex, near the wings closely adherent to the fruit; in upper part (above wings) rosulately expended and sometimes reflexed, widely wedge shaped, slightly convex with broad membranous apexes, on an edge have rare papillate; a surface lineolate by longitudinal furrows. Tepals under wings are hardly convex and smooth; above the wings first incurved and forming a broad, indurated circular bulge, then abruptly recurved and forming an open flower-like cup. Wings: subequal, horizontal, semi-orbicular, or narrower, scarious pale-yellow with a faint rosy-red flush, often slightly hairy, with the broad basis without precisely expressed middle vein and a fan-shaped spreading dense lateral venation; wings are unequally developed: most broad up to 3 mm long and 7 mm wide. Utricle has 2-3 mm in diameter with hardened cap, horizontal.

Seed: small (2,1 mm), horizontal, dark-brown, orbicular, Embryo; large, spirally intorted. Dormancy A_2-B_1. Field germination, because of sclerified fruiting body is low (8-12 %). Viable seeds 78-82%; Stratification (0,5-1 months with temperature 3°C), processing with phytohormones effective and increases germination to 54% Storage: under dry conditions (20-22^0C) is also effective. Seed viability lasts 10-12 months.

S. arbusculiformis **-** fruiting perianth pentamerous of 11-15 mm in diameter. A friable cone, widely wedge-shaped with obtuse apexes, assembles perianth segments above wings; surface colliculate, sculptured with transverse farrows. Under wings: tepals are slightly convex and smooth. Wings: overlapping, horizontal, fan-shaped without precisely expressed middle vein, but with dense spreading lateral venation; subequal, rather stiff, brownish to straw-coloured. Utricle semi-exposed, c 3mm diam. With a weakly hardened cap. Seed: horizontal with spirally twisted embryo.

S. richteri - fruiting of 13-18 mm in diameter. Upper tepals, grey, rigid, strongly pressed to the surface, almost accreted, in the basis widely wedge shaped; to the apex form a deviating column with obtuse extremities. The tepals' surface finely undulate and lineolate has rare papillate accretions. Tepals under wings are slightly convex, on the basis highly pubescent with curly simple hairs; above the wings are first incurved and forming a broad, indurated, circular bulge, often form an open funnel. Wings: horizontal colourless, seldom pink or grey, widely fan-shaped spreading without precisely expressed middle vein, but pierced with numerous rough lateral veins; unequally in size: most broad up to 5 mm in diameter and up to 10 mm wide. Utricle 2-3mm in diameter, with slightly hardened cap; horizontal. Fruit maturation: September-October

Seed: 2,5 - 3 mm in diameter, horizontal with spirally twisted embryo. Dormancy: A_2-B_1; % viable seeds 78-95%. Germination rate: 56-68%. Light dark sequence with alternative (15-28 °C) or freezing temperature stimulates germination. Treatment with gibberellic acid is effective too. Seed longevity 1,-4-1,6 years

S. paletzkiana - fruiting perianth pentamerous of 16-15 mm in diameter. Tepals above wings, darkish, in the basis wide wedge shaped narrowed towards the apex forming a friable column; surface sculptured by lineolate, transversal small-sized, thin primes. Perianth segments under wings slightly convex, at the basis pubescent by rare curly hairs. Wings: very thin, silky shining, horizontal, widely fan-shaped spreading without precisely expressed middle vein, but pierced thin brownish lateral veins; unequally developed: most broad up to 7 mm long and 12 mm wide. Seed 3,0 mm in diameter, horizontal with spirally twisted embryo.

S. orientalis - winged, indehiscent nuciform, monospermous fruits of 7.5-13 mm in diameter. Fruiting perianth including wings 7-10 mm across, connivent above the wings into a loose gently sloping cone; wings: horizontal (7-12 mm diameter) with radial slit; fine venation, reniform, purple or roseate or possibly yellowish turning brown when ripe. Maturation: end of October-November

Seed: orbicular, yellow-dark/brown (from 2.0 to 2.5 mm) closely accreted with thin fruiting body,. Seed coat - 2 celled layer with intermediate cuticle. Embryo large (20-28 mm), spirally intorted, leucophyte with perisperm. Dormancy: B_1; % viable seeds 68-90. Germination 18-52 %. Stratification of seeds (3°C/0,5-1 month) or treatment with phytohormones and washing of fruits (distilled water 2-3 changes) induce germination. Seed viability: 6-8 months. Seed is dispersed by wind.

S. dendroides - fruiting perianth 6-10 mm in diameter. Upper perianth (above wings) is flat and broad at the basis and to the apex shortly pointed, assembled by a truncate cone or an open cylinder; the perianth surface is usually reticulate, alveolate; on edges are often present flat hairy lash. In the middle part of fruiting perianth the precisely designated veins are developed. Wings pale or brownish, more rarely pink have the fan-shaped form; their surface is cover with thin lines, sometimes interrupted. Seed: 1.7-2.0 mm in diam., horizontal with spirally twisted embryo.

S. incanescens - fruiting perianth of 6-11 mm in diameter. Tepals above wings narrowly wedge-shaped, back pilose with stiff ascending hairs and a small hump in the middle part; with distinctly incurved bear-like margins bent together and forming a 5-arched open or closed dome. The perianth surface is evidently reticulate and densely covered by scattered long hairs. Wings horizontal, 3 broad and 2 less broad have the fan-shaped form; its surfaces are covered with oblong lines assembled in groups. Seed horizontal with spirally twisted embryo.

S. sclerantha - fruits of 6 -10 mm in diameter. Upper perianth (above wings) during fruit stage hulled bordered in length with entire margins are assembled in a cone-shaped column. Its surface, especially on margins is covered with long mealy clasped hairs. Lower perianth (under wings) is almost horizontally spreading, slightly concave at the middle. Its surface sparsely covered by long slightly coiled trichomes. Wings horizontal, membranous, colourless or pink almost equal in length and width (2.0 mm long and 2.5 mm wide), hardly overlapping, enlarged to the basis with fine venation. Seed horizontal with spirally twisted embryo

S. implicata - fruiting perianth of 8-12 mm in diameter. Upper perianth segments narrowly wedge-shaped with a small hump are assembled into a conic column. Its surface is abundantly pubescent with mealy, and on the edges by simple, long, thin and curly hairs. Lower perianth is densely covered with short papillae and long direct hairs. Wings: horizontal, free or overlapping with outer parts, wedge to broadly fan-shaped, their base narrow with parallel to slightly divergent margins, in lower half concave, keel absent or present only on the narrower inner tepals. Wings are without obviously expressed central vein; and almost equally developed (about 3 mm long and 4 mm wide); Seed horizontal with spirally twisted embryo.

S. gemmascens - fruiting perianth has 5-8 mm in diameter, straw-or smoke-coloured. Upper part of tepals stiff without hump, wide wedge-shaped, thick –walled with cylindrical filmy apexes that are gathered into a convex friable column. Its surface is covered with malpigipilae hairs that have an appearance of broad fillets with the obtuse narrowed extremities. The surface of tepals above wings has a colliculate sculpture. Tepals under wings are hardly convex, pubescent with rare simple hairs or naked. Wings horizontal, short, thin kidney-shaped or inverse ovate without obviously expressed middle vein, semiorbicular with broad base, unequally developed- three broad up to 2 mm long and 4 of mm wide, other two rather narrow up to 2 mm long and 2,5 mm wide. Seed: horizontal with spirally twisted embryo. Fruit maturation: September-October.

S. vvedenskyi - fruiting perianth pentamerous of 12-14 mm in diameter, rather stiff, brownish; tepals above wings first evenly incurved, strongly arched; broad at the basis, sharply lent to the top form a shovel-shaped column or a very steep cone; the surface - tuberculate, densely pubescent with long ramified hairs. Tepals (under wings) derive into a massive deep cap shaped cavity. Wings horizontal, 3 broad and 2 less broad fan-shaped, short chaotic lines evidently pierce the surface. Seed: horizontal with spirally twisted embryo.

S. aucheri - fruiting perianth has 10-13 mm in diameter. Tepals (above wings) first arched and forming a thickened cushion separated by a cleft from the wings; broad in the base, forming a thickened cavity, smoothly acuminate to blunt and truncated apexes; the upper ½-2/3 erect or recurved, forming a cylinder or funnel. Tepal surface is striate with small grooves, pubescent more or less frequently on edges and on the apex; less often at the base with clasped oblong hairs. Wings: horizontal, 3 broad and 2 narrow fan-shaped, surface drawing by the thin hardly designated long lines. Seed is of 2.5-3.0 mm diam., horizontal with spirally twisted embryo.

S. praecox - fruits of 7-8 mm in diameter enclosed in the pentamerous perianth with a different degree by developed wings. The upper tepals with a rough alveolate surface have the little bit convex strong base with a film bordering and back vertically up narrow - triangular pointed apex (up to 2 mm in diameter). On the surface of upper tepals frequently papillate accretions are revealed. The lower tepals on innerside opposite to the wings are less compact.

Wings: pale yellow, unequally developed: the 3-fan-shaped of 2, 7 mm long and 6-7 mm wide; 2-narrow with triangular appendages up to 1-2 mm long. Wings transparent with fringed margins and roughly distinguishable veins (up to 18 on the largest wing); veins are precisely seen. Seed horizontal (0,21 - 0,83mm), weak - conic form and a spiral coiled embryo. Laboratory germination at 25-28 ^{0} C ranges 67- 78 %.

S. paulsenii - fruits of 10 mm in diameter in perianth consisting from 5 sharply unequal tepals with a different degree by developed wings. Tepal lobes are slender long-acuminate, stiff, forming a beak at the apex up to 2 mm long. The surface of upper tepals is slightly reticulate. The upper perianth tepals at the middle have a hardly visible appendage and its surface is covered with rare papillae. The lower tepals less compact with precisely selected veins. Wings: yellowish, unequal in size: the 3-fan-shaped of 4 mm long and 6- 10 mm wide; 2-awl-shaped up to 2 mm long. Seed is horizontal, conic with spiral coiled embryo.

***S. iberica* -** fruits of 5-6 mm in diameter. The basis of the upper tepals has a hump on the surface with upward thin film trapezoidal apexes (about 1 mm long). The sculpture of upper tepals surface - reticulate - foveate. The lower tepals are less compact with finely venation. Wings unequally developed: the 3-fan-shaped of 1,5 mm long, 2,5-3,5 mm wide.; 2-narrow shovel shape of 1 mm long and 0,6 mm wide. Wings are very thin, transparent with delicate veins (up to 16 on a large wing). Seed horizontal, conic form with a spiral coiled embryo.

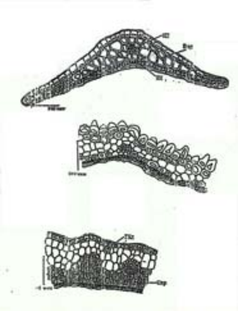
***S. aperta* -** fruiting perianth broadly cup-shaped, 6-11mm diam.; the outer wings 2-3 mm long;

the inner as triangular appendages; tepals on inner side opposite to the wings with a transverse rim, above the wings reflexed forming a stellate structure and exposing the utricle by a 1.5-3.0 mm wide aperture; tepal lobes papery, ½ times to as long as wings; tepals below the wings coriaceou, coalescent; seed horizontal.

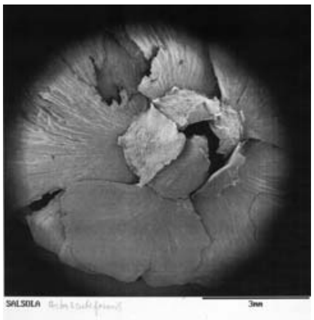
***S. lanata* -** fruiting perianth 12-20 mm in diam. Wings in young stage pink, later light brown, papery, the inner spathulate; cap 3.0-4.5 mm in diam., the upper part funnel-shaped from the recurved white, papery 2-3.0 mm long tepal apices. Seed 2.5-3.5 mm diam., horizontal, but sometimes vertical

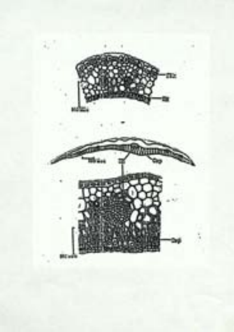
***S. crassa* -** fruiting perianth 12-20 mm in diameter, the upper part forming a steep cone, an open cylinder or a norrow funnel; tepals stiff and brown up to the apex or apical part papery. Seed has 2.-5-3.0 mm diam, usually horizontal, but at first often vertical. Data are summarized and shown in the Fig. 30.

S. arbuscula

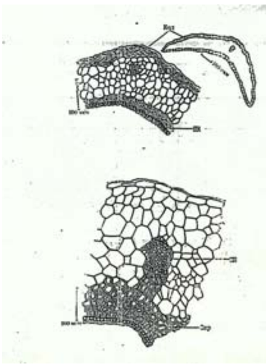


S. arbusculiformis

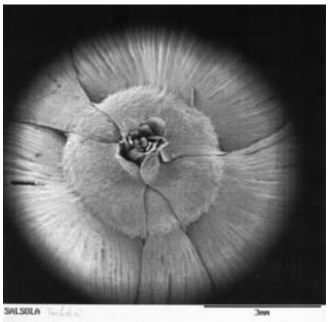


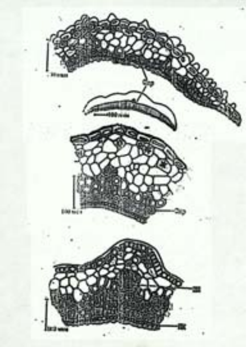


S. paletzkiana

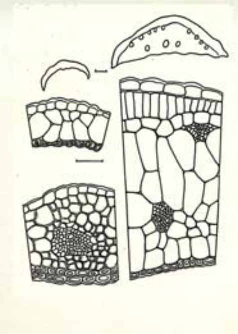


S. richteri

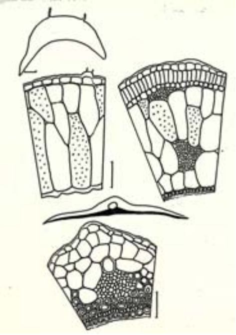




S. dendroides

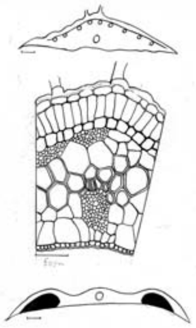


S. incanescencs

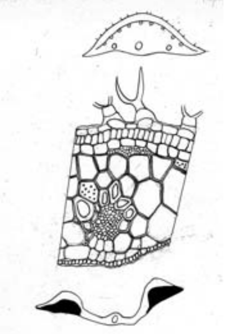


S. gemmascens

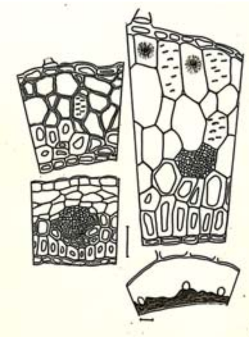
S. sclerantha



S. implicata



S. aucheri



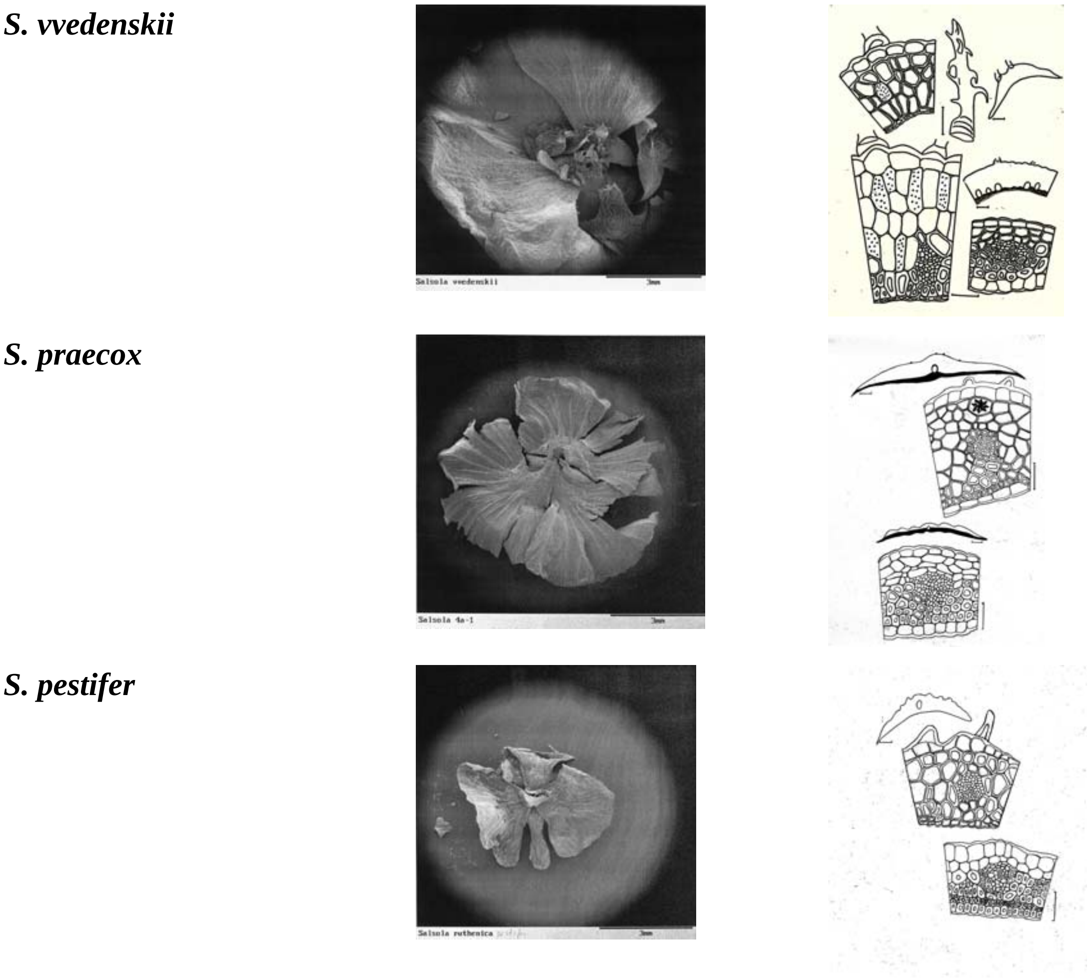


Figure 30. Characteristics of fruit morphology and anatomy within Asiatic genus *Salsola*

Thus, fruits of the studied *Salsola* are dry, monospermous, lyzicarpous, indehiscent with well-developed wings. The weight of 1000 fruits varies from 4.8-6.98 g. Seeds measured on the horizontal axis are 2.5-3.0 mm in diameter, without endosperm and perisperm. Fruits are variable as to size, shape and color (from light yellow to reddish- *S. richteri*; pale yellow to grayish –*S. Paletzkiana, S. arbuscula*). The most distinctive and fairly constant characters seem to be the presence and size of wings and the degree of development and position of the tepals lobes above the wings. Such fruit diversity is conditioned both by phylogenetic relation, tendency and character of specialization of reproductive structures to the extreme arid condition (Werker and Many, 1974; Rilke, 1999; Butnik et al. 2001). By means of TEM and SEM analyses it was inferred that the structure of perianth segments reflects the adaptive evolution of these taxons and plays a more significant role in the species identification than the element of fruit covers. The comparative analysis of fruit morphology has revealed that taxonomic diagnostic features are expressed first of all in the upper leaflets (above the wings) and vertical column (open funnel), whereas bottom leaflets (under the wings) are less identical. Among the species studied, variation of fruits is displayed in the form and color of wings, structure of columns, presence, shape and spatial arrangement of the papillous protuberances (*S. richteri*, *S. arbuscula*) and their absence (*S. Paletzkiana*, *S. arbusculiformis*); in numbers of collenchymatous layers; degree of sclerification and parenchymatization.

The development of five unequal, wide and narrow horizontally spreading wings facilitate the wind seed dispersal and regulation of seeds germination in *Salsola.* There are various inhibitors in the wings of majority chenopods that are accumulated gradually during the seeds maturity (Ionesova, 1970; Shamsutdinova et al, 2000; Gus Gintzburger et al.,, 2003). Partial myxospermy, marked in the cell structure of perianth, is more peculiar for the plants suffered by deficit of water and it's widespread in the fruits and seeds of desert plants (Gutteman and Witztum, 1977; Boesewinkel and Bouman 1984; Takeno at al, 1991). In their opinion the most important function of mucus (slime) is to fix the seeds to the soil and to the animal that facilitate their dispersal and/or to act against seed overheating (Japakova, 1995). Essential significance in defending of embryo is played both by vegetative elements of flower (bracts and bracteoles). Prominent level of sclerification of perianth segments and thickening of pericarp and spermoderma (at *S. richteri* epidermis bearing the papillae–shaped proturbences) are related to the defending of embryo as well. It is determined that the main trend of evolution of many chenopods is toward reduction of structure of spermoderma and pericarp. Pericarp of species studied by us is membranous, thin and contains colored brown pygment in *S. richteri* and black pigment at *S. Paletzkiana*. Anatomy of pericarp is homogeneous for both species and comprises by parenchyma with a different degree of cells walls-thickenings. The pericarp of S. *Paletzkiana* in contrast with *S. richteri* can be easy separated after 1, 5 hours of seeds soaking into the water. Spermoderma of investigated *Salsola* species is formed from two integuments of ovule and as for majority representatives of Chenopodiaceae is reduced up to 2-celled layers with a thin cuticular layer between them. However, the properties of seed quality are determined not only by structure of fruiting covers and spermoderma, but mostly by the level of development of and degree differentiation of embryonal tissues. Embryo is large, peripheral, spirally coiled; cotyledons usually 2, sometimes apical cleft to deeply divide; germination epigeal. All organs of embryo contain proteins and fat without starch. According to Perskaya, 1953 fat is considered not only as a concentrated storage chemical compounds, but it defend embryo from impact of lower and high temperatures.

As results of our investigation on fruit morphology and ultrastructure of Asiatic *Salsola* species diversity we made a conclusion that the perianth during fruit maturation can be well distinguished by perianth segments position and morphology from one side and by anatomy and sculpturing peculiarities of perianth elements from the other. The upper perianth segments (above wings) consist of the less extended base and bending vertically apex. Lower (under wings) perianth segments closely adjoin one another, deriving into a cup shaped cavity. Upper tepals are to some extent superimposed, forming an arch above seed, but never accrete together. The anatomy of upper perianth differs from lower in all *Salsola* species investigated in present work. This is probably because of functional differentiation, when upper tepals during fruits maturation bear both protective and photosynthetic function, as is shown for species of Section *Caroxylon*, to the lower perianth segments the protective function only is assigned. It was also reveled that the species of the certain sections have a set of common structural features and precisely differ by anatomical characteristics of tepals from species of other sections.

Performance of the anatomy of perianth segments during fruit maturation for various *Salsola* species accordingly systematic position of *Salsola* sections is given as following:

The upper perianth tepals for species of Section *Caroxylon* are strongly parenchymatized. Under outer epidermis the two layers of chlorenchyma are developed: a layer of palisade cells and the cubic bundle sheath cells of small-sized vascular tissue; the main vascular bundle usually is dislocated in the center among large cells of parenchyma. *S. incanescens* differs from *S. dendroides* by smaller sized of palisade shaped parenchyma cells and by abundant hydrocyte dotty porous cells, as well by small-sized cells of inner epidermis, which are hard, but uniformly thick-walled. Lower tepals of perianth at *S. dendroides* consist of many rows of izodiametric parenchyma cells with slightly thickened walls that closely adjoin the one layer of thick-walled epidermis cells. *S. incanescens* has a similar structure with the exception of thin-walled parenchyma tissue. At *S. incanescens* the numbers of sclerenchyma, however, is increased up to 2-3 rows. The vascular system is represented by only one central bundle.

Section *Cardiandra* at *S. implicata* and *S. sclerantha* have small distinctions in anatomy of perianth. Common structural patterns are the well developed chlorenchyma, consisting from one layer of palisade cells and numbers of bundle sheath cells of small-sized vascular tissue, great parenchymatization of upper tepals and grouping disposition of sclerenchymatous cells on both edges of lower perianth tepals; a large central vascular bundle on upper perianth segments that enclose sclerenchymatous cells. At *S. implicata*, in comparison with *S. sclerantha,* palisade cells small-sized, the walls of izodiametric parenchyma cells are insignificantly thickened; among them meet the single dotty porous hydrocyte cells.

Upper perianth of *S.gemmascens* (section *Malpigila*) has two-rows of chlorenchyma that consisting of well developed many-rowed palisade, numerous bundle sheath cells and by small-sized vascular tissue. Large parenchyma cells enclose the central vascular bundle. Among them the palisade shaped cells and dotty porous hydrocyte cells are found. Under parenchyma one layer of sclerenchyma is extended. Sclerenchyma cells are distinguishable by extremely thickened walls and very narrow intercellular spaces (at some of them the sizes exceed 1/2 the thickness of perianth tepals). Under sclerenchyma a row of small sized pigmental cells that extends completely around inner epidermis is differentiated. This layer of sclerenchymatous cells in the lower tepals is squeezed. The lower tepals are differentiated by both tissues: thin-walled parenchyma (in the mature fruits; walls of this tissue are partially destroyed) and a row of sclerenchyma with an evident thick-walled cells; one central and two lateral bundles represent the vascular system

Species of section *Belanthera* as *S. vvedenskii, S. orientalis* and *S. aucheri* chlorenchyma is completely absent in the anatomy of perianth segments. Upper and lower tepals consist of 3-4-rows of parenchyma and 2-rows of sclerenchyma tissues. Parenchyma in the upper perianth tepals has large well-differentiated cells, especially at *S. aucheri,* sometimes radial elongated with numerous dotty porous hydrocyte cells at *S. vvedenskii* and slit shaped- in *S. aucheri.* The parenchyma of upper perianth tepals at *S. aucheri* is pigmented (black colour) and contains spheres of unknown origin crystals. Ramified hairs of perianth segments at *S. vvedenskyi* are large, exceeding sometimes the thickness of perianth. The species of this section are distinguishable by the vascular bundles disposition - above sclerenchymatous cells in the middle part of the perianth segments. The numbers of vascular bundles in upper perianth tepals at both species - 5-6, lower - at *S. aucheri* - 4-5, *S. vvedenskyi* - 1 central. Sclerenchyma cells differ between species by sizes and have greatly thickened walls.

The common structural patterns in the perianth anatomy of species from subsection *Arbuscula* are the following: absence of chlorenchyma, large sized cells of outer epidermis with strongly thickened walls and small sized cells of inner epidermis; the central part consists of parenchyma tissues, in which the hydrocyte cells are disperse; sclerenchyma, vascular and pygmental layers consisting of one row of small-sized cubic cells. This number of cubic cells cavities are completely filled with inclusions is appeared at early stages of flower ontogenesis (before flowering), later, at mature fruits the wall of cells is hardly thickened. Each of investigated species can be characterized by a set of anatomical parameters that, probably, play both diagnostic systematic and adaptive significance. For instance, *S.richteri* – the appearance of papillae on the epidermis; the grouping distribution of collenchyma cells under the apex of upper epidermis that amplified the sclerification on all part of perianth; in the parenchyma tissue a partial pygmentation of cells is marked. *S. Paletzkiana* - smooth surface of epidermal cells, 2-3-rows of collenchyma distributed under outer and above inner epidermis, replacing by sclerenchyma at the basis of upper and lower perianth tepals that induce the parenchymatization of upper perianth tepals. *S. arbuscula* – presence of papillae structures on epidermis, many layers and large parenchyma cells with strong thickened walls, absence of sclerenchyma in the uppermost stratums of perianth segments and high sclerification of lower perianth tepals. *S. arbusculiformis* - almost smooth surface of the epidermis, small sized parenchyma cells in the anatomy of upper perianth tepals and a prominent sclerification of lower perianth tepals. The anatomy of tepals and leaves structure differs by absence of the crystal-bearing hypodermis.

The common feature for the species of section *Salsola* subs. *Kali,* such as *S. praecox, S. iberica, S. paulsenii* is the absence of chlorenchyma in upper perianth tepals. The cells of upper and lower epidermis have strong thickened outer walls and rather thin inner walls. But at *S. iberica* the cells of lower epidermis have a uniform strong thickening throughout cell perimeter. On its surface the various types of papillae are developed. Epidermis is somewhat cutinized, producing numerous hairs and glands. The parenchyma cell walls are also thickened. Upper perianth tepals have minor sclerification of cells that is a little bit amplified in the lower perianth tepals. Thin-walled parenchyma cells are more characterized for lower tepals. However, at *S. iberica,* in contrast with other species of this section, in lower tepals parenchyma is uniserial, the wall of sclereids are so thickened that there are only narrow spaces, and under sclerenchymatous tissue the pigmented layer is replaced by a crystals bearing one. According to Botszchantzev,1969; Freitag, 1997; Rilke, 1999; Toderich, unpublished data morphological and structural features of generative organs and, in particular, fruits, were widely used for differentiation and identification of systematic position of species with genus *Salsola*. Botszchantzev, 1969, however, considered it insufficient because of unsatisfactory outcomes. At the basis of his *Salsola* system a complex of morphological parameters, first of all form of leaves and character of its pubescence has been taken into consideration. New criteria in species delimitation, namely the micromorphological surface sculpture and structural diversity of perianth segments during fruit maturation period, described by us for Asiatic *Salsola* groups, precisely has defined the specific and sectional boundaries of genus *Salsola.*

A few data on the perianth anatomy of some species of genus *Salsola* has been given in the literature by Rozanovskii, 1970; Butnik, 1976, 1977, Nigmanova, 1980. The authors, however, mainly paid attention to the structural peculiarities of the lower perianth segments. This approach was justified for a limited purpose of revealing the degree of adaptation of these species to desert extreme conditions. The analysis of variability of perianth structural patterns (from apexes to its lower part), done by us, considerably has expanded review of ways and character of adaptive evolution of fruits within genus *Salsola.*

The differentiation between sections based on the micromorphology of perianth, first of all, strictly distinguished two groups. To the first group belongs species of section *Caroxylon*, *Cardiandra* and *Malpigila,* which are mostly characterized by the development of two-row of chlorenchyma that consists of palisade bundle sheath cells and small-sized vascular tissue. Contrary, for the species of sections *Belanthera, Arbuscula* and *Salsola* sub. *Kali* the chlorenchyma is absent.

High parenchymatization of perianth segments during fruits maturity, radially elongated cells of thin-walled parenchyma, absence of sclerenchyma in the upper tepals, its cholenchymatous thickening of lower epidermis and 1-2 rows parenchyma that closely adhered to the epidermis are peculiar for species of section *Caroxylon* that are considered primary, initial one within genus *Salsola*. Closer to this section by the anatomy of perianth are species of section *Cardiandra,* at which also is absent sclerenchyma in the upper lobes of perianth. But species of this Section have less small-sized and more thick-walled parenchymatous cells and grouping dislocation of sclerenchyma on both margins of lower perianth segments.

Based on Botszchantzev (1969)' opinion and accordingly our studies the first line of evolutionary trends within genus *Salsola* is following: *Caroxylon - Malpigila - Cardiandra*.

S. gemmascens, however, from section Malpigipila is sharply selected by its specific perianth structural patterns. The presence of chlorenchyma in the upper lobes brings together this species with two species of Section *Caroxylon*. In his system Iljin, 1946 referred this species to section *Belanthera.* However, based on leaf morphology, in particular on the presence of hums at the base of leaves in combination with a peculiar pubescence (development of malpigipilae hairs) of assimilative organs and smooth sculpture of anther' appendages Bot schantzev,1969 replaces this species into the separate section named *Malpigila*. Some structural features of perianth anatomy (mostly in its upper part) during fruits maturity stage that were described by us and unusual shape and degree of sclereids wall thickening doubtlessly, distinguish this species from all *Salsola* species of remaining sections.

The second line of species differentiation and evolution within genus *Salsola,* according to . Botszantsev, 1969 was directed at the formation of Section *Belanthera* that has been derived spontaneously from section *Caroxylon*. The structure of perianth as radially elongated very large thin-walled cells of parenchyma and abundance of hydrocyte cells with dot porosity closely related these two sections. At species of section *Belanthera (S. aucher*i and *S.vvedenskyi*) the chlorenchyma is absent; schlerenchyma is presented only by a few rows (1-2) of cells in upper tepals and evident development of sclerenchyma at lower tepals perianth. A characteristic indication is the disposition of 5-6 vascular bundles in one plane by an average part upper tepals of perianth, whereas at other sections or as at *Caroxylon, Cardiandra, Malpigila* - 1 large central and 7-8 small-sized under vascular sheath bundles, or as at section Arbuscula and Salsola - 1 large central vascular bundle.

The third line of evolution of genus *Salsola* was going towards *Caroxylon- Arbuscula - Salsola.* At species of sections *Coccosalsola*, *Cardiandra* and *Salsola* the surface of perianth is covered by various types of papillae that differ between species by size and abundance of their distribution. Species of section *Coccosalsola* sub. *Arbuscula (S. arbuscula, S. arbusculiformis, S. richteri, S. Paletzkiana*) differ from each other by size and abundance of their distribution. Species of section *Arbuscula (S. arbuscula, S. arbusculiformis, S. richteri, S. Paletzkiana)* differ from each other by a significant thickening of epidermis cells, massive sclerification, development of kollenchyma in the perianth apexes *(S. Paletzkiana),* and comparative small sized of cells of all perianth tissues. Hydrocyte cells can be like dots (*S. arbusculiformis)*, crack shaped or reticulate (*S. richteri, S. Paletzkiana*) porosity. On some structural indexes of perianth species of section *Salsola* are approached to species of section Arbuscula, but differ from them by the thick-walled parenchyma and rather larger thin-walled epidermis cells; *S .iberica* is distinguishable by uniform thickening of inner epidermis walls of lower tepals of perianth, as well as by the development of crystall/salt bearing layer that is, perhaps, transformed from pygmental.

The analysis of structural features of perianth segments has shown a direction and variety of specialization of each fruit tissue stipulated by shedding or emerging of those or other elements, modifications in the form and sizes of cells, character of a thickening of cell walls etc. Epidermis can be rather thin-walled (internal walls), but, as a rule, at all investigated species the outer walls are thickened. *S. dendroides, S. incanescens* (section *Caroxylon)* and *S. iberica* (section *Salsola*) are selected by uniform thickening of all walls of epidermis. The evolution of parenchyma goes from radially elongated large thin-walled cells to small sized cells thick-walled izodiametric shape cells. In the same direction the cells of sclerenchyma are changed from very large radial elongated form to small sized izodiametric form. Two directions of adaptation are detected for species of genus *Salsola.* The large parenchyma and sclerenchyma cells are positively correlated with the development of strong pubescence, whereas in almost non- pubescent species (exception short papillae for a few species) the small sized parenchyma with thickened walls is observed.

Increasing of sclerification, availability of pigments and tracheids like cells holding a moisture, abundance of crystals in the perianth tissues also promote the protection of embryo from unfavorable conditions. The development of wings on a median line of perianth segments stipulates the anemohorous way of seed dispersion, characteristic for arid regions with extensive open spaces.

Thus, detailed analysis of morphology and anatomy of perianth during fruit maturation stage has revealed new criterias of species delimitation within complicated polyphyletic genus *Salsola* showing their systematic significance in submission of adaptive evolution of fruits to extreme desert habitat conditions.

5.2. Seed storage, type of dormancy and ecology of germination

As shown in Table 5 there is a direct relationship between fertility of pollen, mode of reproduction and quality of seed. Usually, the higher fertility of pollen is observed in the flowers arranged in the lower and middle part of generative sprouts during the maximum flowering period of plants.

Table 5. Pollen fertility, genome, anatomy and biochemistry in woody *Salsola* species in relation to their seed quality characteristics

Nomenclature	*S. arbuscula*	*S. arbusculiformis*	*S . richteri*	*S. Paletzkiana*
Fertility of pollen (%)	15.3-82.45	25.0-64.8	50.0-86.12	no data
Genome	no data	no data	2n=18, 36,54,72	2n= 18
Reproduction	Sexual, partenocarpy	Sexual, asexual (apomictic), partenocarpy	Sexual, vegetative (cuttings)	Sexual, getative (cuttings)
13C/12C carbon discrimination value ($^{0}/_{00}$ PDB)	-12.71 –12.95 leaves -13.61 -14.0 fruits	- 23.6 -24.4 leaves -26.29-26.31 flowers -23.47-23.63 fruits	-12.0-12.3 leaves -12.21- 12.9 flowers -12.20-12.3 fruits	–13.13 -13.35 ves -14.00 –14.08 its
Anatomy/ biochemistry	C$_4$-Sals(+H) NADP-ME (Both in cotyledon, leaves and bracts)	IP/C$_3$ (cotyledons) SYMP/C$_3$-C$_4$ (leaves and bracts)	C$_4$-Sals(+H) NADP-ME (Both in cotyledon, leaves and bracts)	C4-Sals(+H) NADP -ME (Both in tyledon, leaves d bracts)
Seed quality	Dt:A$_2$-B$_1$;	Dt: A$_2$-B$_1$;	Dt:A$_2$-B$_1$;	Dt:A$_2$-B$_1$;

	Vs: 42-78% Ls: 7-8 month; Gs: 26-54%	Vs:24-56%; Ls:7-8 months; Gs:12-38 %	Vs:40-74%; Ls: 12 months-1,5 years; Gs: 30-52 %;	Vs:46-88%; Ls:10-12 onths; Gs: 18-34 %
Seed treatment	L/Str. (0.5-2.0 months;30°/28° C)	L/Str. 1.5-2.5 months day/night cycles sequence with A/t 25/10° C; removal of fruit covers	Light/dark cycles 15/28° C; organic acids	Light/dark cycles 15/28° C; Removal of it covers

Dt-type of dormancy; Vs-viability of seed; Ls-longevity of seed; Gs-rate of germination; L/str- long-term stratification; A/t- alternative temperatures

Seeds of high vigor and of best quality occur primarily at this time and on the part of the plant, which is flowering at this time. Environmental factors mostly affect the fertility of pollen, and less strongly, pollen size. Pollen maintained viability for 1-2 hours after dehiscence depending on atmospheric water potential. Other factors such as high temperature can also negatively affect pollen fertility. In natural *Salsola* populations this phenomenon is usually overcome by the copious quantities of pollen that are shed. The formation of high partenocarpic seeds is very common for studied species. It was determined that the development of empty seeds in woody *Salsola* complex depends on female, especially stygma/style receptivity, as well as on the process of embryo development (zygotic and/or parthenogenetic) and fruit development. This peculiarity is most characteristic for *S. arbusculiformis,* where two fitness components: sexual and apomictyc is simultaneously functioned.

Results of field experiments and laboratory investigations showed that woody *Salsola* species had a low rate of seed germination both under laboratory and field experiments despite of high percent of viable seeds (with fully developed embryo), except *S. arbusculiformis*. We also found that high degree of sclerification of perianth is one of the main reasons of lower rate of seed germination. According to our data fruit covers contain various inhibitors and it needs special temperature control and/or chemical treatments. Destruction of intact of seed coat or removal of fruit covers was more effective to increase rate of seeds germination in *S. Paletzkiana*. A short-term dormancy was found for the woody *Salsola* species (8-10 months, rarely 1, 5 years) depending on the storage conditions. Dry storage conditions alternate with low temperatures usually stimulate the seed germination. Optimum germination occurs 12-28 ^{0}C. Seedlings also exhibit some level of frost and salt tolerance. The early seed germination gives Salsola species an advantage in winter/spring perennial pastures system.

In addition an evident tendency toward vegetative propagation was also marked for woody Salsola species, especially for *S. richteri* and *S. Paletzkiana*. However the technique of vegetative propagation of these species should be developed that can be a useful tool for Seed Company in controlling rangeland use in research scale planting.

CHAPTER 6. Vegetative floral organ micromorphology, ion/translocation mechanisms and photosynthetic pathways

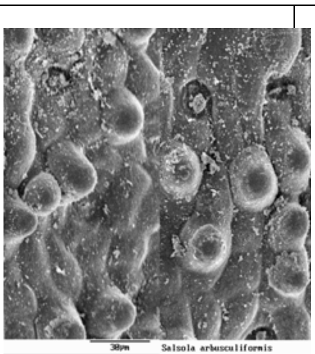
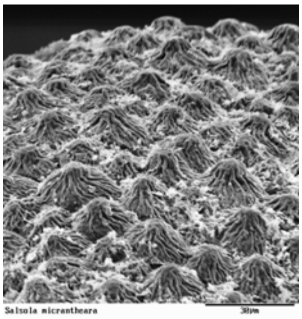
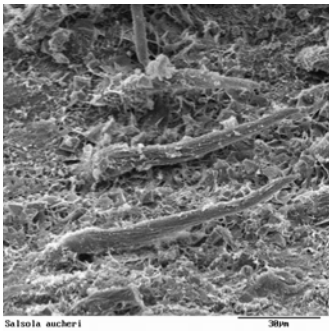
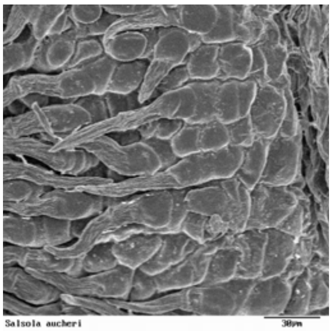
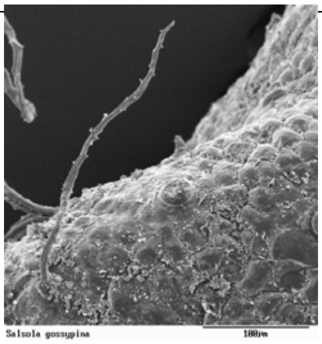
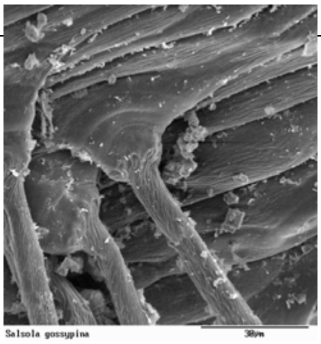
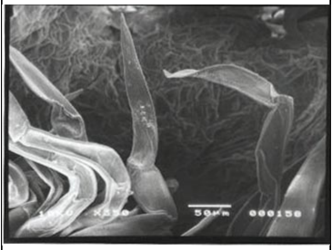
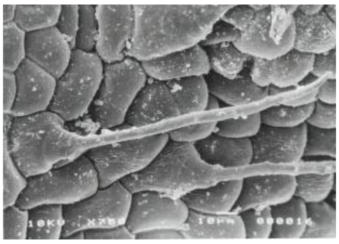
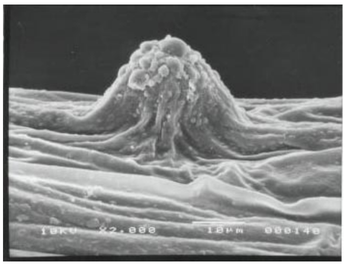
6.1. Diversity of morphology of trichomes, hairs and perianth stomata in some taxa of Salsola

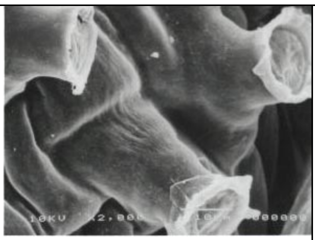
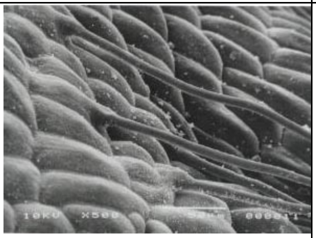
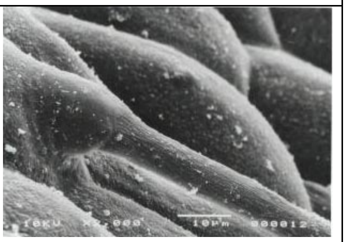
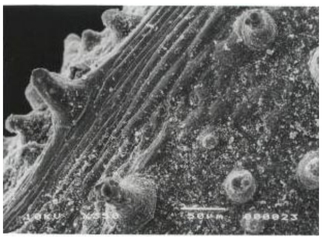
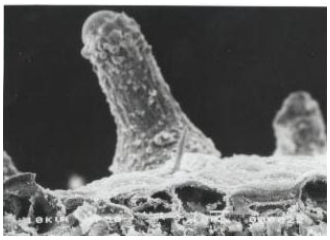
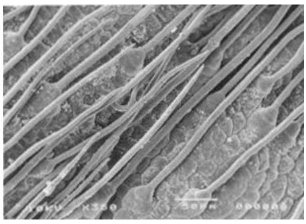
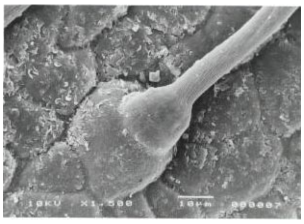
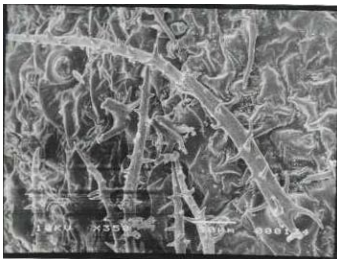
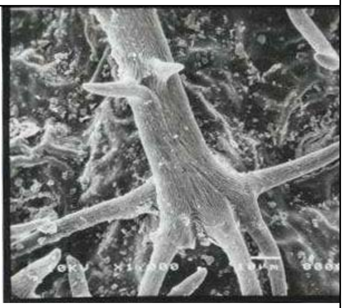
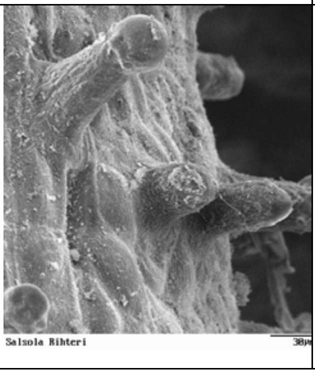
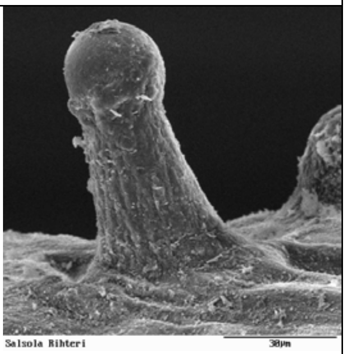
The glandular trichomes are a structure of the plant leaf/perianth surface, which are usually in direct contact with surroundings. By their physical properties and by the production of different chemical products they play a great defensive role against herbivores and pathogens, in the salt secretion, plant pollination and in other interactions between plants and environments.

Trichomes are highly variable appendages of the epidermis including glandular (or secretory) and nonglandular hairs, scales, papillae etc. Although trichomes vary widely in structure within larger and smaller groups of plants they are sometimes remarkably uniform and may be used for taxonomic purposes. Still now there is neither a satisfactory nor well-accepted classification of trichomes for high plants (Behnke, 1984). The importance of the micromorphology and distribution of glandular trichomes for the taxonomy of some species and subspecies have to be reconsidered. Trichome morphology and ultrastructure can also be used as valuable markers of the evolutionary level of the taxons. The pronounced variability of glandular structures can be related to the phenotypic responses to salinity or contaminated environments. Ulbrich,1934 in particular uses them in the delimitation of the sub-families of Chenopodiaceae and these categories in his treatment are fairly homogenous with regard to trichome type. Later Carolin et al., 1983, have investigated trichomes morphology and its classification within Chenopodiaceae and Amaranthaceae. Morphological traits of trichomes and/or hairs provide a key for easier identification and the delimitation of the closely related taxa in different flowering groups. Concerned genus *Salsola* Freitag, 1997 showed the dependence between the anatomy/morphology of trichome type in some *Salsola* species of Iranian flora.

Our study was undertaken to assess the validity of trichome characters in the precise identification of species belonging to genus *Salsola,* as well as to find a correlation among morphological trichome traits with harsh desert environments. The main trichome types for

Asiatic species of *Salsola* are schematically shown in the Fig. 31.

 *S. arbusculiformis*		 *S.micranthera*
S.aucheri		
S.gossypina		
 *S. gemmascens*	 *S. incanescens*	 *S.aperta*

S. leptoclada		
S.crassa		
S.iberica		
 *S.lanata*	 *S.lanata*	 *S. lanata*
S.orientalis		
S.richteri		

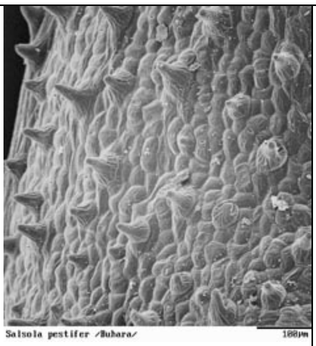
S. pestifer (Kyzylkum desert ecotype)		
S.sclerantha		

Figure 31. Diversity of trichomes morphology (by SEM) in some species of *Salsola*

The species of Asiatic genus *Salsola* exhibited the two unicellular trichome types described early by Carolin,1983 for the families Chenopodiaceae and Amaranthaceae. Using the indumentum characters we defined that the examined *Salsola* species could in fact be allocated to different sectional groups. Densities of unicellular and multicellular trichomes in both bract/bracteoles surfaces, as well as number of cells composing the stalk of multicellular trichomes were subjected of nonparametric analysis of variance (data not shown). On the bracts/bracteoles and tepals (perianth segments) of 28 species, representing all sections of the genus *Salsola* different types of glandular and non-glandular hairs were found.

Our results showed that the trichome characters studied possesses different values for each species and that they might be valuable when identification is impossible using macromorphological parameters. Trichomes have highly variable appendages of the epidermis including glandular (or secretory and nonglandular hairs, scales, papillae). Trichomes of Asiatic *Salsola* species we have classified into a few morphological categories. Some of these categories are: hairs, which maybe unicellular or multicellular; glandular or nonglandular; scales or peltate hairs; water vesicules, which represent enlarged epidermal cells. Glandular hair – a trichome having a unicellular or multicellular head composed of secretor cells, which is usually borne on a stalk of non-glandular cells that vary in degree of differentiation.

For the majority species of *Salsola* – non glandular clothing trichomes, unbranched, uniseriate, multicellular are composed of one or two basal epidermal cells and of one or six cells arranged in one row. Their surface is usually covered by cuticular micropapillae lacking on basal part of the trichomes. The glandular structures are usually bicellular, comprising a basal and cap cell, and are referred to as salt glands, trichomes or microhairs.

Based on the above-mentioned analysis we have proposed the following classification of glandular structure for genus *Salsola:*

A- papillae, the most simple and common type of glandular hairs in the genus *Salsola* scales. The huge or sessile glands that can be found in species of section *Salsola* and sect. *Arbuscula* consist of a short stalk of two parallel cells and multicellular glands. Often the cuticula is removed.

B- peltate trichomes with one basal cell , one stalk cell, and glandular head; the subcuticular space is remarkably large.

C- unbranched, short glandular hairs, stalk bi-or multiceseriate, gland spherical, basal biseriate with two very short cells and a few secretory cells.

D- long capitate trichomes , which have usually one (sometimes two) basal cells; the stalk composed of one to four cells (the upper one is often shorter and marked as neck cell and one cell head; sometimes with small subcuticular space)

E- simple two-armed , unbranched glandular hairs . The stalk cells are usually thin-walled. This type of glandular hairs could only be found on the bracts/bracteoles and tepals of *S. gemmascens* (sect. *Malpigila*)

F- An unusual type of salt glandular structure was described for *S. carinata*. The terminal cell(s) for many *Salsola* species is always end bluntly. On top of the stalk cell, extremely thin-walled cells form a single originally ornamented ring, while the thick cuticle of the stalk cell remains as a cylindrical scar.

The unicelled and stiff trichome on multicellular base is one of most frequently found type within genus *Salsola*. This type of uniseriate smooth trichomes that are mostly common for species of section *Salsola* and *Physurus* have no noticeable difference in texture between the body and at the base, which is more or less bulbous. However, it remains to be explained if long (as a case of species of section *Physurus*) and short as was described for *S. paulsenii, S. praecox, S. pestifer, S. iberica)* trichomes represent two different kinds of trichomes or two different developmental stages of the same. Dense epidermal-cell protrusions or few-celled of well developed smooth trichomes, which were described for some species of sect. *Physurus,* obviously, indicate that these species are tolerant to extreme dry and saline habitats.

Our results showed that Asiatic annual species, especially from sect. *Salsola* sub.*Kali* are clearly separated from those annual species of the same section from Europe. They differ from

Asiatic species of *Salsola* not only by the morphology, but also by the density of unicellular trichomes on both bract/bracteoles surfaces. Micropapillate unicellular trichomes as seen from figures are highly specific to *S. paulsenii, S. praecox, S. pestifer, S. iberica.* The closely related annual European species of section *Salsola*,sub. Kali in particular *S. ruthenica* and *S. kali* are similar with Asiatic annual *Salsola* species in most instances, except for the density of glandular trichomes on the bract/bracteoles surfaces. *S. ruthenica* and *S. kali* are associated with the smooth bract/bracteoles surface or with a presence of slightly developed papillae a soft protuberance structures. This phenomenon, perhaps, indicates to co-species relationships between the Asiatic and European species of genus *Salsola*. Although the abundantly development of various types of trichomes within desert Asian *Salsola* species might be well correlated with the desert ecological factors.

Wide morphological variations exhibit species of sect. *Cardiandra* and *Belanthera*, which mostly possess both uni-and multicellular trichome types (bladder cells –structural organization) those usually, are globose or club-shaped and readily distinguishable from unicellular papillae and sharp-pointed prickles.

The 2-armed or detached smooth trichomes called ‘Malpigilian hairs’ seem highly specific to species of sect. *Malpigila*, while vesicular and various glandular structures were best described for species of sections *Cardiandra* and *Belanthera.*

Species of section *Caroxylon* are clearly separated from all other species of genus *Salsola* by the development of branched and/or dendric trichome types.

In some cases it has been established that a high concentration of variations accumulates in the vacuole of terminal cells of bladder trichomes and are released probably by rupture of the cytoplasm and cell-walls described by Thomson, 1975. In such case the collapsed cell gives the characteristic mealy appearance of the epidermis of so many of the Chenopodiaceae. Thus, using morphological characters, mainly related to epidermal structures (by SEM analysis), we find that the *Salsola* species complex could in fact be divided into two groups: species with salt-producing trichomes/hairs and salt-accumulating (with specific salt/storage cells) plants. This is an indication that different mechanisms and strategies for the sequestration and regulation of the salt ion concentration in the plant tissues are operated in the stem and leaf succulent halophytes and in the recreto-and pseudohalophytes of the Kyzylkum flora. The ability of some desert chenopods to accumulate significant amounts of nitrates and/or oxalates has been noted in the literature (Baslavskaja 1946; Kingsbury 1964; Everist 1974; Erejepov 1978; Fuller and McClintock 1986; Loweres and Yeo, 1988; Ungar, 1991; Sandquist and Ehleringer, 1997; Judd and Ferguson 1999, Butnik, 2001). The spiny leaves or fruits or chemical constituents of them are known to cause skin irritation of animals (Mitchell and Rook, 1979).

In addition, the natural plant-cellular mechanism of salt/metal removal and tolerance provided by this study should permit the development and testing of more informed hypotheses regarding adaptations required for colonization and survival of plants, growing under extremely harsh and simultaneously contaminated desert environments.

It is worth noting here that the multicellular trichomes of vegetative sterile elements of floral bracts, bracteoles and perianth segments of some chenopods and graminous plants are related to salt and heavy metal removal. In some cases, it has been established that a high concentration of various ions accumulates in the vacuole of bladder trichomes terminal cells. The rupture of cuticle or cell walls since collapsed gives the characteristic mealy appearance of the epidermis in many Chenopodiaceae species (Tomson 1975; Carolin 1983). There are two types of glandular trichomes (salt glands) found by us in *Salsola* species that contradict the literature data concerns the absence of salt glands in chenopods (Carolin, 1983). It may be that they are not strictly homologous, particularly since both occur in annual *Salsola* species. We suggest that the different appearance of terminal cells by these two types is due to differences in function connecting both with the accumulation of various ions and /or secretory processes. A comparative morphology study of closely related annual *Salsola* species from highly contaminated desert soils (Kyzylkum) and unpolluted steppe soils (Europe) show an increase of succulent bracts/perianth segments consistent with Kyzylkum chenopods. Epidermal vesicles were rarely recorded here. The prickles, as single celled hairs with relatively thin cellulose walls, and thick cuticles, as in some annual chenopods, may represent the final stage in the reduction of uniseriate hairs (type 3 and 4 according to Carolin, 1983 classification. We are inclined to consider various morphological types of hairs described mostly for *Salsola* species as part of the same transformation series. Probably they perform different functions. However, little is known about the origin and significance of such kind of transformation, especially when they occur on the same plant.

Stomata apparatus diversity in genus *Salsola*. The stomata are openings (the stomatal pores, or apertures) in the epidermis bounded by two specialized epidermal cells, the guard cells, which by changes in shape bring about the opening or closure of the aperture. Stomatal frequency within representatives of genus *Salsola* varies greatly. It varies on different parts of the same leaf/or leaf –like organs and on different leaves, bracts/bracteoles of the same plant and is influenced by environmental conditions. In bracts/bracteoles of examined *Salsola* species stomata occur on both sides or mostly or only on one side, usually lower. Stomata also vary in the level of their position on the epidermis. Some are even with the other epidermal cells; others are raised above or sunken below the surface (as the case of *S. lanata, S. crassa).*

The two features just discussed for genus *Salsola*, the number of stomata per unit area and the positional level of the guard cells with respect to other epidermal cells are so variable that they are of little of taxonomic value. The more frequently used taxonomic character is the appearance of the stomata as seen from the surface, especially with reference to the nature and orientation of the neighboring cells (Essau, 1966). The stomatal counts indicate a great variation in the absolute number per unit area, probably due to differences in variety (species) and ontogenetic stage of leaf-like organs.

6.2. Salt accumulation, silicification, wax deposit associated with epidermal structures of the inflorescence bracts and bracteoles

The analysis of average values of trace element composition in the various types of soils of the Central Kyzylkum deserts show high levels of Hg, Cu, U, As, Zn, Mo, Ni, Sr, Co (Table 6). Coefficients of concentrations ($K_k=C_f/C_k$) of above-mentioned heavy metals exceed 1.0. Soils contaminated with As, Zn, Ni, Mn, Cu, and Sr has been defined to be mostly toxic and widely distributed in sandy Kyzylkum Deserts. Nickel is of natural origin and in the soils it occurs in form the rich nickel-cobaltum rock types, particularly of Palaeozoic age. Concentrations of nickel in soils are in the ranges of 60-70 ppm. The mobility of As, Cu, Zn (along with other heavy metals and their accumulations) are highly facilitated by both chemical properties of soils and the aridity of the climate of the Kyzylkum Deserts.

It is noted that the technogenic pollution by heavy metals, organic pollutants is concentrated around mining and tailing waste deposit zones and is located exclusively in foothills areas of Kul'dzhuktau, Auminzatau, Tamdutau, Dzhemtau, Aristantau and Bucantau mountain ranges, located in the Central Kyzylkum

Table 6. Average values of trace metals composition in the soils of the Central Kyzylkum Deserts

Chemical elements	$(C_k)^*$, ppm in the soil according Klark)	Average containing (C_f), ppm	Coefficients cf concentration (K_k)
Be	6	1	0.2
Cd	0.5	0.19	0.4
As	5	7.7	1.5
Hg	0.01	0.048	4.8
Pb	10	8	0.8
Zn	50	51	1.0
Co	10	8.1	0.8

Cu	20	57	2.9
Mo	2	2.3	1.2
Ni	40	40	1.0
Sb	-	1	-
Cr	200	55	0.3
Ba	500	400	0.8
W	-	4	-
V	100	89	0.9
Mn	850	340	0.4
Sr	300	190	0.6
U	1	2	2.0
Th	6	8.2	1.4

(Vinogradov, 1957 and Malyuga, 1963)

Tailing sand soils contaminated with cadmium, copper, iron, nickel, manganese, chromium, lead and zinc are colonized by plant and animal species that have developed strategies for avoidance of and/or tolerance to metal toxins. One possible avoidance strategy is for plants to prevent the uptake of potentially toxic metals. This mechanism is not strongly developed in vascular, arid-land plants, although tolerant plants may restrict metal uptake to varying degrees. The concentrations of some metals (indicated in the Table 5) were only unusually high in the accumulator's plants.

Our experiments have demonstrated that only a restrict number of the Kyzylkum sandy/deserts species have the ability to translocate, to high concentrations, a wide variety of elements, such as: Fe (15-4170); Zn (9.0-50.0); Pb (0.1-7.6) ; Ni (0.0-3.7); Cr (0.1-50.0) ; Sr (0.0 –793.0); or trace levels (e.g. As (0.1-1.9); Co (0.1-2.7); Th (0.1-2.5); Cd (0.1-0.18).

A survey of much the Kyzylkum halo-metallophyte flora has revealed a few species in Uzbekistan, mainly from genera *Salsola* (both annuals and perennial ones), *Haloxylon, Halothamnus, Kallidium, Anabasis, Tamarix, Artemisia, Peganum, Zygophyllum, Smirnovia, Poa, Allysum, Carex, Euphorbia, Frankennia, Lycium.* The plant families most strongly represented are the Euphorbiaceae, Tamaricaceae, Chenopodiaceae, Poaceae and poorly Asteraceae, Fabaceae and Cyperaceae. However, future work is needed to:

- select optimal genotypes from Kyzylkum desert flora and to initiate a program of it's seed multiplication;determine the mechanisms of their hyperaccumulation and hypertolerance ;isolate the genes involved. It may then be possible to genetically engineer these traits into higher biomass crops by making them transgenic and make the process of heavy metal phytoextraction more efficient.

Several authors have pointed out that the use of plants, which hyperaccumulate heavy metals in their aerial parts could be an economically efficient method for cleaning the soil (Kiekens et al. 1982; Williams et al. 1994; Leblane et al. 1999; and Escarre et al 2000). Significant progress has been made in recent years in developing native or genetically modified plants for the remediation of contaminated environments (Wu et al., 1993; Rugh et al 1996; Heaton 1998; Meagher et al 2000).

The timing of salt excretion with plants organ development is of critical importance, not only for our understanding of the cellular mechanism involved, but also because salt/toxin accumulation could interfere with animal diets. Chemical defenses may be the most important characteristic which plants employ to protect themselves against forage-grazing selection by many livestock and wild animal species. The study of chemical compounds (origin, localization etc.) for Asiatic desert plants are of great interest because they are often specific to a particular plant species or genus and must therefore have been designed to serve a particular protective function. The analysis of average values of trace elements composition in the various types of soils of the Central Kyzylkum deserts showed high levels of Hg, Cu, U, As, Zn, Mo, Ni, Sr, Co. The coefficients of concentrations ($K_k=C_f/C_k$) of heavy metals exceeded 1.0. Soils contaminated with As, Zn, Ni, Mn, Cu, Sr have been defined to be mostly toxic and widely distributed in sandy Kyzylkum Deserts. Nickel originates in rock rich in nickel and with cobalt, particularly of Paleozoic age. Concentrations of nickel in soils are in the ranges of 60-70 ppm. Mobility of As, Cu, and Zn, along with other heavy metals and their accumulations, is highly facilitated by both chemical properties of soils and aridity of Kyzylkum deserts climate. It was determined that pollution by heavy metals and organic pollutants is concentrated around mining and tailing (waste) deposit zones, and exclusively in the foothills areas of Central Kyzylkum, such as: Kul'dzhuktau, Auminzatau, Tamdutau, Dzhemtau, Aristantau and Bucantau mountain ranges.

Our experiments demonstrated that only a restrict number of the Kyzylkum flora species had the ability to accumulate high concentrations a wide variety of elements (Table 7). A survey of the Kyzylkum halo-and metallophyte flora has revealed a few species in Uzbekistan, mainly from the following genera: *Salsola* (both annual and perennial species), *Haloxylon, Halothamnus (Aellenia), Halostachys, Kalidium, Anabasis, Tamarix, Artemisia, Peganum, Zygophyllum, Aeluropus, Eremopyrum, Poa, Allysum, Carex, Euphorbia, Frankenia, and Lycium.* The plant families most strongly represented as accumulators are the Euphorbiaceae, Tamaricaceae, Chenopodiaceae, Poaceae, while the families Asteraceae, Fabaceae, Cyperaceae and Zygophyllaceae were less well represented. Specimens of *Triticum sp*. (Poaceae), growing on the cultivated foothill fields of Central Kyzylkum, showed high concentrations of iron (up to 2547 ppm) in the aerial dry matter of the plants. *Artemisia diffusa* (Asteraceae) had remarkably high Zn levels, above 5020mg/kg, and it deserves being described as a hyperaccumulator. The species *Haloxylon aphyllum*, *Tamarix hispida*, *Artemisia diffusa*, some species of *Salsola* and *Peganum harmala* all demonstrated a strong tendency to translocate strontium.

Table 7. Average values (mg/kg) of trace elements in the aboveground dry matter of field-grown plants of Central Kyzylkum region

Plant species	Fe	Mn	Sr	Pb	Zn	Cu	Mo	Cd	V	As	Sb	Se	Ni	Co	Cr	Th	
Alhagi	315	36,1	170,5	0,0	26,2	8,3	2,7	0,1	0,7	0,1	0,0	0,2	2,5	0,3	1,5	0,1	
pseudoalhagi	280-350	29-43	85-256	0,0	17-35	7-10	2-3	0-0,1	0,5-0,9	0-0,2	0,0	0-0,3	2-3	0,3	1-3	0,1	
Peganum	865	38,2	234,3	0,3	24,2	7,2	2,5	0,1	2,0	0,1	0,0	0,5	2,0	0,5	3,2	0,3	
harmala	15-3310	14-86	0-793	0-3,6	14-58	3-13	0-6,4	0-0,2	0-11	0-0,3	0-0,2	0-0,2	0-6	0,1-2,7	0-11	0-2,5	2
Carex	395	22,3	65,7	0,5	17,2	8,9	2,2	0,2	1,8	0,0	0,1	0,0	1,6	0,2	2,4	0,1	
physodes	250-580	19-26	48-104	0-3,2	11-28	3-21	0-4,6	0,1-0,4	1,4-2,5	0,0	0-0,1	0,0	0,9-2,8	0,2-0,3	0,9-4,7	0-0,2	1
Poa bulbosa	280	24,6	53	0,0	18,8	9,1	3,6	0,18	3,1	0,0	0,02	0,0	2,0	0,14	4,4	0,08	
Carex pahystyllis	685	71,5	57	0,4	16,8	7,6	2,6	0,2	1,5	0,2	0,1	0,5	5,3	0,3	24,6	0,1	
	500-870	18-25	21-93	0-0,8	16-18	7-9	0-5,2	0,1-0,2	1,2-1,8	0-0,4	0-0,1	0,3-0,6	1-9	0,2-0,4	2-47	0,1-0,2	1
Artemisia diffusa	932	38,1	123,6	0,4	23,3	11,6	3,1	0,1	2,4	0,2	0,0	0,3	3,3	0,5	3,7	0,3	
	117-5020	15-128	13-980	0-7,5	9-72	3-25	0-9,3	0-0,4	0-15	0-1,9	0-0,5	0-7,6	0,5-12	0,1-1,9	0,5-14	0-1,2	4
Triticum sp.	2547	62,7	82,3	2,4	25,3	15,3	1,3	0,2	7,1	0,1	0,2	0,2	5,6	1,1	20,6	0,8	
	440-4650	10-150	27-135	0-7	16-38	6-25	0-3,6	0,1-0,4	1-14	0-0,6	0,1-0,5	0-0,5	1-13	0,3-2,2	2-50	0,1-1,5	3
Haloxylon aphyllum	454	42,0	146,3	0,3	19,2	5,8	2,7	0,1	0,6	0,1	0,0	0,2	3,6	0,2	2,1	0,1	
	100-2600	18-82	53-1041	0-4	11-41	2-13	0-7,1	0-0,2	0-3,4	0-0,4	0-0,2	0-1	0-24	0,1-1,1	0,3-23	0-0,8	1
Salsola L.	569	41,6	153,6	0,5	20,8	6,7	1,6	0,1	2,0	0,1	0,0	0,9	1,8	0,4	2,0	0,1	

	160-1880	16-93	21-508	0-7,6	8-50	3-12	0-5,6	0-0,5	0-12	0-0,5	0-0,2	0-13,6	0-4	0,1-0,8	0,5-5,5	0-0,7	2
Tamarix Hispida	2960	74,0	264	0,0	20,1	6,4	0,9	0,09	8,1	0,0	0,09	0,2	5,7	3,08	8,5	0,87	
Ferulaassa-foetida	755	32,2	147	0,1	21,3	21,4	1,5	0,1	1,8	0,0	0,1	0,0	2,1	0,3	3,2	0,2	
	510-1100	25-50	116-166	0-0,5	17-33	9-54	1-2	0-0,4	1,1-2,6	0,0	0-0,2	0,0	1,2-3,7	0,2-0,4	1,2-3,6	0,2-0,3	

From the standpoint of metal accumulation, *Artemisia diffusa* was mostly inferior to *Tamarix hispida, Carex pahystylis, Triticum sp.* *Salsola spp.* showed a multi-element accumulation capability with regard to nickel, chromium, strontium and iron. The plant species exhibited differences in their ions/metals distribution characteristics (Fig.32).

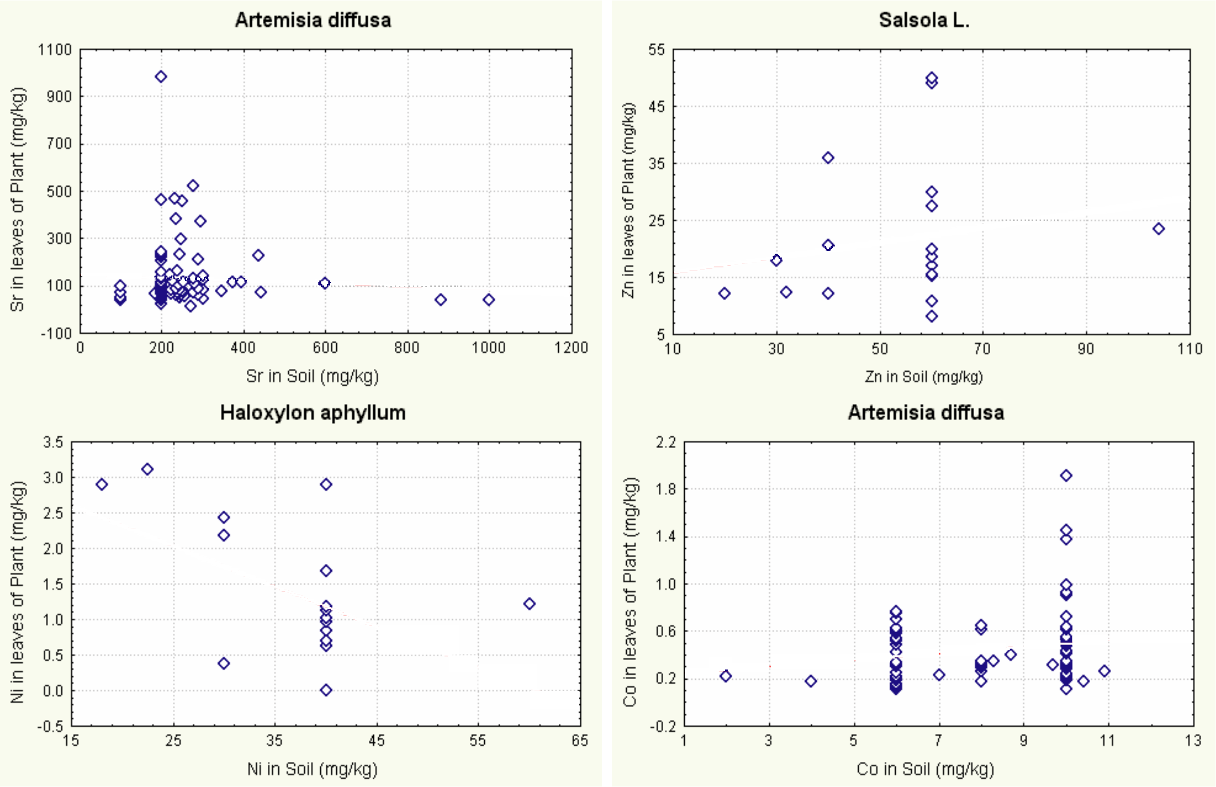


Figure 32. Ions/metals distribution characteristics in various desert taxons

The representatives of genus *Salsola* maintained the ions of Zn in their tissues over a wide range of soil-metal concentrations, indicating hyperaccumulation. Conversely, Zn extraction by *Artemisia diffusa* is relatively high in relation to the comparatively small variation of soil Zn concentrations. The relationship between the concentrations of Co in the plant tissues of *Salsola* species and soil was curvilinear, showing that this taxon is capable of accumulating large concentrations of Co across a wide range of soil concentrations. A few species, among those studied taxons described as ion-accumulators, recorded high survivability and high seed germination rate, but with a low biomass production.

Our analyses show that these desert plants, grown on metalliferous or salinized soils, tend to accumulate the highest ion concentrations in epidermal and subepidermal tissues, including various glandular structures of bracts/bracteoles and perianth segments. Salt glands that are recognized as structures of varying degree of specialization, actively involved in the elimination of solute, mineral elements on the surface of the vegetative organs are very common for Asiatic desert plants. Excretion occurs predominantly on the adaxial surface and is uniformly localized along the lateral walls of the grooves. Salt glands vary somewhat in different genera in that they may be sunken, semi-sunken or located above the epidermis as in the majority of investigated chenopods and gramineous species. In chenopods and in graminous species glandular structures are usually bicellular, comprising a basal and cap cell. Slight variations in morphology of the basal and cap cells of glandular hairs were described mostly with annual species of genus *Salsola, Aeluropus litoralis* and *Eremopyrum orientale,* which appear to be related to their efficiency of salt secretion (Toderich et al., 2003). The analogy was described for *Cynadon* and *Distichlis* species (Thomson et al 1988) where large flask-shaped, sunken basal cells and dome-shaped cap cells secrete salts more efficiently than trichome-like glands with narrow basal and cap cells as in *Sorghum halapense* (McWhorter et al 1995) and *Sporobolus virginicus* (Naidoo 1998).

We frequently observed epidermal vesicles and papillae in desert species. As seen on the Figs. 33 and 34, such type of epidermal structures have a large, bladder cell attached to a stalk composed of one or more cells that in turn is attached to an epidermal cell. Comparative study of two annual taxonomically close related *Salsola* species from steppe soils of Europe (Poland) and Kyzylkum metalliflerous/salinized sands revealed that salt secretion become prominent and salt glandular structures are formed abundantly only when plants are exposed to high contaminated environments. Under such conditions an evident increasing of succulent bracts was consistency noted with Kyzylkum chenopods.

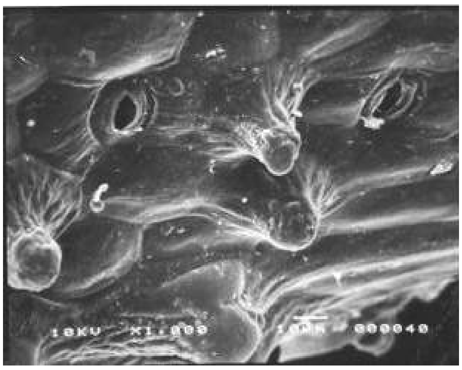


Fig.ure 33. The morphology of vesicular-and short peltate trichome on bracts of *Salsola pestifer* (Buchara ecotype).

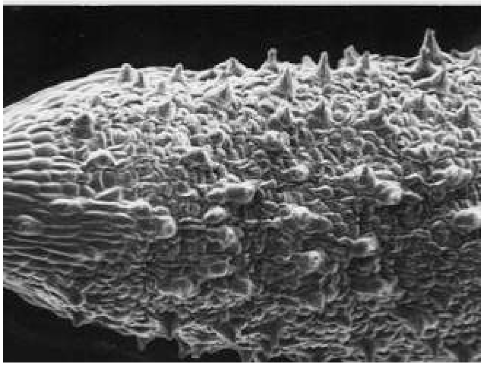


Figure 34. Epidermal surface view of mature bracts of *Salsola .pestifer* (Buchara ecotype). Glandular structures have a strong localization, especially on adaxial side, which is mostly exposed to environmental impact. X 750

We suggested that the vesiculate hairs of some Asiatic annual *Salsola* are considerably involving in cellular salt secretion mechanisms. Although in the opinion of Luttge 1971, this might not be taken strictly as a secretor process, these trichomes are considered salt glands review since their function is obviously a specialized mechanism for the removal salt from the leaves. The emission of salt in these vesiculated hairs is apparently the result of the rupturing and collapses of bladder cells (Luttge, 1971). The presence of papillas on the epidermal cells as was described for *S. praecox*, *S. iberica* and *S. pestifer*, their thick outer walls, cuticle and submerged stomata seemingly protect assimilatory organs against excess transpiration. Annual C_4- herbaceous species, known in practice of pasture economy of Uzbekistan as “solyanki" differ by salt-glands/trichomes morphology (shape of their head: mainly clavate or capitate or also in the number of constituent cells composing their stalk) and its density on the epidermal surface. Variation in salt glands /trichomes density is believed to be mainly the effect of stress/desert environmental factors and even herbivore pressures (Johnson, 1975). These parameters potentially could be used as discriminating characters between different ecological halophytes groups. For instance the *Climacoptera* complex has a unicellular non-glandular trichomes or hairs possessing a smooth or micropapillate (warted surface), while the bract/bracteoles surface of many dry/sclefiried *Salsola* species has an undulating epidermal surface with numerous salt glandular structures and tall adaxial ridges alternating with deep grooves. On the ridges of annual *Salsola* species we found various papillae and prickle hairs, as well as secreted salts, which appear as crystals. Crystaline deposits were more abundant on the adaxial organ surface because of the higher gland frequency (s 35- 36).

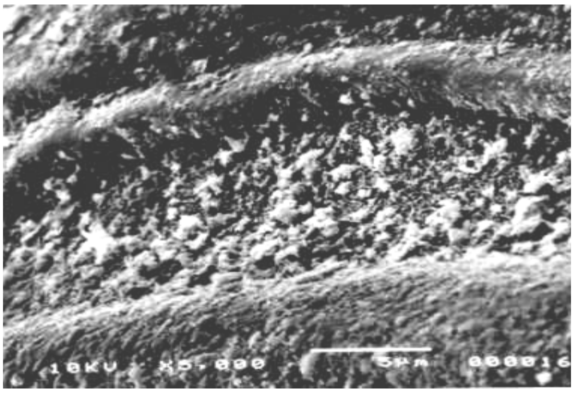


Figure 35. The adaxial surface of bracts S. *iberica* with ridges and salts whic appear as crystals.

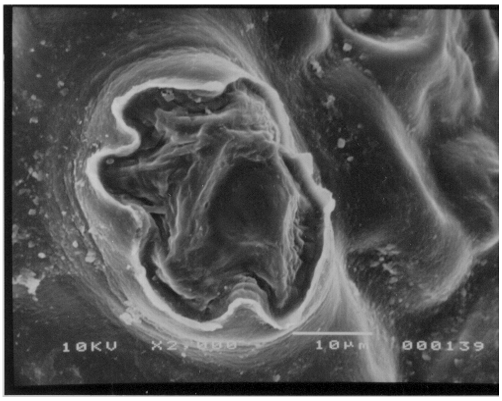


Figure 36. SEM microgrphs showing t patterns of crystaloid structure in the bra tissues of *S. orientalis*.

Salt glands (bladder cells–structural organization) usually are globose or club-shaped and readily distinguishable from unicellular papillae and sharp-pointed prickles. An ornamented, porous cuticle overlies the epidermis. The cuticle is distinctly thicker over the area that adjoins basal and epidermal cells than over the cap or other parts of the epidermis. The cuticle is separated from the outer cap cell wall, resulting in the formation of a salt collecting chamber or cuticular cavity. The cuticular cavity we noted for species of *Salsola* (both annual and perennial*), Aeluropus litoralis* and *Eremopyrum orientale* is similar to those in *Spartina, Cynadon* and *Distichlis* (Thomson, 1975) and probably represents a temporary collecting compartment where secreted salts accumulate prior to elimination from the leaf. The ions seem to be compartmentalized in small vacuoles and transported to the cuticular cavity, prior to exclusion from the vegetative and reproductive organs either through cuticular pores or by rupture of the cuticle (Yordoan 1998, Naidoo 1998).

An unusual type of salt glandular structure was described for *Salsola carinat*a: the terminal cell(s) is always end bluntly. On top of the stalk cell, extremely thin-walled cells form a single originally ornamented ring, while the thick cuticle of the stalk cell remains as a cylindrical scar (figs. 37-40).

Figure 37. Salt gland of Salsola paulsenii comprising flask-shaped basal cell, dome-shaped cap cell an raised cuticular chamber

Figure 38. Micromorphology of landular hairs of Salsola sclerantha and wax-epicuticular inclusions partially surrounding it

Figure 39. SEM micrograph showing
surface features and morphology of
non-glandular, unicellular hair of brac
in *Cimacoptera lanata*

Figure 40. Untypical morphology of sa
gland, occurring on the epidermal
bract's surface of *Salsola carinata*
(Central Kyzylkum ecotype) .

Cross-sections of bracts and bracteoles of many *Salsola* species shows that different tissues carry out water and salt-accumulating functions: swollen epidermal cells (in all species), large–celled hypodermis and water bearing parenchyma. Size, shape and/or their density should be recognizing by the location and deposits of salt/ions into specific (salt- storage) cells. The displacement of salt ions in the flower organs of some *Salsola* species by means of fluorescent microscopy reveals an abundance of mineral ions in the tissues of sterile of flower like sepal's elements or anther connective cells. However ions dislocation has never been observed in male-and female gametophytes or in embryos (Figs. 41-44).

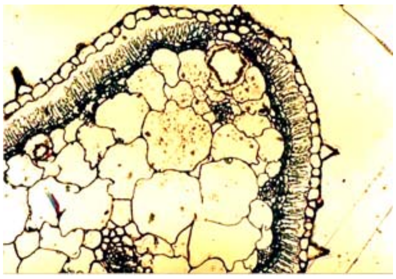


Figure 41. Cross-section of succule
bract of *Salsola praecox*; central pa
is occupied by 3-4 layers of water
storing parenchyma cells with sma
salt crystals. 10 X 60 (1µk)

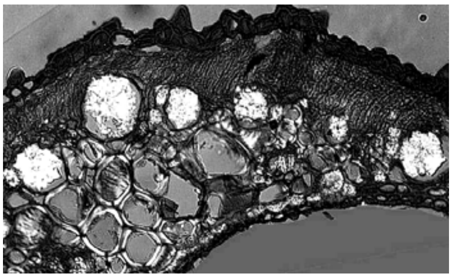


Figure 42. Anatomy of bract tissue
Salsola arbusculiformis. Differe
types of crystals in the subepiderm
salt-storage cells. 10 X 60 (3.0 µk)

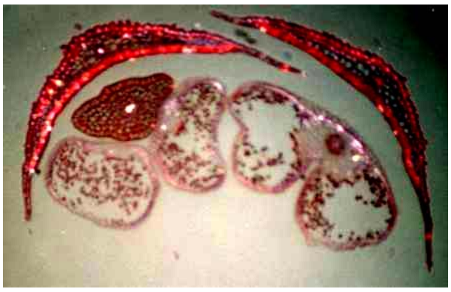


Figure 43. Cross section of anther
Salsola arbuscula. The salt io
location in pollen grains (ma
gametophyte) is absent. 10 X
(1µk)

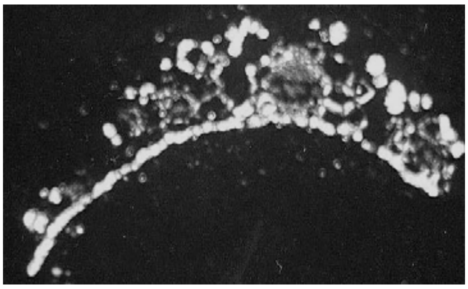


Figure 44. The fluorescent microsco
image of bract of *S. arbusculiform*
with the location of salt/ions in it. 10
60 (1µk)

Figures 41-44. Cross section of vegetative organs of flowers shown different cellular mechanism of ion/salt translocation

Occurrence of calcium oxalate crystals in leaves and seed coats of poisonous plants was described by Fuller and McClintock, 1986. It was suggested that the concentrating of oxalate crystals was almost absent in the root and stems. The presence of crystals in the outer covering of seeds may play a role in changing soil pH, thereby providing a more favorable condition for plants survival.

Structurally, SEM methods revealed a high diversity in the micromorphology of epicuticular wax (epicuticular secretion), mostly occurring as specific crystalloids on the plant surface of these desert plants. Cuticular wax partially covers the mature pricle-hairs, papillas and long cells of outer epidermis of bracts/bracteoles of some perennial *Salsola* species (Figs 45, 46). Unfortunately the nature and molecular organization of such wax deposits is still unknown for desert plants. Therefore we shall use the term crystalloids (epicuticular wax crystalloids) proposed by Barthlott et al., 1998, which recognize this uncertainty. There is also evidence in the literature that chemically these waxes consist of alkanes, long-chain alcohols, ketones, esters of long-chain fatty acids, cyclic compounds like phytosterols, pentacyclic triterpenoids and epicuticular flavonoids (Barthlott 1994; Barthlott et al.1998). However, there are still contradictory opinions concerning waxes deposition. Hall et al 1965 suggested that waxes could be exuded to the outer cuticular surface through pores, while Hallam, 1970 and Mahllberg, 1991 suggested excretion through lamellate regions onto the cuticle. Glandular trichomes in such case enhance a plant capacity to accumulate large quantities of volatile components and transport them to the cuticular surface for vaporization from the gland surface.

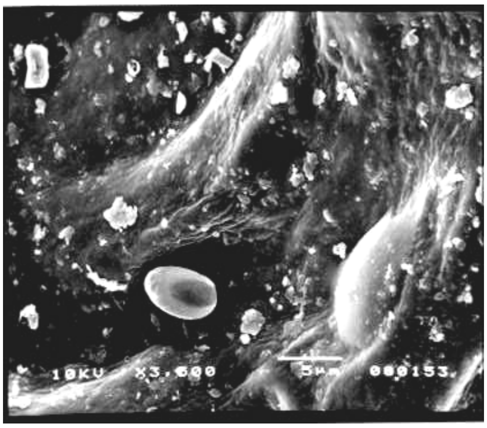


Figure 45. Scanning micrograph of *Salsola orientalis* bract epidermal surface with various salt crystaloids (or epicuticular inclusions) on it.

Figure 46. Silicon X-ray distribution image of mature inflorescence bracts in E*remopyrum orientale (Poaceae)* X 3000

A comparative developmental study of floral organs of various chenopods and gramineous species revealed that Si accumulation was greatest on the adaxial trichomes of inflorescence organs of *Eremopyrum orientale, Bromus tectorum* and *Aeluropus litoralis,* collected from highest contaminated lands from the Bukhara oasis. The localization of small siliceous particles on the inflorescence bracts of *Eremopyrum orientale* that is concentrated mostly on the surface of epidermis around stomata. Crystalloid types in *Salsola* taxons are characterized by uniformly distributed small irregular-shaped platelets; occasionally they have also a parallel orientation around the stomata. In some chenopods species platelets occur in clusters too. The similar silicification process associated with trichomes and other epidermal structures of the inflorescence bracts was described for *Phalaris canariensis L* (Poaceae). There is an opinion that the silification may be synchronized with the deposition of wall substances, such as lignin, suberin and phenols (Sangster and Wynn Parry, 1981). Silicon deposition patterns and localization in bracts has been described for different groups of flowering plants Sangster et al., 1983. Siliceous hairs and particles have been suggested as possible causative factors of human oesophageal cancer (Hodson et al., 1983).

Electron microscopic X-ray analysis of salt glands secretion products with different representatives of *Salsola* has revealed the localization of variety of mineral elements and ions. Prismatic crystals secreted by glands primarily contain cations Na, K, Ca, and anions Cl, SO_4, carbonate, although other ions such as Mg, Si, Sr also were detected. We believe that our findings require further studies on a wider range of plant material in respect to structural and genetic variation and their relation to bioremediation of contaminated desert ecosystems.

Summarizing the results of this chapter we have concluded that tailing sandy and saline soils, contaminated with Cd, Sr, Cu, Fe, Ni, Mn, Cr, Pb, Zn, various toxic salts and organic pollutants are colonized by plant species that develop strategies for avoidance and/or tolerance to metal toxins. One possible avoidance strategy is for plants to prevent the uptake of potentially toxic metals, especially into the reproductive organs like pollen grain (male gametophyte) and embryo. This mechanism still is not strong analyzed in arid vascular plants, although tolerant plants seem to restrict salts and metal uptake to varying degrees. It was found that salt (minerals and ions)-accumulating glands are mostly common in families Poaceae, Tamaricaceae, Chenopodiaceae, and Frankenaciaceae, but only occurred in a few scattered species from Plumbaginaceae, Zygophylaceae, Fabaceae, Lamiaceae. Many species of these families are known to have glandular structures, but in many instances further investigations are needed to determine their secretion products.

Using morphological characters, mainly related to epidermal structures (by SEM analysis), we find that the Salsola species complex could in fact be divided into two groups: species with salt-producing trichomes/hairs and salt-accumulating (with specific salt/storage cells) plants. This is an indication that different mechanisms and strategies for the sequestration and regulation of the salt ion concentration in the plant tissues are operated in the stem and leaf succulent halophytes and in the recreto-and pseudohalophytes of the Kyzylkum flora. The ability of some desert chenopods to accumulate significant amounts of nitrates and/or oxalates has been noted in the literature (Baslavskaja 1946; Kingsbury 1964; Everist 1974; Erejepov 1978; Fuller and McClintock 1986; Judd and Ferguson 1999; Butnik et al., 2001). The spiny leaves or fruits or chemical constituents of them are known to cause skin irritation of animals (Mitchell and Rook 1979). In addition, the natural plant-cellular mechanism of salt/metal removal and tolerance provided by this study should permit the development and testing of more informed hypotheses regarding adaptations required for colonization and survival of plants, growing under extremely harsh and simultaneously contaminated desert environments. The existence of great diversity in photosynthetic pathways of Asiatic *Salsola* species, as well as in their CO_2 assimilation organs anatomy and biochermical features also is evidence related to plant's growth, survival, and reproduction in these continental deserts (Butnik et al 1991; P'yankov et al 2001, 2002).

It is worth noting here that the multicellular trichomes of vegetative sterile elements of floral bracts, bracteoles and perianth segments of some chenopods and graminous plants are related to salt and heavy metal removal. In some cases, it has been established that a high concentration of various ions accumulates in the vacuole of bladder trichomes terminal cells. The rupture of cuticle or cell walls since collapsed relates this process probably cells gives the characteristic mealy appearance of the epidermis in many Chenopodiaceae species (Tomson 1975; Carolin 1983). We suggest that the different appearance of terminal cells by these two types is due to differences in function connecting both with the accumulation of various ions and /or secretory processes. A comparative morphology study of closely related annual *Salsola* species from highly contaminated desert soils (Kyzylkum) and unpolluted steppe soils (Europe) show an increase of succulent bracts/perianth segments consistent with Kyzylkum chenopods. We are inclined to consider various morphological types of hairs described mostly for *Salsola* species as part of the same transformation series. Probably they perform different functions. However little is known about the origin and significance of such kind of transformation, especially when they occur on the same plant.

The use of heavy- metal tolerant flora to reclaim soils could represent both a practical and economically viable alternative strategy. Halophytes and simultaneously metal tolerant arid/semiarid plants may be used for phytoremediation of areas contaminated with toxic salts and heavy metals. The plants that were found growing well in natural metalliferous and/or high saline sandy habitats we include as metal tolerant and/ or facultative metallohalophytes. We suggest that for bioremediation purposes there should be interest in any species that consistently has a metal/salt removal potential. Since several "hyperaccumulators" are characterized by small biomass production, the use of selected metallohalophytes species, as phytoremediators capable of accumulating high amounts of toxic ions should be considered.

In addition of a great interest is the usage of local floral resources for land phytoremediation, the introduction of new succulent halophyte species with high adaptability to severe waterlogging for forming protective water-saving mechanisms. The cultivation of halophytes (C_3 and C_4 plants) both native and introduced may limit long-distance salt spreading and improve the vitality and growth conditions for local species, when cultivated in combination plantations. And since stress conditions frequently trigger defense mechanisms based on the production of specific biological active metabolites of pharmaceutical or industrial importance, halo-metallophytes of the South part of Aral Sea Basin could constitute a valuable source of cash compounds. These characteristics may offer a new and valuable source of income to local populations and favor the movement from crowded impoverished towns to prosperous rural communities

6.3. The occurrence of C_3/C_4 photosynthesis in the leaf-like organs of some *Salsola* species under Kyzylkum desert conditions

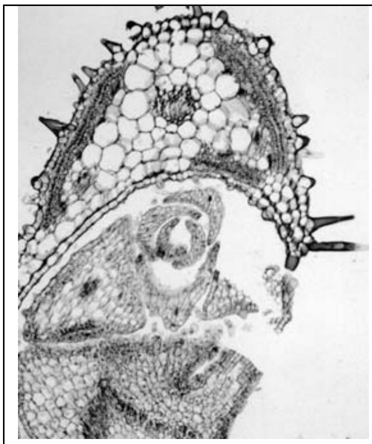
Diversity in anatomy of assimilation organs and their photosynthetic pathway has been marked within representatives of genus *Salsola*. Two anatomical types, Salsoloid and Sympegmoid (Carolin et al. ,1975; Butnik, 1979; Toderich, 1992; Toderich et al, 2002; Voznesenskaya et al, 2002; and Freitag et al, 2002) occur in leaves of species of *Salsola.* It was also determined that some species with Salsaloid anatomy have NAD-ME C_4 photosynthesis, whereas others have NADP-ME C_4 subtype (P'yankov et al., 1997, 2001). Plants with Sympegmoid anatomy have C_3-like C^{13}/C^{12} carbon discrimination values (Akhani et al., 1997б P'yankov et al, 1997). Variations also occur in structural and biochemical features in cotyledons (P'yankov et al, 1998, P'yankov et al., 1999). Two non-Kranz anatomies, Atriplicoid and Salsoloid, are found in *Salsola* cotyledons (Butnik, 1979 P'yankov et al., 1998). Finally, Kranz-type cotyledons and leaves may or may not contain a hypodermis. The result is a number of unique combinations of structural and biochemical photosynthetic types in leaves and cotyledons in species of Salsoleae. So, multiple origins of C4 photosynthesis as was described for the families of Poaceae, Cyperaceae, Asteraceae and Zygophylaceae appear likely within Chenopodiaceae and the diversity of photosynthetic types and anatomical structures in the tribe *Salsoleae* suggests a dynamic pattern of photosynthetic evolution within this single tribe.

From our phenological observations and experimental results, it seems very likely that structural polymorphism of floral organs and sexual reproduction system in some Asiatic *Salsola* species are coupled with the diversity of photosynthetic pathways and anatomy of the CO_2 assimilative organs.

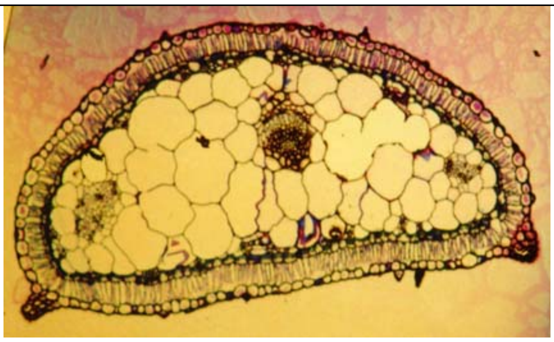
S. arbusculiformis manifest a Sympegmoid leaf and bracts anatomy and non-Kranz bundle sheath cells (Voznesenskaya et al. 2001;Toderich, unpubl. data). Other species of Section *Coccasalsola* forming a unique "plant functional group" can be united by Salsoloid (with hypodermis both in leaves and reproductive organs) or a "Crownary –centrical Kranz type of photosynthetic cell arrangement (Voznesenskaya and Gamaley, 1986). The Salsoloid type of Kranz assimilation tissues anatomy is always associated with the C_4 syndrome (Jacobs and Vesk,1975; Freitag, 1997b) that is well support by represented in tab.7 C_4 like $^{13}C/^{12}C$ carbon discrimination values in leaves, flowers and fruits with a range of – 12.0 - 14.08. Such similarity of anatomical and biochemical features is well coordinated with developmental stability of reproductive system noted by us for *S. arbuscula, S. richteri* and *S. Paletzkiana.*

However, plants of *S. arbusculiformis* from their natural habitats with Sympegmoid leaf and bracts anatomy maintained their $^{13}C/^{12}$ $C_{3/}C_4$ carbon fractionation values in the range from - 23.6 - 26.31 throughout their ontogeny, although significant variation was found within plant organs with 2.69 $^{0}/_{00}$ in flowers. In addition *S. arbusculiformis* is characterized by a set of primitive embryological features such as ana-campylotropous, crassinucellate, bitegmic ovule, autogamy (self pollination /fertilization system) , narrow specialization of sexual reproductive system that may be an evidence of lower reproductive plant functional activities leads to the lower level of seed set, seed viability and their seed germination energy. It is also known that C_3 is the primary type of photosynthesis in relation to C_4. Apparently there is a strong connection between structural floral and fruits traits and their physiological and biochemical activity throughout their ontogeny. The anatomy of bracts in the different Asiatic species of *Salsola* we studied in relation to their photosynthetic activity (Figs. 47, a-d).

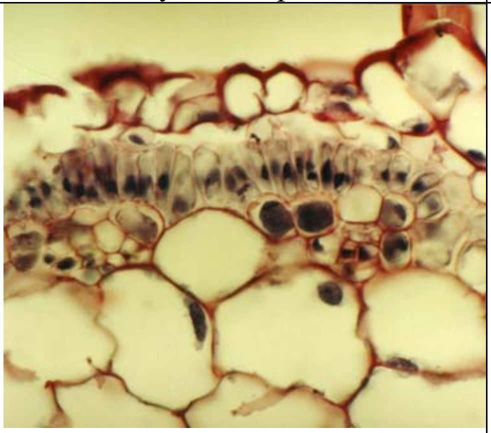
Figures 47. Photosynthetic activity of reproductive organs of *Salsola* praecox



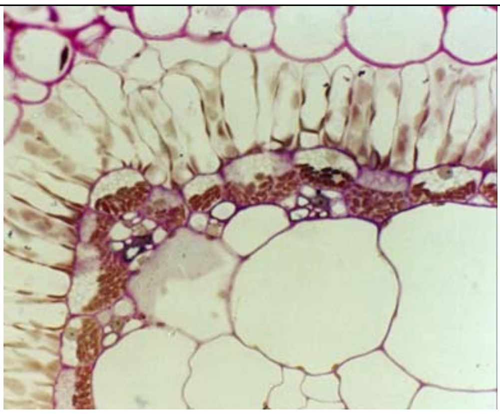
a)the first stage of differentiation of sclerenchyma of *S.praecox*



b) Salsaloid bracts anatomy and indefinite Kranz bundle sheath cells of *S.praecos* during budding stage



c). Cross section through bracts of*S. praecox* during flowering proces Kranz bundle sheath cells is visible



d) Cross section through bract of *S. praecox* during fruit maturation

Photosynthetic activity of reproductive organs was insignificantly in budding stage with some increasing during flowering processes and gradually decreasing during fruit maturation (tab.8.).

Table 8. The C^{13}/C^{12} carbon isotope analysis for indication of C_4 or C_3 photosynthesis activity in leaves, flowers and fruits for different *Salsola* species collected in Uzbekistan

N/N	Nomenclature of species	Plant organs	$^{13}C/^{12}C$ ($^{0}/_{00}$, PDB)		Collected sit description
	Section *Caroxylon*		Range	Mean	
1.	*Salsola dendroides* Pall.	Fruits (1)	-12.52– 12.73	-12.63	Coll. in 1954, Herb. Inst.of Bot. S-Pet. Russia
		Flowers (23)	-11.57	-	Fix. 1999,. T.Matyunina U. Japakova , Karakal-Pakstan
		Flowers (39)	-13.29–13.18	-13.24	Western Tyan-shan, Chatkal ridge in 1974 b Nabiev
2.	*S. incanescens* C.A. Mey	Fruits (2)	-13.75–13.58	-13.67	Coll. in 1978, Herb.of Inst. of Bot. S-Pet. Russia
		Leaves (59)	-13.89-13.90	13.90	Gulistan , Sep. 2000 by A. Butnik and H. Freita
3.	*S. orientalis* S,G. Gmel.	Flowers (28)	-14.73- 14.55	- 14.69	S-W Kyzylkum, 1999 by K.Todeich, T. Matyunina
		Leaves (56)	-13.87–13.86	-13.87	
4.	*S. micranthera*	Flowers (29)	-15.50–15.63	15.57	On sands, Central Fergana by Nabiev, July 1974

	Section *Coccosalsola (*Ulbrich)Botcs sub./sec. *Arbuscula*				
5.	*S. arbusculiformis* Drob.	Fruits (3)	- 23.47-23.63	-23.55	Coll. in 1910, Herb.of Inst. of Bot. S-Pet. Russia
		Flowers (37)	-26.31- 26.29	-26.30	Collec. 1980 by A. Butnik, Inst. of Botany Acad. Sci.Uzb.
6.	*S. arbuscula* Pall.	Fruits (4)	-4.86-4.71 (?)	- 4.79	Herb.of Inst. Of Bot. S-Pet. Russia
		Laves (60)	-12.82-12.96	12.89	Sothwestern Kyzylkum in 1997 by T. Matyunin
7.	*S. drobovii*	Fruits (5)	-25.65 -25.93	- 25.79	Coll. in 1963, Herb. Inst. of Bot. S-Pe Russia
8.	*S. Richteri* Kar. et Litv.	Fruits (7)	-12.25–12.30	- 12.28	Coll. in 1970, Herb. Inst. of Bot. S-Pe Russia
		Flowers (24)	–11.91-12.04	-11.98	Fix. U. Japakova in 200 ,Karakalpakstan, Lake Auzkat
		Flowers (36)	-12.21–12.34	- 12.27	Collected by A. Butnik U.Pratov 1973, Kyzylkum sands
9.	*S. paletzkiana* Litv.	Fruits (6)	14.08- 14.00	14.04	Collec. In 1989, u. Japakova , Kyzylkum

		Leaves (41)	-13.35–13.13	13.24	Coll. By A. Butnik in May, 1974, Kyzylkum
10.	*S. montana* Litv.	Flowers (26)	-20.97–20.95	20.96	Fix. by Tsukervani 1974 mountains
		Flowers (35)	-24.63–25.58	24.60	Tyan-Shan mour August, 1974 b U.Pratov
		Leaves (54)	-23.08-22.96	-23.02	Tyan-Shan mountains 1974 by Tsukervanik
11.	*S. pachyphylla* Botsch.	Flower (21)	20.88-20.92	20.90	July 1974 b ukervanik
	Section *Coccosalsola* (Ulbrich) Botsch. sub./se *Coccosalsola*				
12.	*S. foliosa* (L.) Shrad	Flowers (34)	-11.90–12.05	-11.97	Plateau Usturt, 1970 b Sarybaev
		Leaves (45)	-11.86- 12.07	-11.97	Usturt plateau, Karakalpakstan, coll. By Sarybaev in 1970
	Section *Salsola* sub. *Kali* (Ulbrich)				
13.	*S. praecox* Litv.	Fruits (8)	-12.11-12.06	-12.09	Coll. in 1932, Herb.of Inst. of Bot. S-Pet. Russi
		Leaves (46)	-12.76–12.75	12.75	Coll. In Kyzylkum 1976 by A. Butnik
		leaves (57)	-13.17–13.21	13.19	Buchara oasis in 1999 by Matyunina

14..	*S. aperta* Pauls.	Fruits (9)	-11.97- 11.88	-11.93	Coll. In 1932, Herb.of Inst. of Bot. S-Pet. Russia
		Flowers (33)	-11.74- 11.71	11.73	Southwestern Kyzylkun June, 1972 by Pratov
		Leaves (50)	- 12.88-12.69	12.78	Kyzylkum Desert in 1972 by A. Butnik
15..	*S. tamariscina*	Fruits (10)	-11.94-11.93	-11.93	Coll. in 1935, Herb.of Inst. of Bot. S-Pet. Russia
16..	*S. paulseni* Litv.	Fruits (11)	-11.24–11.21	-11.22	Coll. In 1931, Herb.of Inst. of Bot. S-Pet. Russia
		Flowers (32)	-13.00- 13.16	- 13.08	Sands, Central Fergana deserts, July , 1974 by Nabiev and Pahomova
		Leaves (53)	-12.00-12.15	-12.08	Fergana sands in 1974 b Tsukervanik
17.	*S. pestifer* A. Nelson	Leaves (58)	-13.42-13.43	-13.42	Fix. in Buchara oasis in 1999 by K.Toderich and K.Toderich
	Section *Belanthera*				
18.	*S. tomentosa*	Fruits (12)	-13.01-12.81	-12.91	Coll. in 1983, Herb.of Inst. of Bot. S-Pet. Russia
19.	*S. aucheri* (Mog.) Bge	Fruits (13)	- 13.20-13.31	- 13.25	Herb.of Inst. of Bot. S-Pet. Russia
		Flowers (25)	-12.5– 12.46	12.50	Fix. U. Pratov in 1979, Kungrad, Karakalpaksta
20.	*S. Vvedenskyi* Iljin. et N p.	Fruits (14)	-12.99- 13.05 -	- 13.02	Collected in 1970

21..	*S. gossypyna* Bge.	Flowers (22)	-14.56-14.71	-14.63	Fixation 1974 by U.Pratov , Kopetdag
	Section *Malpighpilla*				
22.	*S. gemmascens* Pall.	Fruits (15)	-12.95-12.92	-12.93	Coll. In 1915 by Androsov, Herb.of Inst. of Bot. S-Pet. Russia
		Flowers (38)	-12.76–12.66	- 12.71	Collec. On takyrs in Kyzylkum in 1977.
	Section *Cardiandra*				
23.	*S. sclerantha* C.A.Mey	Fruits (16)	-13.45-13.34	-13.40	Coll. in 1968, Herb.of Inst. of Bot. S-Pet. Russia
		Flowers (27)	-13.92- 14.08	-14.00	Fix. K.Toderich July 1999, S/W Kyzylkum (embryo develop.)
		Leaves (47)	-13.00- 13.00	- 13.00	Coll. In Kyzylkum in 1974 by A. Butnik
		Leaves (48)	-15.12- 15.14	- 15.13	Coll. In Kyzylkum in 1994 by A. Butnik
24.	*S. forcipitata* Iljin.	Fruits (17)	-12.79-12.86	-12.82	Coll. in 1970, Herb.of Inst. of Bot. S-Pet. Russia
25.	*S. turkestanica (?)*	Fruits (18)	-10.00-9.94	-9.97	Coll. in 1953, Herb.of Inst. of Bot. S-Pet. Russia
		Leaves (51)	-12.26–12.15	12.21	Chatkal range (Western Tyan-Shan) in 1974 by Tsukervanik

26.	*S. carinata* C.A. Mey	Fruits (19)	-12.25-12.44	12.35	Coll. in 1970, Herb.of Inst. of Bot. S-Pet. Russia
	Section *Physurus*				
27.	*S.lanata* Pall. (by H.Freitag, 1997 and Flora Iranica) or *Climacoptera lanata* (by Botchantsev, 1969, Pratov, 1986)	Fruits (20)	-13.20-13.18	-13.19	Herb. Inst. of Botany, Acad. Of Sciences Uzbekistan, 1977
		Flowers (31)	13.72-13.84	13.84	Buchara oasis in 1999 b K.N. Toderich
		Leaves (42) leaves (44)	-12.92–12.86 13.48 –13.46	-12.89 - 13.47	Coll. A. Butnik May, 1975, Kyzylkum desert Coll. A. Butnik, June, 1979, Kyzylkum
28.	*S. crassa (Climacoptera crassa)*	Flowers (30)	-13.85–13.83	- 13.84	Kyzylkum bot. exper. station , 1979
29.	*S. ferganica (Climacopter ferganica)*	Leaves (43)	-12.16- 12.06	- 12.11	Coll. A. Butnik in 1979 Kyzylkum
		Leaves (52)	-13.11- 13.03	-13.07	Kyzylkum in 1995 by A Butnik
30.	*S. roshevtzii* Iljin.	Flowers (40)	- 13.99-14.01	14.00	Central Tyan-Shan (Kuntogdy natural boundary in 1974 by Tsukervanik and Nabie
		Leaves 5)	-13.05-13.09	-13.07	Mountains Tean-Shan i 1974 by Tsukervanik

Great floral micromorphology and anatomical diversity of assimilative and floral like organs (bracts, bracteoles) were described for some annual *Salsola* species, contrasting by their growing habitats. It was found that *S. pestifer, S. praecox and S. paulsenii* are similar in photosynthesis types: C4-Sals (-H) both in leaves, cotyledons and bracts.

Differences were revealed in the anatomy of bracts. All Asiatic annual *Salsola* species of section *Salsola* sub. *Kali* have so-called Salsoloid (Carolin et al, 1975) or ‘crown centric’(Voznesenskaya and Gamaley, 1986) Kranz leaf and bracts anatomy. The first features of differentiation of bracts and bracteoles chlorenchyma cells are marked at the early stage of pollen sacs development, reaching a maximum during blooming stage. Cross sections of fruits perianth of many annual *Salsola* species during its maturity also show an insignificant development of chlorenchyma tissue. The similar situation was described for the species of section *Belanthera*. In bracts or fruiting body of this type, chlorenchyma is represented by two layers of green cells positioned around the periphery of the organs: the outer layer is composed of palisade mezophyl cells and the inner layer is composed of palisade mezophyll cells and inner layer of bundle sheath cells. The main vascular bundle with greatly thick-walled in the centre, surrounded by the water-storage tissue, and only small peripheral bundles have contact with cholernchyma. It is known that all species with Salsaloid Kranz anatomy in photosynthetic organs (irrespective of whether these are leaves, stems, cotyledons or bracts) have C_4 type photosynthesis (P’yankov and Vakhrusheva, 1989; Toderich, 1997; P’yankov et al 1999, 2000). However, chlorenchyma of *S. ruthenica,* consisting of palisade and Kranz cells, is interrupted by longitudinal colenchymatic ridges

6.4. Sexual reproduction, photosynthetic pathways and biochemical linkage

We suggested that the C_4-syndrom evolved in the leaves and only later extended to the cotyledons and floral organs. Sex expression of flower’ organs have been most marked for *S. ruthenica* (European species) that may be related with the habitats, where this species was recently introduced and naturalized. This is a good evidence of origin and diversification of *Salsola* from Asia to Europe. Analysis of karyotype revealed that these two species have the same number of chromosome 2n=18.

Annual C4- Asiatic *Salsola*, known in pasture economy of Uzbekistan as “solyanki differ from European by salt-glands/trichomes morphology (shape of their head: mainly clavate or capitate and its density. Abundant papillae prickle hairs and secreted salts secretion between ridges on bracts/bracteoles surfaces of annual Asiatic *Salsola* are described. Frequently salt glands are globose or club-shaped and readily distinguishable from unicellular papillae and sharp-pointed prickles. These parameters could be used as discriminating characters between different ecological halophytes *Salsola* groups. Variation in the indumentum density is believed to be mainly the effect of stress/desert environmental factors and/or even herbivores pressure.

Floral structure diversity (hypoginous disk, stigma, ovule, anthers), pollen grain morphology and fruit anatomy are clearly defined, suggesting their potential value as diagnostic characters concerning taxonomic and evolutionary linkages within Chenopodiaceae, particularly genus *Salsola*. Remarkable examples of intraspecific variation in pollen grain traits have been described for C/D ratio, thickness of exine, size and numbers of pores. These parameters being more conservative than other flowers and fruits traits were discovered to be highly specialized and support the evident cladistic grouping of some critical species within genus *Salsola.* Diversity in the anatomy of fruits reflects ways and character of adaptive coevolution of woody *Salsola* taxons and plays a more significant role in the species identification than other elements of floral organs. For instance at *S. richteri* and *S. Paletzkiana* the direction of adaptive specialization to the xeric-arid conditions going towards the intensification of sclerification of fruiting perianth and increasing of size and number of cells layers of pericarp and even embryo tissues. The presence of pygments in the fruits covers, singular hydrocytic cells, partial myxospermy and development of membranous layer in the spermoderma intense the defending function against sun radiation. A fully development of embryo organs and differentiation of their tissues indicate the completely readiness of embryo of *Salsola* species to the germination. Seed dispersal is manifested by the development of large and wide wings; all elements of fruiting cover and embryo organs of studied species has adaptive value pygmentation, partial myxospermy, thickenings of external walls; membranous and aleironic layers in the spermoderma, intensification of succulence features as a results of well development of aerial parenchyma, abundant of reserve store nutritional substances, which stimulate the good defending of embryo from extreme deserts environments.

We found out that Asiatic *Salsola* species of section *Arbuscula* from *Coccosalsola* section with both C_4 and C_3 photosynthesis types represents a unique example of the evolutionary convergence of ecological, structural, physiological and biochemical traits. The great range of variation, far more marked in ploidity of genome and fruit structures than in floral and pollen morphology explains the high phenotypic plasticity and good adaptation of *S. richteri* and *S. arbuscula* to various geographical and ecological desert habitats. Controversy, *S. Paletzkian*a and *S. arbusculiformis* are characterized by narrow structural specialization of reproductive organs, partly seeds to germinate only on the sandy or stony gypsumferous soils that, perhaps explained the strict local distribution of this species in Central Asian Flora.

The embryological data of perennial Asiatic woody *Salsola* species from their natural habitats presented in this paper lead us to the conclusion , that *S. arbusculiformis* by it reproductive biology is evidently not close allied with S. arbuscula, *S. richter*i and *S.*

Paletzkiana, despite these species form a taxonomic separate monotypic subsection *Arbuscula* in *Coccosalso*la section. (Botschantzev 1969; Freitag 1997). This supports a view that many arid plants being morphological and taxonomic closely related develops a specific “plant reproductive functional system” that ensure them to reproduce and survive in extreme desert conditions. Our anatomical, biochemical and physiological data in regard to the C_3 and C_4 pathways of photosynthesis in limits of *Coccosalsola* complex both in leaves and reproductive organs confirm that this delimitation is well founded. Based on morphological features, Akhani et al., 1997 recently mentioned that section *Coccosalsola* could be most primitive group of *Salsola.* However high specialized centric type anatomy of mesophyll of cotyledons of *S. arbuscula*, *S. richteri* and *S. Paletzkian*a indicate on their relatively younger phylogenical group. *S. arbusculiformis* manifest a unique combination of structural and biochemical phosynthetic types in leaves and cotyledons within genus *Salsola* (P’yankov et al., 1997; Voznesenskaya et. al. 2001). In addition several aspects of the species’ ecology indicate on reproductive assurance in this taxon as an adaptive explanation of selfing control for surviving under extreme desert condition. First, *S. arbusculiformis* typically occurs in small patchy geographical isolated populations or singular individuals, where the availability of outcross mates might be limited. Floral biology of *S. arbusculiformis* supports the hypothesis that mating between close relatives is expected to reduce the number or vigor plants. Second, embryological data showed that S. arbusculiformis produces simultaneously self-reproduced, sexual and apomictic seeds in the absence of pollinators. This feature perhaps is a main reason of lower viability and seed germination both under field and laboratory condition.

Based on whole plant morphological features, sexual reproduction and functional systems, as well as ecological habitats and geographical distribution of Asiatic *Coccosalsola* complex we assumed that S. *arbusculiformis* might be the primitive and primary originated in Central Asia.

CHAPTER 7. Isoenzymatic and karyological studies of some *Salsola* species

The extremely high morphological variability of the annual species of section *Salsola*, sub.*Kali (*Ulbrich) has been known for a long time and has led to the description of several species, subspecies and varieties (Ulbrich 1934; Pratov 1986). The biogeographical, morphological and ecophysiological characteristic of species belonging to this section has also been studied in relation of their systematic position (Butnik 1984; Rilke and Reimann 1996; Li et al. 2000, Toderich et al, 2004b, 2005). The genetic variation of *Salsola* species within their native ranges in Europe and Asia is not well known (Ryan and Ayres, 2000) as well as other plants from arid regions (Schuster et al., 1994). Another unanswered question is to what extend their great morphological variability represents genetic, developmental or environmental differences (Rilke and Reimann 1996; Woinicka-Poltorak et al., 2002).

The present study was conducted in an attempt to estimate the genetic variation and describe the variability and genetic structure of population for three annual species like *Salsola lanata* (revised in this study as. *Climacoptera lanata*), *Salsola praecox* and *Salsola pestifer*, which grow under desert and highly saline conditions of the southern KyzylKum Desert in Uzbekistan.

We examined eight enzyme systems, which were coded by different numbers of loci in particular species: 14 in *S. lanata*, 17 in *S. pestifer* and 16 in *S. praecox.* In the population of *S. lanata* three loci GDH B, GOT B, PGM B, that occurred in the two *Salsola* species were not observed. Locus G6PD A was found only in *S. lanata*, and locus PGI A only in *S. pestifer*. We observed a null allele in locus MDH C in *S. lanata*. The general pattern of isoenzymatic bands of *S. pestifer* and *S. praecox* were similar for all loci except PGI A, which was observed only for *S. pestifer*. In *S. lanata*, the enzymes G6PD, PGM, GOT, GDH and PGI are coded by different numbers of loci than in S. *pestifer* and *S. praecox.* Zymograms of the all examined loci are presented in Fig. 48 as they were seen on the gels. As seen from Tab. 9 and 10 loci 6PGD and MDH of *S. lanata* clearly differ from those of S. *pestifer* and *S. praecox.* Frequencies of alleles and genotypes particular enzyme loci are the proportion of polymorphic loci (at 0.99 criterion, Nei 1987) was rather low and ranged from 5.9% for S. *pestifer* and 12.5% for *S. praecox* to 21.4% for *S. lanata* (Tab. 10). The χ^2 test confirmed the significance of differences in allele PGI C2 and genotype PGI C1/2 frequencies between S. *lanata* and *S. praecox* and between S. *pestifer* and *S. praecox.* Overall, 18 alleles and 18 genotypes were found in S. *pestifer* and *S. praecox,* and 17 alleles and 17 genotypes were found in S. *lanata.*

Table 9. Frequencies of alleles in the studied species: *S.l- Climacoptera lanata, S.p-Salsola pestifer, S.x-Salsola praecox.*

Locus/allel	**S.l**	**S.p**	**S.x**
6PGD A			
1	1,000	1,000	1,000
6PGD B			
1	1,000	1,000	1,000
DIA A			
1	1,000	1,000	1,000
DIA B			
1	1,000	1,000	1,000
G6PD A			
1	1,000	-	-
G6PD B			
1	1,000	1,000	1,000
GDH A			
1	1,000	1,000	1,000
GDH B			
1	-	1,000	1,000
GOT A			
1	1,000	1,000	1,000
GOT B			
1	-	0,741	0,859
2	-	0,259	0,141
MDH A			
1	0,984	1,000	1,000
2	0,016	-	-
MDH B			
1	1,000	1,000	1,000
MDH C			
1	0,906	1,000	1,000
null	0,094	-	-
PGI A			

1	-	1,000	-
PGI B			
1	1,000	1,000	1,000
PGI C			
1	0,969	1,000	0,823
2	0,031	-	0,177
PGM A			
1	1,000	1,000	1,000
PGM B			
1	-	1,000	1,000

Table 10. Frequencies of genotypes in the studied species: *S.l- Climacoptera lanata,* S.p-*Salsola pestifer*, S.x-*Salsola praecox.*

Locus/geno-type	**S.l**	**S.p**	**S.x**
6PGD A			
1/1	1,000	1,000	1,000
6PGD B			
1/1	1,000	1,000	1,000
DIA A			
1/1	1,000	1,000	1,000
DIA B			
1/1	1,000	1,000	1,000
G6PD A			
1/1	1,000	-	-
G6PD B			
1/1	1,000	1,000	1,000
GDH A			
1/1	1,000	1,000	1,000
GDH B			
1/1	-	1,000	1,000
GOT A			
1/1	1,000	1,000	1,000

GOT B			
1/1 1/2	-	0,483	0,719
MDH A	-	0,517	0,281
1/1			
1/2	0,969	1,000	1,000
MDH B	0,031	-	-
1/1			
MDH C	1,000	1,000	1,000
1/1			
null	0,906	1,000	1,000
PGI A	0,094	-	-
1/1			
PGI B	-	1,000	-
1/1			
PGI C	1,000	1,000	1,000
1/1			
1/2	0,938	1,000	0,645
PGM A	0,063	-	0,355
1/1			
PGM B	1,000	1,000	1,000
1/1			
	-	1,000	1,000

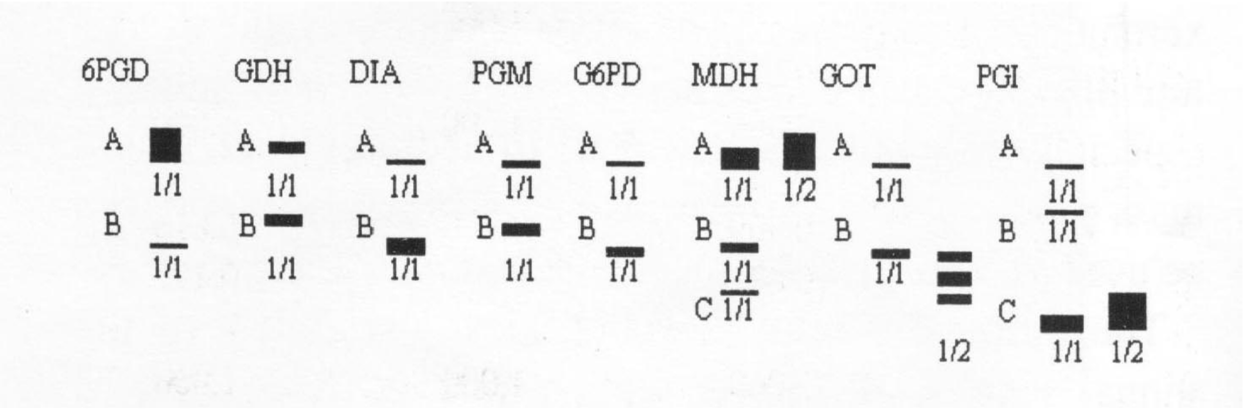


Figure 48. Zymograms of observed genotypes in particular enzymes loci.

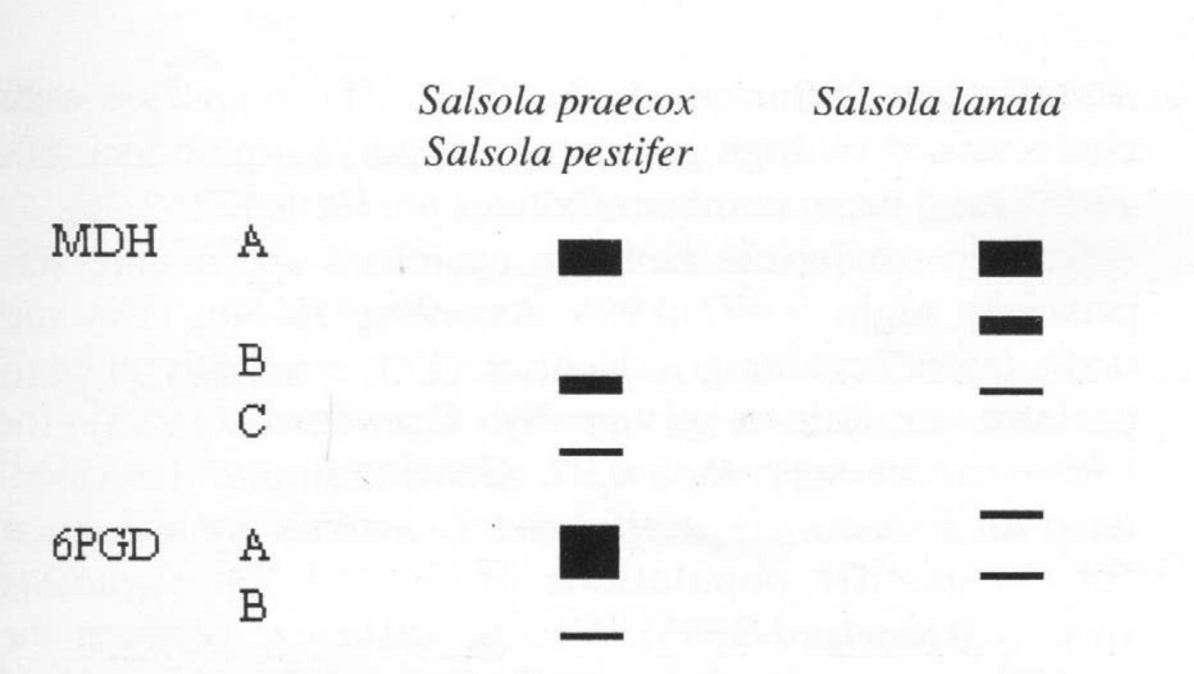


Figure 49. The differences in patern loci of two enzymes between *Salsola pestifer, Salsola praecox* and *Salsola lanata* .

Parameters describing genetic diversity indicate a very low level on variation on the investigated species. The mean number of alleles and genotypes per locus was very low: from 1.1 in *S. pestifer* and *S. praecox* to 1.2 in *S. lanata* for both parameters. The mean observed heterozygosity Ho (average over loci) was the highest for *S. praecox* (0.159), intermediate for *S. pestifer* (0.129) and the lowest for *S. lanata* (0.031). In all the investigated species there was a significant excess of heterozygotes (test χ^2) as indicated deviation from Hardy-Weinberg equilibrium *S. lanata* and *S. pestifer* have similar values of genotype polymorphism index Pg (0.025 and 0.029 respectively), as opposed to *S. praecox*, which has the highest genotype polymorphism (0.054).

Values of genetic distance based on allele DN and genotype DH frequencies are summarized in Table 10. In both cases the smaller genetic distance was found for the pair *S. lanata - S. pestifer* and the largest for *S. pestifer - S. praecox*. Chromosome number *2n=18* was the same for three investigated species and is presented at Fig. 49.

In the Tables 11 and 12 is given the main genetic parameters calculated for the studied species: A/L-mean number of alleles per locus, G/L-mean number of genotypes per locus, H_e-expected heterozygosity, H_o-observed heterozygosity, F-Wright's fixation index, P_g-genotype polymorphism index.

Table 11. The characteristics of main genetic parameters of three annual desert species

Populations	**% of loci polymorphic***	A/L	G/L	H_e	**H_o**	**F**	**P_g**
S. lanata	7,1	1,2	1,2	0,019	0,031	-0,675	0,025
S. pestifer	5,9	1,1	1,1	0,023	0,129	-4,733	0,029
S. ecox	12,5	1,1	1,1	0,033	0,159	-3,768	0,054

Table 12. **Genetic distances and similarities according to Nei (belove diagonal) and according to Hedrick (above diagonal) between the studied species.**

	genetic distance			**genetic similarities**		
	S.lanata	***S.pestifer***	***S.praecox***	***S.lanata***	***S.pestifer***	***S.praecox***
S.lanata	-	0,0011	0,0076	-	0,999	0,992
S.pestifer	0,0007	-	0,0119	0,999	-	0,988
S.praecox	0,0024	0,0029	-	0,998	0,997	-

There are few karyological accounts of *Salsola* species. Nevertheless, even with the small amount of data available the positive correlation between high levels of ploidy and large pollen grains revealed for different flowering plants does not exist within subgenus *Salsola* (Hindakova and Schwarzova, 1980, Toderich et al., 2000). Our data show the same number of chromosomes for each studied species (2n= 18). However further investigations are necessary to confirm this hypothesis.

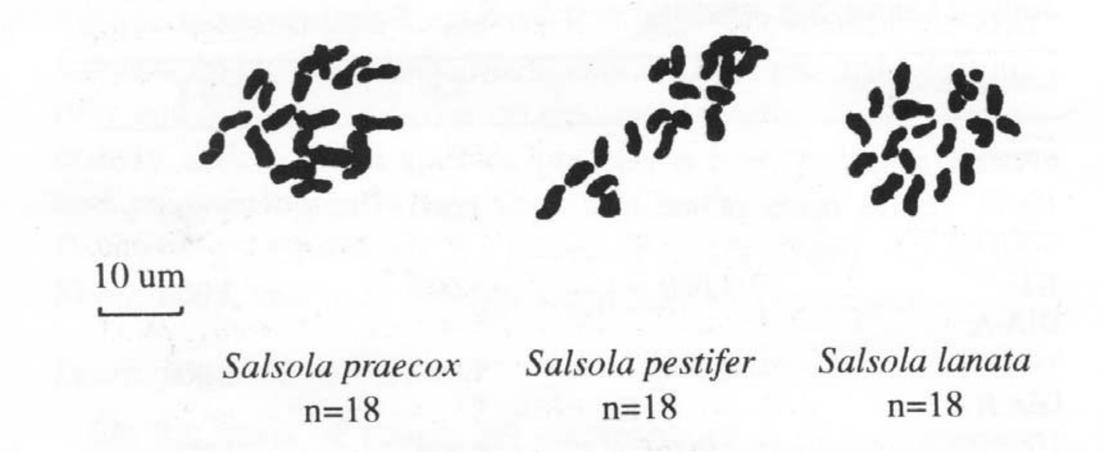


Figure 49. Chromosome number of *Salsola pestifer, Salsola praecox* and *Salsola lanata.*

Thus, as were described in this chapter the populations of examined three taxons show enzyme monomorphism in majority of enzyme loci. The number of examined (14-17) was quite representative for estimation of population variation, thus such a low genetic differentiation of the studied taxa is noteworthy. This fact may be a characteristic feature of the family Chenopodiaceae, as indicated by data for diploid and tetraploid *Chenopodium* species (Crawford 1979; Wilson 1981, 1988a) and for *Salsola tragus* (Ryan and Ayres, 2000) and Salsola komarovii (Kim and Chung, 1995), where high percentage of monomorphic loci are observed. Values of the calculated genetic parameters indicate a very low genetic diversity of the studied species. A low genetic variation was also detected in *Chenopodium* spp. by Crawford and Wilson (1979).

Wilson, 1988a, b reports that wild and cultivated populations of *Chenopodium quinoa* from the Andes share a low level of allozyme variation with no distinction between domesticated and wild populations. A low level of intraspecific variation by RAPD markers was also found within six species of this genus by Ruas et al., 1999. Contrary, high level of genetic variation was observed in four dominant arid species in Arizona: *Encelia farinosa, Larrea tridentata, Gutierreza microcephala and Coleogyne ramosissima* (Schuster et al. 1994). Theses species were characterized by high percentage of polymorphic loci (50-78.9%) and mean number of alleles per locus (2.0-2.28).

Genetic similarities between examined by us *Salsola* species are surprisingly high: 0.996-0.999 according to Nei (IN) and 0.988-0.999 according to Hendrick (IH), especially in comparison to values given by Crawford, 1983 for *Chenopodium spp.:* 0.35-0.97. Genetic similarities calculated for *S. lanata, S. pestifer* and *S. praecox* are as high as for conspecific populations of several *Chenopodium* species (Crawford 1983). Genetic distances between the studied taxa are much lower (0.0007-0.0029) than values estimated by Nei (1976) between species 0.1-0.2 and between subspecies 0.02-0.1. Such a high isozyme monomorphism of *Salsola* species may be due to very narrow environmental conditions; under which only highly specialized organisms can survive. This conclusion is in concordance with the hypothesis of Hamrick et al. (1979). The authors suggest that strong directional selection might result in lower levels of genetic variation in arid plant populations. According to Golding, 1994 environment factors also shape frequencies of alleles, thus taxa experiencing similar conditions may exhibit similar allele frequencies. The above genetic data suggest that a significant component of the great morphological variation of the examined taxa may result from phenotypic plasticity. By contrast, Rilke and Reimann, 1996 present that differential saline tolerance of *Salsola kali* from northern Europe suggests some genetic differentiation.

The lack of activity of the four loci in the population of *S. lanata* as well as the presence of the unique G6PD A locus, distinguishes its genetic structure from those of *S. pestifer* and *S. praecox*. The lowest heterozygosity, Wright's fixation index and genotype polymorphism index support this. High salinity regimes of the habitats may be responsible for genetic distinctiveness of *S. lanata*. Despite it, a very high genetic similarity (0,999) was found between populations of *S. lanata* and *S. pestifer*. These surprising data may due to unclear systematic position of *S. lanata*. It was first described as *Salsola lanata* sec. *Eusalsola* (Ulbrich, 1934) or sect. *Physurus* (Iljin, 1937). Because of several unique morphological traits of leaves, flowers and fruits it was separated as a genus *Climacoptera* by Botshantsev, 1969 and Pratov, 1986, while Hedge et al., 1997 replaced this taxon again to genus *Salsola* sect. *Physurus*. From palynological point of view Toderich et al., 2000 consider *S. lanata* as distinct species belonging to genus *Climacoptera* closely related to genus *Salsola*.

What distinguishes two *Salsola* species is the lack of G6PD A locus and the presence of the polymorphic locus GOT B. The more differentiating locus for *S. praecox* seems to be PGI C, which allele and genotype frequencies were significantly different from those of the remaining two species.

In our study we found that pattern of the two 6PGD loci seems to be very similar (or the same) to the type B of Californian *S. tragus* (regarded as synonym for *S. pestifer*) described by Ryan and Ayres, 2000. They suggest, on the basis of electrophoretic and cytological analysis, that two distinct isoenzymatic types (A and B) of 6PGD and GOT enzymes are in fact two different species. The number of chromosomes estimated in *S. pestifer* ($2n=18$) confirms, that the investigated plants belong to the Californian type B of this species.

In conclusion, the results of this chapter, as well as works of Crawford and Wilson, 1977; 1979, Crawford, 1983; Ryan and Ayres, 2000, demonstrate the usefulness of electrophoresis for exploring the genetic diversity and taxonomic position of taxa of family Chenopodiaceae. Obviously, our findings based on the analysis of the only few populations of each species, are preliminary and require further studies on wider plant material in respect to genetic variation and its relation to environmental conditions.

CHAPTER 8. Adaptive strategy and evolutionary trends in Asiatic genus *Salsola* its taxonomic relations within Centrospermae

Reproductive strategies of haloxeric Asiatic *Salsola* species and its adaptive significance-

Palynological; analysis of 24 species of genus *Salsola*, mostly growing under desert, semidesert and less under mountainous conditions of Central Asia allow us to define a set of palynological traits for differentiation , especially if the species studied are phylogenetically remote or belong to different subgenera. However, not various categories have been distinguished in the general pollen type, in some cases species have not been separated on the basis of their pallynology. As results of our data and considering the set of the species studied, we can accept the separation of only one *Climacoptera* pollen type within genus of *Salsola.* Graphic representation of the pollen size and C/D relation for each taxon under study reveals the lack of clear discontinuities among most of the genus *Salsola* representatives. This homogeneity in the measurements of quantitative values of palynological traits together with uniformity in genesis of reproductive organs and processes shows that despite the external polymorphism and variability of floral morphology the pollen grain does not reflect the variability shown by macroscopic characters. Also worthy of mention is the high degree of overlapping in their range of variation. In this review work, which includes a large number of taxa, the range of variation of quantitative parameters of pollen grains, as well as in the surface of the tectum, and to a lesser extent in the aperture types and exine ultrastructures, raises the fundamental question of the adaptive significance of entire set of structural, morphological and physiological diversity. . There are some correlations between the function of the pollen grain, which is to transfer the male gametophyte and to insure germination, and certain characteristic of the exine. In spite of the homogeneity of the pollen morphology, the discreet differences found in this study, especially for species of sections *Physurus, Salsola* sub. *Kali* (Ulbrich), sub. *Arbuscula* and *Belanthera* can contribute to clarifying the relationships between species of the same natural group of the genus *Salsola.*

Protection from desiccation during transfer of pollen grain is basic and the architecture of the pollen wall could logically be interpreted as an adaptation to minimize the effects of water loss: the spherical or derivates other shapes, i.e., the foot layer and tectum, whose spatial separation is maintained by the collumelae, provides maximum support and rigidity. Adaptations for polyporate pollen grain type germination are more conspicuous: preformed breaks in the exine expedite the release of the nuclei; more than one potential exit would permit rapid germination no matter what area of the grain might be in contact with the stigma. A function has been attached to the chamber between the foot layer and tectum: storage of recognition substances that initiate the process of male gametophyte germination. The apertures also function as harmomegathic mechanisms (Wodehouse, 1935). The range of variation in the surface of tectum, and to a lesser extent aperture specificity and exine sculpture, which spans such a large number of taxa of Chenopodiaceae family, raises the fundamental question of the adaptive significance of the variation. There are some correlation between the function of the pollen grain, which is to transfer the male gametophyte and to ensure germination, and certain characteristics of the exine.

The great diversity in the surface of the tectum is another matters altogether. in Heslop-Harrison, 1971 concept.: "Evidently if we are not to assume that pollen wall sculpturing are no more than meaningless manifestations of a kind of morphogenetic virtuosity, we must accept that there is a high adaptive component, and that diversity has resulted from selected forces." But has all of the diversity been the result of selective forces? or all possible structure-function correlations in pollen morphology, that of pollen-pollination vector has probably attracted the most attention and produced the least consistent results. Leuenberger, 1976, after examination of 600 species in the Cactaceae (order Centrospermae) reported, "the data obtained so far do not support the assumption that clear correlations exist between exine sculpturing and pollination types. Taylor and Levin, 1975 reported similar and wider conclusions in the Polemoniaceae. In their discussion they note, "it is appropriate to question of this point whether different exine organization patterns reflect adaptations to different pollen dispersal mechanisms. The data presented in our work do not substantiate such a relationship." Nor did they find a relationship between pollen ornamentation and environmental parameters. And, while conceding that features of wall configuration might prove to be correlated with some parameters, Taylor and Levin, 1975 considered the adaptive significance of the various patterns to be a matter of conjecture. (It should be added that none of the Polemoniaceae in comparing with tribe Salsoleae are to be wind pollinated).

However, in our case critical may be the need to control desiccation in wind-pollinated grains that occurs in majority species of *Salsola*. In this transfer method each individual grain has the entire surface exposed to climatic stress. Most wind-pollinated species have the pollen grain with well developed pollenkitt, an oily-waxy coating that prevents or reduces evaporation from the surface of the pollen grain. The pollenkitt also causes the grains to clump together, and during transfer those grains in the interior of these sticky masses are protected from physical damage as well. Wind pollinated grains lack, apparently, adaptations which would reduce water loss.

On the other hand, the predominantly wind-pollinated Amaranthaceae and Chenopodiaceae have grains with numerous small pores, fewer but larger pores or larger and recessed pores. Structural modifications that provide additional support, such as a thick tectum and/or robust columellae, may function to counteract the desiccating properties of the apertures. The adaptive significance of the tectum diversity has become more obscure with an increasing number of results of observations with which appears contradictory. In particular, there are two somewhat paradoxical phenomena that are difficult to reconcile in a limited framework of structure/function. On the one hand, quite diverse tecta or even pollen morphologies occur within the same genera, while, on the other hand, the same or very similar, specialized tecta and sometimes pollen morphologies occur in unrelated genera of widely separated families. The first phenomenon is well known and there are numerous examples. Three examples from our own studies can be cited. The large genus *Tourneforia* has four pollen types, one of which, III, is remarkably distinct (Nowicke and Skvarla, 1974). In vegetative and floral morphology *Podophyllum emodi* and *P. peltatum* are obviously closely related, but polynologically they are widely separated (Nowicke and Skvarla, 1979). Polygonum may have the greatest pollen diversity in the angiosperms (Faegri, 1956; Hedberg, 1974; Nowicke and Skvarla, 1977).

The second phenomenon depends upon the demonstration or proof of pollen similarity, and for the most part the discovery of very similar pollen in widely separated families is the direct result of a technological advancement, the scanning electron microscope. The examples may not be as numerous as in the first case, but it is only a matter of time. If palinologists and systematists accept the view that pollen variation has a high adaptive component, then all the diversity of pollen in closely related species, or the similarity of pollen in widely separated taxa, can be attributed only to selective forces.

Although Taylor and Levin, 1975 avoid the use of selective forces, the following quotation from their Phylogenetic Iterpretations is of considerable interest: “Scanning electron microscopy may prove to be a very valuable tool in elucidating species relationships within the various systematic families, especially if pollen morphology is largely free from the confronting elements of parallel evolution. Implicit in such argument is the proposition that congruity in wall architecture is not the product of parallel evolution, but is the manifestation of long-standing structural similarity dictated by common ancestry. We fail to identify any environmental conditions, biotic or abiotic, which may account for parallel evolution within order Centrospermae. The adaptive radiation in pollen morphology leading to major ‘pollen lineages’ ostensibly was initiated and nearly completed long ago, in contrast to more recent differentiation within genera for other aspects of their pollination biology.” The lack of success in identifying environmental conditions and/or selective forces, either on the part of Taylor and Levin, 1975 or us, does not deny their existence. But the discovery of similar pollen in widely separated taxa could be interpreted as evidence that some pollen variation stems from relictual adaptations. The most plausible explanation of the close similarity of specialized pollen morphologies in the Chenopodiaceae, Caryophyllaceae and the Amarathaceae would be common ancestry. But if the adaptive significance of pollen characteristics is obscure in the present, it is unlikely to be clarified in the past.

Important arguments come from re-evaluation of classical characters, e.g. trichome types, structure of leaf base and leaf insertion, anther appendages and configuration of the hypogenous disck. They are supported by biochemical subtypes of C_4 photosynthesis and by the results of new comparative studies on the anatomy of fruits. First application of molecular markers has proves that Salsola in its present circumscription is highly polypheletic.

A concept of "plant functional reproduction system" (PFRS) based on common structural floral, fruits and functional (photosynthetic pathways and biochemistry type) features of some woody *Salsola* species has been considered. Quantitative palynological data was subjected to multivariate analyses and confirmed the monotypic taxonomic relation of woody-shrubby species within Asiatic genus *Salsola*. We suppose that sexual reproduction mechanism and CO_2 fixation pathway diversities of tree-like Salsola species, detected in this study, are an important factor for its seed production and survival under desert harsh environments. The structural polymorphism of floral organs is coupled with the diversity of pathway and anatomy of the CO_2 assimilative organs. Species with C_4-MADP-ME pohtosynthesis and Salsoloid type of Kranz-anatomy both in leaves and reproductive organs forming a unique "functional reproductive plant group" were most resistant plants to various ecological arid habitats. Ana-campylotropous, crassinucellate ovule, autogamy (self pollination /fertilization system), and narrow specialization of sexual reproductive system linked with Sympegmoid –type structure and C_3 –like ^{13}C values both in leaves and reproductive organs testify the ancient origin of *S. arbusculiformis*, from which *Salsola* species with C_4– syndrome must have derived recently. Evolutionary changes in the mating system of *S.arbusculiformis* and *S.montatna* under extreme desert environments through advantages of self-fertilization, reproductive assurance (when pollinators are scarce), geographical restricted distribution (growing preferentially on rocks, crushed stones or other ancient substrates) and reproductive isolation between sympatric species support a strong tendency to inbreeding depression in this taxon. The coexistence of two fitness components (sexual and apomictic) in *S. arbusculiformis* we estimate as structural adaptive modifications of reproductive organs enable plants to survive and reproduce fruits under extreme continental desert conditions. By means of SEM analyses it was defined that structure of perianth segments reflects ways and character of adaptive coevolution of these taxons and plays a more significant role in the species identification than other elements of floral organs.

Interspecific variations in external seed morphology and tepals anatomy of the taxa examined does not completely support subgeneric segregation given by Botschantzev,1969; Botschantzev et al. 1989; Freitag, 1997, Rilke, 1999. The overall patterns of variation and the structuring of diversity in seed morphology are significantly correlated with pollen grain morphology and ultrastructure.

General Conclusion

The present thesis provides the first multi-disciplinarily studies and comprehensive survey of Asiatic Genus Salsola based on their morphology, structural, eco- physiological and genetic variability in relation to their taxonomy, evolutionary trends and adaptation to the harsh desert stressful conditions. A special attention has been focused primarily on morphology and embryology of reproductive organs at the species and even populations levels. It was hoped that pollen and morphologyfruit morphology might supplement a taxonomical revision of the genus *Salsola,* tribe *Salsoleae* (*Chenopodiaceae*), since, in spite of different geographical distribution, important macromorphological characters for the distinction of many species within this genera cannot be found.

Firstly 24 (*S. montana, S.aperta, S. gemmascens, S. incanescens,, S. arbusculiformis, S. pachyphylla*, S.aucheri & *S. gossypina* and more than 8-10 populations for the species with a large geographical distribution such as *S. arbuscula, S. richteri, S. paletzkiana, 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)* native both annual and perennial species from different ecological zones of Uzbekistan were analysed regarding pollen grain/flower organs, fruits morphology and ultrastructure.

Uniformity on the ultrastructure of pollen grain with only exception of *S. lanata* and *S. crassa* (revised as *Climacoptera* complex) has been detected. Two distinguishable types of pollen grain: 1- Salsola type – include species with small to medium large, wall thick pollen grains; 2- *Climacoptera* type- aperture region consists of flecks of reduced, angular enktexine underlain by lamellar plates of more and less distinctive endexine similar to species of Amaranthaceae was described. Three morpho-structural groups within genus *Salsola* has been delimitated based on complex of quantitative parameters of pollen grain: type of apertures, number and degree of pore sinking, pollen grain sizes, exine thickness, pore number and its area, nanospinules and minute holes densities on the mesoporial exine; echinus number on pore, interpore distance and chord (C/D ratio) value. A less conspicuous link exists between *S. subaphylla* (confirmed by our studies as *Halothamnus*) and species of section *Physurus*, such as *S. lanata* and *S. crassa* (revised *as Climacoptera*) all of which have large, sunken, well configured pores with densely spinulose aperture membrane. Pollen morphology of these two Sections differs clearly from all investigated Salsola species in C/D ratio; fairly large grains and almost absence/or presence of minute extexine perforations Remarkable examples of intraspecific variation in pollen grain morphology have been described for the C/D ratio. The C/D value was discovered to be highly specialized supporting the evident delimitation of investigated Salsola species and appears to be more conservative than some flowers and fruits characters**.** C/D ratio and implied pores number as taxonomic traits rest upon their constancy within well-defined species and show a high similarity between closely related species. Index form that comprises the numerical value by the ratio between the length of polar axis and diameter (P/E) could be also considered as an informative taxonomic parameter useful for the species delimitation. High polymorphism of all diagnostic indexes of pollen grain has been detected for the annual species of Section Kali: *S. ruthenica, S. praecox, S. pestifer, S. paulsenii, S.aperta, S.tragus* The similarity of palynological features of *S. ruthenica* with other species of this section, however, supports the relationship of the Asiatic and European group of Section *Salsola* sub. *Kali.* Euclidean distance of overall pollen traits was used to compute the dissimilarity matrix, and the tree was made, which clearly indicates that Asiatic genus Salsola almost reflect current taxonomic boundaries, i.e. species belonging to the same section are grouped together with exception of evident delimitation of species of section *Physurus* into the separate genus *Climacoptera* , as well as *S. subaphylla* into a seprate genera *Halothamnus*. Woody-shrubby species of subsection Arbusculae section *Coccosalsola* forms taxonomically separate monotypic subsection *Arbuscula* of section *Coccosalsola*., while annual species of Section *Salsola* are partitioned in both clusters, i.e. *S. aperta* and S. paulsenii, which typically belong to taxa of section Kali (Salsola) are included near species of section Arbuscula and Belanthera. Based on the morphology of pollen grain, perianth and fruits analyzing we concluded that from the systematic point of view the position of *S. aperta* should be reconsidered.

Set of structural features of fruit anatomy comprising sculpture of perianth surface, size, shape of fruit tepals and wings evidently distinguished species within sections and even genus *Salsola* among other genera of order Centhrosperma. The most distinctive and fairly constant characters seem to be the presence and size of wings and the degree of development and position of the tepals lobes above the wings. It was assumed that fruit diversity is conditioned both by phylogenetic relation, tendency and character of specialization of reproductive structures and through them the adaptation of *Salsola* species to the extreme arid condition, especially salinization. Taxonomic diagnostic features of fruits are expressed first of all in the upper leaflets (above the wings) and vertical column (open funnel), whereas bottom leaflets (under the wings) are less identical. Among the species studied, variation of fruits is displayed in the form and color of wings, structure of columns, presence, shape and spatial arrangement of the papillous protuberances;in numbers of collenchymatous layers; degree of sclerification and parenchymatization. Partial myxospermy widespread in the anatomy of seeds of *Salsola* halo- and xerohalophytic species like *S. rigida, S. paulsenii, S. lanata, S. pestifer, S. gemmascens, S. arbuscula* species should be related to the soil salinity and deficit of water. In our opinion the most important function of mukus (slime) is to fix the seeds to the soil and/or animals that facilitate their dispersal or to act against seeds overheating. Bracts and bracteoles due to prominent level of sclerification of perianth segments, as well as thickening of pericarp and spermoderma plaid an essential role in embryo protection. The main evolutionary trend in fruit anatomy is toward reduction of structure of spermoderma and pericarp. New criteria in species delimitation, namely as micromorphological surface sculpture and structural diversity of perianth segments during fruits maturation was also described, which precisely delimitated species boundaries within genus *Salsola,* as well as identified the adaptive evolution of fruits to extreme desert habitat conditions. Increasing of sclerification, availability of pigments and tracheids like cells holding moisture, abundance of crystals in the perianth tissues also promote the protection of embryo from unfavorable desert conditions. The development of wings on a median line of perianth segments stipulates the anemohorous way of seed dispersion, which are mostly characteristic for many other syatematic groups of desert plants like species of genus *Haloxylon, Suaeda, Calligonum* , grown almost unde the same dryland environments. Thus, detailed analysis of morphology and anatomy of fruit stage has revealed new criteria of species delimitation within complicated polyphyletic genus *Salsola* shown their systematic significance in submission of adaptive evolution of fruits to extreme desert habitat conditions. The differentiation between salsola sections was based on the micromorphology of perianthstrictly distinguished two groups:species of section *Caroxylon, Cardiandra and Malpigila*, which are mostly characterized by well developed two-layered chlorenchyma that consists of palisade bundle sheath cells and small-sized vascular tissue from one side and species of sections *Belanthera, Arbuscula and Salsola* subsection *Kali* in the fruit anatomy of which the chlorenchyma are completely not differentiated.

Additionally, high parenchymatization of perianth segments during fruit maturation, radially elongated cells of thin-walled parenchyma, absence of sclerenchyma in the upper tepals, its cholenchymatous thickening of lower epidermis and 1-2 rows parenchyma that closely adhered to the epidermis are peculiar for species of section *Caroxylon*,which has been considered as initial and primitive sections within genus *Salsola*. Closer to this section by the anatomy of perianth are species of section *Cardiandra*, at which also is absent slerenchyma in the upper lobes of perianth. But species of this Section have less small-sized and more thick-walled parenchymatous cells and grouping dislocation of sclerenchyma on both margins of lower perianth segments. *S. gemmascens,* however, from section *Malpigila* is sharply delimitated by its specific perianth structural patterns. The presence of chlorenchyma in the upper lobes brings together *S. gemmascens* with species from the *Caroxylon.* Section. Based on leaf morphology, in particular on the presence of hums at the base of leaves in combination with a peculiar pubescence (development of malpigipilae hairs) of assimilative organs and smooth sculpture of anther' appendages we agreed with Boschantzev, 1969 to replace *S. gemmascens* into the separate section named *Malpigila.* Some structural features of perianth anatomy (mostly in its upper part) during fruits maturity stage that were described by us and unusual shape and degree of sclereids wall thickening doubtlessly, distinguish this species from all *Salsola* species of remaining sections.

The second line of species differentiation and evolution within genus *Salsola,* according to our studies was allocated to the formation of Section *Belanthera*, which has been, probably, derived spontaneously from section *Caroxylon*, although the fruit tepals anatomy consisted from radially large thin-walled, elongated cells of parenchyma with abundantly developed porous hydrocyte cells closely related *Malpigila* section to the *Caroxylon.*

The third line of evolutionary trend within genus *Salsola* was going towards *Caroxylon-Arbuscula –Salsola* sub.*Kali* differentiation. For the almost all investigated species of these sections the surface of perianth is covered by various types of papillae that differ between species by size and abundance of their distribution. Species of section *Arbuscula: S. arbuscula, S. arbusculiformis, S. richteri, S. Paletzkiana* and *S. montana* differ from each other by size, morphology, number of papillae and their distribution on the epidermis of vegetative organs. Species of section *Arbuscula (S. arbuscula, S. arbusculiformis, S. richteri, S. Paletzkiana)* differ from each other by a significant thickening of epidermis cells, massive sclerification, development of collenchyma in the perianth apexes *(S. Paletzkiana),* and comparative small sized of cells of all perianth tissues. Hydrocyte cells can be like dots (*S. arbusculiformis)*, crack shaped or reticulate (S.richteri, S.paletzkiana) porosity. It was also detected that by some structural indexes on morphology and anatomy of perianth the majority species of section *Salsola* sub. *Kali* are approached to species of section *Arbuscula,* but differ from them by the thick-walled parenchyma and rather larger thin-walled epidermis cells; *S .iberica* is distinguishable by uniform thickening of inner epidermis walls of lower tepals of perianth, as well as by the development of crystall/salt bearing layer that is, perhaps, transformed from pygmental.

Interspecies differences were detected in the glandular structures (trichomes , hairs, papillae, salt glands), which are evidently developed on the surface of vegetative organs of flowers. Our preliminarily studies distinguished 6 morphological groups of indumentum frequentlky occurring for Salsola species. Specialized dense epidermal-cell protrusions or few-celled of smooth trichomes were described for some representatives of section *Physurus,* which obviously, indicate that these species possess a high salt tolerance to dry and saline environments. Wide morphological variations exhibit species of sect. *Cardiandra* and *Belanthera,* which mostly possess both uni-and multicellular trichome types (bladder cells –structural organization) those usually, are globose or club-shaped and readily distinguishable from unicellular papillae and sharp-pointed prickles. We found out that various mechanisms and strategies for regulation of the salt ion concentration in the plant tissues are operated in the stem and leaf in both succulent halophytes and in the recreto-and pseudohalophytes of Asiatic *Salsola* complex.

Desert *Salsola* annual and perennial species compared with mountaneous representatives showed a prominent ability to accumulate significant amounts of nitrates and/or oxalates in the vegetative flower organs. Secreted salts usually appeared as crystals, which are more abundant on the adaxial organ surface because of the higher gland frequency. Cross-sections of bracts and bracteoles of many *Salsola* species show that different tissues carry out water and salt-accumulating functions. Cell size, shape could be identified by location and accumulation of salt/ions into specilized (salt- storage) cells or tissue. The displacement of salt/ions into the cellular tissue for some *Salsola* species (by means of fluorescent microscopy) revealed their maximum abundance in leaves, sterile elements of flower and anther connective cells, while ions dislocation has never been observed in the male-and female gametophytes and embryo. Structurally, SEM methods revealed a high diversity in the micro-morphology of epicuticular wax (epicuticular secretion), mostly occurring as specific crystalloids on the plant surface. The presence of crystals in the outer covering of seeds may play a role in changing soil pH, thereby providing a more favourable condition for plant survival. Electron microscopic X-ray analysis of salt glands secretion products with different representatives of Salsola has revealed the localization of variety of mineral elements and ions. Prismatic crystals secreted by glands primarily contain cations Na, K, Ca, and anions Cl, SO_4, carbonate, although other ions such as Mg, Si, Sr also were detected. Thus, *Salsola* species represents high interest in phytoremediation processes cleaning up toxic salts and heavy metals. Specific biological active metabolites for pharmaceutical or industrial use could be also detected from *Climacoptera* species, which would constitute a valuable source of cash compounds.

By our studies it was determined that *Salsola* complex represents a valuable source of species to explore the variation and evolution of C_3/C_4 anatomy and cellular natural mechanisms to salt/drought stress factors in flowering plants; photosynthetic activity of reproductive organs was insignificantly in buds stage with some increasing during flowering processes and gradually decreasing during fruit maturation. We suggested that the C_4-syndrom were primarily evolved in the leaves and only later extended to the cotyledons and floral organs. Sex expression of flower' organs have been most marked for *S. ruthenica* (European species) that may be related with the habitats, where this species was recently introduced and naturalized. This is a good evidence of origin, species formation and further dispersion of Salsola species from Central Asia through African continent to Europe. From the phylogenetic point of view the history of genus *Salsola* is a striking example for the evolutionary convergence of morphological, ecological and biochemical traits. One of the adaptive strategies that are correlated with morphology, ecology and even taxonomy is photosynthetic type. Different types of CO_2-fixation, namely C_3 and C_4 or intermediate C_3-C_4 were described for different representatives of genus *Salsola.* (Toderich et al., 2008). Even with the small amount of data available in the present thesis the positive correlation between high levels of ploidy and large pollen grains has been revealed. Our preliminarily results demonstrate the usefulness of electrophoresis for exploring the genetic diversity of species populations, which occurred useful for the discussion of taxonomic position of *Salsola* taxons alone and between different genera of the Chenopodiaceae family.

Based on whole plant morphological features, sexual reproduction and functional systems, as well as ecological habitats and geographical distribution of Asiatic genus *Salsola* we concluded that woody species, in particularly *S. arbusculiformis* was primitive and primary with an origin in Central Asia. Some suggestions were formulated for better understanding of the relationships within genus *Salsola* and different representatives of order Centrospermae. We have summarised that *Salsola* species palynologically are closely related to genus *Suaeda, Camphorosma, Chenopodium*, *Haloharis, Sarcobatus, Traganum* from Chenopodiaceae, as well as to the type II of pollen morphology found in Caryophyllaceae, Portulacacea, Phytolacaceae and Amaranthaceae.

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