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► **To cite this version:**

Mehdi Dehghani, Morteza Djamali, Hossein Akhiani. Pollen morphology of the subfamily Salicornioideae (Chenopodiaceae s.s.) in Eurasia and North Africa. *Palynology*, 2021, 45 (2), pp.245-258. 10.1080/01916122.2020.1784304 . hal-02879003

HAL Id: hal-02879003

<https://amu.hal.science/hal-02879003v1>

Submitted on 23 Jun 2020

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Pollen morphology of the subfamily Salicornioideae (Chenopodiaceae s.s.) in Eurasia and North Africa

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Abstract

Pollen morphology of 40 specimens of 15 species belonging to eight genera in the subfamily Salicornioideae (Chenopodiaceae), was studied using Light (LM) and Scanning Electron Microscopy (SEM) to evaluate the taxonomic importance of pollen characters. Pollen grains were characteristically pantoplyporate with 31-51 evenly distributed pores on the surface. Tectum and operculum are covered with minute spinules, typical of other members of Chenopodiaceae, with minor differences among different genera and species. Perforation was only seen in *Halostachys belangeriana* at high magnification. Pollen characters studied in this study include pollen and pore diameters, number and density of apertures, interporal distance (chord), chord/pollen diameter ratio, pore diameter/pollen diameter ratio as well as spinule density on tectum and operculum. Despite extreme uniformity in pollen morphology there is good evidence supporting currently known phylogenetic relationships and generic delimitations within the Salicornioideae subfamily. The significant differences in pollen characters among populations of *Halostachys belangeriana* and *Halocnemum strobilaceum* may indicate genetic diversity or polyploidy in different populations. The pollen characters provide limited taxonomic value in the Salicornioideae subfamily which may come from habitat homogeneity of all species growing in hypersaline marshes and inland hygrohalophytic communities.

Keywords: Amaranthaceae, Caryophyllales, Irano-Turanian region, Mediterranean region, palynology, pollen-habitat relationship.

Introduction

Chenopodiaceae s.s., includes 105 genera and 1400 to 1700 species (Hernández-Ledesma et al. 2015; Akhani et al. 2016), with worldwide distribution but most abundant in deserts, semi-deserts and saline soils in temperate and subtropical regions (Kühn et al. 1993; Zhu 1995; Kadereit et al. 2003). The family has been subjected to extensive molecular studies during the past two decades, representing one of the most phylogenetically well-known families in Caryophyllales with seven distinct subfamilies including Chenopodioideae, Betoideae, Corispermoideae, Salicornioideae, Suaedoideae, Camphorosmoideae and Salsoloideae (Kadereit et al. 2003; Akhani et al. 2007; Kadereit et al. 2010; Wen et al. 2010; Fuentes-Bazan et al. 2012). The inclusion of Chenopodiaceae in its closely related family Amaranthaceae has also been suggested by many morphological, serological and molecular studies (e.g. Malligson 1922; Judd et al. 2002; APG IV 2016) although there are some recently published studies considering them as two separate families with quite different global distributions and habitat preferences (Hernández-Ledesma et al. 2015).

Salicornioideae subfamily is a monophyletic clade with 13 genera and about 100 species (Ball et al. 2017; Piirainen et al. 2017). The genera *Allenrolfea* Kuntze (three subshrub and shrubby species), *Heterostachys* C.A.Mey. ex Schrenk (two shrubby species) and the species *Arthroceras subterminale* (Parish) Piirainen & G.Kadereit and *Mangleticornia ecuadorensis* P. W. Ball, G. Kadereit & Cornejo (a relict shrubby species in Ecuador and Peru) are distributed restrictively in America. All 44 species of *Tecticornia* Hook f. (comprising nearly half of the species in the subfamily) are endemic to Australia except for *Tecticornia indica* (Willd.) K.A.Sheph. & Paul G.Wilson which stretches along the tropical coasts of Asia and Africa and *T. australasica* in Northern Territory, Queensland and New Guinea. *Salicornia* L. (25-30 species) and *Sarcocornia* A.J.Scott (28 species) are distributed worldwide with eight and 11-15 representatives in Eurasia, respectively. Other genera including *Arthrocaulon* Piirainen & G.Kadereit (two species), *Halocnemum* M.Bieb., (two species), *Halopeplis* Bunge ex Ung.-Sternb. (three species), *Kalidium* Moq. (six species), *Halostachys belangeriana* (Moq.) Botsch and *Microcnemum coralloides* (Loscos & J. Pardo) Buen are mostly Eurasian (Kadereit et al. 2007; Shepherd and Wilson 2007; Steffen et al. 2010, 2015; Biondi et al. 2013; Sukhorukov and Nilova 2016; Ball et al. 2017; Piirainen et al. 2017). Altogether some 35 species are distributed in Eurasia and North Africa, of which 15, representing all genera of the region (except for *Tecticornia indica*), are included in this study.

The members of this subfamily are a group of hygro-halophyte plants with succulent and predominantly articulate stems, reduced leaves and inflorescences of spikelets comprised of minute reduced flowers (Kühn et al. 1993). These morphological modifications allow them to tolerate the harsh conditions of their habitats, especially high salinity and extreme physiological drought (Waisel 1972; Short and Colmer 1999), but at the same time cause many taxonomic problems due to a lack of morphological characteristics, leading chenopod researchers (Kadereit et al. 2007; Akhani 2008) to consider the genus *Salicornia* something of a nightmare!

The members of Salicornioideae subfamily form vast communities in coastal and inland saline soils (Akhani 2004) and play a major role in providing water and energy to wild and domestic animals in halophytic pastures. Some genera, such as *Halostachys*, *Halocnemum* and *Kalidium* with a high yield, are traditional fodder for livestock (Zhao and Feng 2001; Squires and Ayoub 2012); these genera are also known to accumulate Na^+ and Cl^- in their tissues, harvest and removal of which might be a solution for soil desalinization (Zhao et al. 2002, 2005; Matinzadeh et al. 2013; Matinzadeh et al. 2019). In addition, there are many studies showing the potential medical uses of species of the Salicornioideae subfamily, including anti-oxidant and antimicrobial (Liu et al. 2010, 2012), anti-phytopathogenic (Hong-bing et al. 2009), and anti-diabetic (Bang et al. 2002) properties.

Salicornia seeds, with their unique lipid constitution, contain 25-30% oil and protein, comparable to those of soybean and cottonseed (Glenn et al. 1998), highly valuable not only for wildlife and domestic livestock but also a great potential source for oil production in highly saline soils where no glycophyte is able to grow. In addition, *Salicornia* shoots are edible and its seeds are of high nutritional value due to the presence of sulphur-rich proteins (Jha et al. 2012).

In palaeoecological studies using pollen as a hydroclimate proxy, high frequency of chenopod pollen is often interpreted as an aridity index (e.g. El-Moslimany 1987, 1990; Zhao and Herzschuh, 2009), causing inaccuracy in reconstructing past vegetation and climate since some chenopods, including members of Salicornioideae, are not characteristics of desertic and dry conditions but rather represent halophytic communities occupying humid saline soils (Dehghani et al. 2017). Distinction between halophytic and non-halophytic desertic species is thus of high importance in Quaternary palynological investigations (Djamali et al., 2008a). The family Chenopodiaceae is stenopollinous (Wodehouse 1935; Erdtman 1969; Lu et al. 2019), the pollen grains are monad and exclusively polyaperturate with tiny spinules on both tectum and operculum (Nowicke 1975; Skvarla and Nowicke 1976). There are a few comprehensive pollen morphological studies in Chenopodiaceae treating the whole family (Monoszon 1951, 1952; Dambach 1993), Suaedoideae (Dehghani and

Akhani 2009) and Salsoloideae subfamilies (Toderich et al. 2010) and Atripliceae tribe (Olvera et al. 2006), resulting in important taxonomic, ecological and biological applications. Local studies focusing on pollen morphology of single or few genera of the family are also available (McAndrews and Swanson 1967; Uotila 1974; Perveen and Qaiser 2012). However, despite the ecological and taxonomical importance of the subfamily Salicornioideae, there is no detailed survey examining pollen morphology in this group.

In this study, we aim to evaluate the taxonomic importance of pollen morphology in reflecting phylogenetic relationships and delimiting genera and species of the subfamily Salicornioideae from Eurasia and North Africa.

Materials and methods

Plant material and nomenclature

Pollen morphology of 40 specimens of 15 species belonging to eight genera under the subfamily Salicornioideae was studied using Light (LM) and Scanning Electron Microscopy (SEM) (Table 2). The study covers all genera distributed in Asia, Europe and North Africa except for *Tecticornia indica* (due to lack of polliniferous material in accessible specimens). The material used in this study was obtained from herbarium samples deposited in the Halophytes and C₄ Plants Research Laboratory, School of Biology, University of Tehran (Hb. Akhani), Université de Montpellier (MPU) and Muséum national d'histoire naturelle (P) (Appendix). The name of genera and species is based on latest accepted morpho-molecular concepts (Kadereit et al. 2006; Shepherd and Wilson 2007; Akhani 2008; Hernández-Ledesma et al. 2015; Piirainen et al. 2017), except for *Sarcocornia* in which we follow the classical circumscription of the genus *Salicornia* sensu Kühn et al. (1993) considering *Sarcocornia* as a separate genus.

Light and scanning electron microscopy

Polliniferous materials were treated using acetolysis technique (Erdtman 1969) in which the pollen bearing organs undergo six minutes treatment with acetolysis solution (one part concentrated sulphuric acid and nine parts acetic anhydride) in 90° C followed by centrifuging for five minutes in 3000 rpm and washing with distilled water (for more details see Dehghani and Akhani 2009). Pollen grains were then mounted in glycerin jelly. Using a Nikon H III Ophthot-2 light microscope equipped with Motic Image Plus 2 software, 50 mature pollen grains were photographed at ×1000 in two focal points; one at high focus to show exine surface structures, and the other at mid focus to show the exine structure. Pollen morphological data including pollen and pore diameters, chord distance (see below for definition) and exine thickness were measured using calibrated Motic Image Plus 2.0 software. Since pollen grains are geometrically spherical and pores are circular in shape, one each of the pollen- and pore diameters were measured as pollen and pore sizes respectively. Chord distance was obtained by measuring the distance between one edge of a pore and the opposite edge of neighboring pore. Other characters namely, number of pores, pollen grain area, pore area, pore density in 100μ², pore diameter/pollen diameter ratio and chord/pollen diameter ratio (C/D) (McAndrews and Swanson 1967; Campbell 1992) were calculated in Excel software (Table 2). Pollen surface area is a function of pollen diameter and was calculated using the equation $SA=4\pi r^2$, where SA is surface area and r is the sphere radius, in order to calculate pore density on pollen surface. The nomenclature for description of the pollen morphology follows that of Erdtman (1966, 1969).

In order to prepare the samples for SEM studies, pollen grains were mounted on carbon pasted stubs and covered with 10 nm gold using a Magnetron Sputter Coater. At least three micrographs of the whole pollen grains and a surface close up micrograph at ×10000 were taken for each sample with a Hitachi Su 3500 electron microscope (Central Laboratory at University of Shahid Beheshti, Tehran).

The average density of spinules on $2\mu\text{m}^2$ of tectum area and the average number as well as density of spinules on operculum were counted and calculated based on three to five SEM observations. The visibility of perforations at $\times 10000$ magnification was also documented (Table 2).

Statistical analyses

The means and standard deviations of all data were calculated using Microsoft Excel software. Pore number estimation was obtained according to the formula provided by Campbell (1992) in which the number of pore or any other evenly distributed objects on a spherical surface equals: $N = 540/[\arcsin(C/D)]$ where N= number of pores, C= the distance between two adjacent pores and D= pollen diameter (Table 2).

Finally, a matrix of 40 specimens (samples) and 10 quantitative pollen grain characters (variables) was provided. Using Euclidian distances, the variation of pollen characters was investigated by Principle Component Analysis (PCA) in PAST V. 3.14 software (Hammer et al. 2001). Variance-covariance matrices were computed from which eigenvalue and eigenvector matrices were derived, based on which PCA biplot was extracted.

Results

The LM and SEM micrographs of eight genera and 15 species of Salicornioideae subfamily from Eurasia and N Africa are presented in Figs 1-4. Table 1 represents all studied species/populations in this study and their life forms, distribution ranges, Chorotypes and ecological types. Pollen grains in all studied samples of the subfamily are monad, pantopolyporate, tectate, spheroidal or subspheroidal in shape, with pores distributed evenly on the tectum. Tectum and operculum are covered with spinules, perforations are very minute and only in one case (*Halostachys belangeriana*) are visible at magnification of $10000\times$. Pollen size averages of different species range from 18.16 to 36.13 μm in diameter and average pore numbers vary from 31 to 51 in examined species of this subfamily. The means and standard deviations of pollen character measurements from light and electron microscopy are presented in Tables 2. A summary of pollen morphological results and important findings for each genus is also provided in the same table.

Arthrocaulon Piiirainen & G.Kadereit (= *Arthrocnemum* auct. non Moq.) (Fig. 1 A-B; Fig. 3 A-B). Pollen morphology of four accessions of the Eurasian and north African species, *A. macrostachyum*, studied by light microscopy, showed a continuous variation in terms of size, pore number and the distance between adjacent pores. Pollen diameter ranges from 24.30-27.52 μm , pore number varies from 35-44 and chord distance is between 5.88 and 7.11 μm in four examined accessions (Table 2). According to electron microscopy images of the sample from Pakistan (Akhani 16531) average densities of spinules on operculum and on $2\mu\text{m}^2$ of tectum are 5 and 5.8 respectively, which are the lowest numbers compared to all other studied species in the subfamily (Table 2).

***Halocnemum* M. Bieb.** (Fig. 1 C-D; Fig. 3 C-D). Four representatives of the widely distributed species *Halocnemum strobilaceum* were examined in this study. Pollen diameter in populations of this species ranges from 19.18 to 23.24 μm , pore number varies from 34-36, and chord distance is 5.04-6.08 μm (Table 2). The sample collected from Semnan (Akhani 24152) shows larger pollen with bigger pores, longer chord distance and thicker exine compared with the other three populations that show insignificant variations in pollen traits among them (Table 2). Pollen in this species shows the highest number of average spinules per $2\mu\text{m}^2$ of tectum area (16 spinules in $2\mu\text{m}^2$) in comparison with other studied species (Table 2).

***Halopeplis* Bunge ex Ung.-sternb.** (Fig. 1 E-J; Fig. 3 E-H). All three species of the genus are included with six representatives, in our study. Pollen diameter in this genus ranges from 21.36-25.72 μm , pore number varies from 31 to 37, and chord distance is 5.45-6.77 μm (Table 2). Pollen

characters in studied populations of the genus *Halopeplis* display continuous variations with the exception of *H. pygmaea* (Akhani 24170) which shows larger pollen size (three micrometers bigger than other studied samples) (Table 2). The average densities of spinules on operculum and on $2\mu\text{m}^2$ of tectum for two studied species of this genus vary from 6.8 to 7.3 and 8.8 to 14.13, respectively (Table 2).

***Halostachys* C. A. Mey.** (Fig. 1 K-L; Fig. 3 I-J). Pollen morphology of seven populations of this monotypic Eurasian genus was studied here. There is a significant variation in pollen morphology of studied samples (Table 2, Fig 5). Pollen diameter in this genus ranges between 21.36 and 25.72 μm , pore number varies from 31 to 37, and chord distance is 5.45-6.77 μm (Table 2). Of all samples of the subfamily Salicornioideae studied here by electron microscopy, only in one studied sample of *H. belangeriana*, are pollen perforations visible at magnification of 10000 \times .

***Kalidium* Moq.** (Fig. 1 M-P; Fig. 3 K-K; Fig. 4 A-B). Two out of five species of this Eurasian genus with four representatives were included in our study. Pollen diameter ranges from 18.16 to 22.90 μm , pore number varies between 32 and 37, and chord distance is 5.34-6.02 μm (Table 2). *K. wagenitzii*, an Anatolian endemic, shows the smallest pollen grain in the whole subfamily with the highest pore density. The two studied species are distinguishable based on pollen diameter (18.16 μm in *K. wagenitzii* and 20.15-22.90 μm in *K. capsicum*) and pore densities in $100\mu\text{m}^2$ of tectum (3.07 in *K. wagenitzii* and 2.23-2.66 in *K. capsicum*). A population of *K. capsicum* (Akhani 24164) shows larger pollen size and a higher but overlapping pore number in contrast to the other two populations with highly similar pollen characters (Table 2).

***Microcnemum* Ung.-Sternb.** (Fig. 1 Q-R; Fig. 4 C-D). This monotypic genus includes two disjunct subspecies in western areas of the Mediterranean region and western areas of the Irano-Turanian region (subsp. *coralloides* from Spain and subsp. *anatolicum* from Iran), which show close pollen morphological characters. Pollen diameter is 25.31-25.91 μm , pore number varies between 34 and 36 and chord distance ranges from 6.74 to 6.86 μm (Table 2). In *Microcnemum coralloides* subsp. *anatolicum* both tectum and operculum of the pollen grains are densely occupied by spinules (Fig. 4, C-D, Table 2).

***Salicornia* L.** (Fig. 1 S-T; Fig. 2 A-F; Fig. 4 E-j). Twelve specimens belonging to five species of this genus were investigated in this paper. Pollen diameter ranges from 22.21 to 27.88 μm , pore number varies between 38 and 46 and chord distance is 4.81-6.38 μm (Table 2). In agreement with close morphological similarities among various species of *Salicornia*, the pollen characters of different taxa do not show significant differences, making it impossible to distinguish any pollen type or group. (Fig. 5).

***Sarcocornia* A. J. Scott** (Fig. 2 G-H; Fig. 4 K-L). The two studied populations of *S. perennis* in this paper show a significant difference in pollen diameter between them (27.62 versus 36.13 μm). Pollen in this genus represents the biggest pollen and pore sizes and the highest pore number on the tectum comparing to all other studied samples in the subfamily (Fig. 5).

Multivariate analysis

Fig. 5 shows the scatter plot of Principle Component Analysis (PCA) on pollen data measured under LM. The contributions of PCA axes 1 and 2 to the total variance are 67.99% and 27.11%, respectively. The horizontal axis correlates with pore diameter and the vertical one is mainly associated with pore number. All studied accessions of *Arthrocaulon macrostachyum* are located at a relatively short distance from one another in the positive side of the PCA horizontal axis. Studied samples of *Kalidium* are also gathered together in the PCA diagram (Fig. 5). All species of *Salicornia* are placed on the negative side of the PCA horizontal axis and positive side of the PCA vertical axis, far away from two examined samples of its closely related genus, *Sarcocornia*. In

Halocnemum only the sample collected from Semnan (Akhani 24152) stands distant from the other three samples in the PCA biplot. This is the case with the genus *Halopeplis* in which only a sample of *Halopeplis pygmaea* (Akhani 24170) is distant from its group (Fig. 5). The distribution of the seven samples of *Halostachys* is more interesting, as four samples are grouped together while other three samples are distributed on the other side of the diagram (Fig. 5).

Discussion

Pollen grains provide monophyly and taxonomic signals

Pollen morphology of all genera in the subfamily Salicornioideae distributed in Asia, Europe and North Africa studied in this research indicates a general uniformity of pollen grains in this subfamily. Similar results were obtained by Monoszon (1952) in a study on pollen grains of Chenopodiaceae growing in the former Soviet Union. In spite of a high degree of overlapping, the distribution of the different genera on the PCA biplot is in consensus with new taxonomic delimitations at genus level suggested by molecular evidence (Kapralov et al. 2006; Ball et al. 2017; Piirainen et al. 2017). In accordance with many morphological similarities among members of this subfamily, the variations and overlapping in pollen traits can be due to natural variation (plasticity) or genetic differences among different populations and various closely related taxa. Pollen morphological characters in the two subspecies of *Microcnemum coralloides* does not support recent morpho-molecular findings that suggest the two subspecies of *M. coralloides* (subsp. *coralloides* endemic of Iberian Peninsula and subsp. *anatolicum*, a SW Asian endemic) are genetically distinct taxa. In the case of *Arthrocaulon macrostachyum* there is not enough data on genetic variation of this widely distributed species, and therefore we can consider the distinction either as a reflection of genetic diversity among different taxa or natural variation among one species. It is interesting that despite the differing habit, habitat and geography of these two genera (*Microcnemum* as a small annual inland halophyte, but *Arthrocaulon* as a shrubby salt marsh plant), both phylogenetic results and pollen morphological data show their close affinity (Piirainen et al. 2017) (Fig.5). The similarity of seed protein profiles of three genera *Microcnemum*, *Arthrocaulon* and *Sarcocornia* (Yaprak and Yurdakulol 2007) is also supported by our PCA plot of pollen data (Fig.5). Moreover, the close phylogenetic affinities between *Halocnemum* and *Halostachys* (Kapralov et al. 2006; Ball et al. 2017; Piirainen et al. 2017) is also reflected by pollen morphological data (Fig. 5). On the other hand, the completely different distribution of *Halostachys belangeriana* populations (a monotypic genus) on our PCA diagram and the isolation of one specimen of *Halocnemum strobilaceum* (Akhani 24152) from other studied samples of this ditypic genus may indicate the presence of cryptic taxa in these genera, or the existence of local variation. Similarly, some cases have been observed in studied specimens of *Halopeplis pygmaea* and *Kalidium caspicum* which need to be studied if such variation in pollen morphology is related to any genetic difference or polyploidy variation (Fig. 5). Due to the succulent nature of many Chenopodiaceae, the interspecific differences between closely related species is often very difficult to assess, resulting in some discrepancy of species delimitation by different authors. An interesting case of such complexity was found in the formerly supposed monotypic genus *Bienertia* Bunge (Hedge 1997). Detailed studies on co-cultivation have revealed that the two species *B. sinuspersici* and *B. kavirense* can be distinguished further (Akhani et al. 2005, 2012).

In spite of continuous interspecific and intergeneric variations in pollen, all annual *Salicornia* specimens are grouped closely together in our PCA diagram (Fig. 5), indicating that pollen traits are consistent with the genetic proximity of the taxa, yet the separation of the species based on pollen characters is not feasible. Ghaffari et al. (2006, 2015) reported *S. persica* in central Iran as tetraploid ($2n=4x=36$) and other examined taxa of *Salicornia* as Diploid ($2n=2x=18$). However, there is no clear relationship between pollen traits in diploid and tetraploid species of *Salicornia*.

The noticeable pollen morphological differences between the two populations of *Sarcocornia perennis* can be attributed to the difference in ploidy levels; two chromosome numbers ($2n = 18, 36$)

have been reported for this species (Shepherd and Yan 2003). Therefore, it is likely that the Guillon 3895 specimen with the largest pollen grain in the whole subfamily is tetraploid but the Bouby 4951 specimen might be diploid, which causes the deviation in their distribution in the PCA diagram (Fig. 5). The pollen morphology data is not consistent with the assimilation of the perennial *Sarcocornia* into annual *Salicornia*, as has recently been proposed by molecular data (Steffen et al. 2010, 2015; Piirainen et al. 2017).

Pollen of *Kalidium wagenitzii* shows the smallest size in the whole subfamily, and is distinguishable from pollen of *Kalidium caspicum* based on pollen size and pore density (Table 2). These two species show significant morphological differences (Kadereit et al. 2006; Ball et al. 2017; Piirainen et al. 2017). In *Kalidium wagenitzii*, the leaves are tubular, while they are reduced in *Kalidium caspicum* and the stem is articulated. Due to these differences, *Kalidium wagenitzii* was originally described under the genus *Kalidiopsis* (Aellen 1967). The diversity centre of *Kalidium* is Central Asia, where four additional species are growing. Lu et al. (2019) described a *Kalidium*-pollen type among studied species of Chenopodiaceae from the eastern arid Central Asia which is characterized by the presence of isolated spines on pore membrane and pore diameter of 1-3.5 μm . All Salicornioideae species in this study fall into the same category of pore diameter. However, we did not consider the character of microechina on pore membrane in our study.

Pore number and habitat moisture

The application of pollen characters is limited in the taxonomy of the highly complicated groups under Salicornioideae. However, there are hints that indicate some pollen grain traits do correlate with habitat conditions. For example, in a study of pollen characters in the Suaedoideae subfamily it was found that very often higher numbers of pores are positively correlated with wet saline soils. Furthermore, it has been shown that C_3 taxa in *Suaeda* Forssk. Ex J.F. Gmel. growing in wetter soils are characterized by higher pore numbers (Dehghani and Akhani 2009).

The most common pollen types in Angiosperms are monocolpate (in monocots) and tricolpate (in dicots). While exine provides protection for the pollen grains, apertures play three major roles including water and gas exchange with the environment, pollen tube germination and harmomegathy (Wodehouse 1935; Payne 1972). The last is a process in which pollen shape changes to adapt to the smaller or larger size of cytoplasm caused by dehydration or hydration (Wodehouse 1935; Punt et al., 2007) with apertures playing the most important role (Heslop-Harrison, 1979). Phylogenetically, the pantoporate pollen type is a derived form with at least 66 independent origins, occurring in 57 families of angiosperms particularly in the species of Caryophyllales (Prieu et al. 2017). Prieu et al. (2017) argue that pantoporate pollen distribution among angiosperms comes from positive short-term selection (such as accelerating water absorption and hence pollen germination) and negative long-term selection (for example the possibility of pollen desiccation during pollination) since this pollen type occurs frequently but with limited diversification and hardly fixed in large taxonomic groups. Multiple origins of pantoporate pollen is explained by the unique mechanism in which position and number of future apertures are determined by callose deposition (Albert et al. 2014) but reversion to the ancestral state is almost impossible (Matamoro-Vidal et al. 2016). The high rate of convergence in pantoporate pollen grains reflects the essential ecological determinism in the formation of this pollen type which may address the high similarity of pollen morphology in Salicornioideae species.

All members of the subfamily Salicornioideae are C_3 species, except for some species of *Tecticornia* (not included in this study) (Shepherd and Wilson 2007; Voznesenskaya et al. 2008) occupying salt marshes, inland and saline soils around salt lakes and rivers, hence sharing a uniform pollen grain closely related to those of Chenopodioideae and the genus *Suaeda* (Monozson 1952; Uotila 1974; Dambach 1993; Akhani et al. 2003; Dehghani and Akhani 2009), but completely different from pollen of most members of the Salsoloideae subfamily, occupying more xeric habitats (Monozson 1951, 1952; Dambach 1993; Toderich et al. 2010; Authors unpublished data). A simple conclusion

of these comparisons is that habitat moisture determines, to a large extent, the most taxonomically important character of chenopods' pollen grain, namely pore number. This finding can be very useful in interpreting fossil pollen to infer past vegetation and ecology of the earth, since pollen of Chenopodiaceae is one of the most predominant pollen grains in lake sediments in drylands of SW Asia (e.g. Wick et al. 2003; Djamali et al 2008b). In many studies, high frequency of Chenopodiaceae pollen has been interpreted as an aridity index but there are different types of chenopod pollen indicating different ecosystems and different soil hydroecological conditions (Dehghani et al. 2017). We hypothesize that developing an operculum covered with increasing numbers of spinules and reducing the number of pores in the course of evolution may have been a strategy to reduce water loss during pollen transferring.

Conclusions

We conclude that pollen characters are of limited taxonomic value in Salicornioideae subfamily due to high similarity in pollen morphology, however, current taxonomic relationships and delimitations of the genera are relatively shown in multivariate analysis of pollen characters. It is likely that the uniformity of pollen characters in this subfamily comes from the similar ecological conditions in which the members of Salicornioideae grow. The pore number and possibly the presence of opercula and spinules may indicate the evolutionary responses to aridification in SW Asia. This last finding could shed light on paleoenvironmental interpretations of fossil pollen grains. A pollen type definition based on different pollen characters, especially the pore numbers and pore structure, may help to infer more precise environmental information from the Chenopodiaceae pollen which forms one of the most dominant components of fossil pollen assemblages in semi-arid regions of the world.

Acknowledgments

This paper is part of the PhD thesis of the first author which was supported by a scholarship from University of Zabol and an additional grant provided by the Iranian Ministry of Science and Technology for six months research in the Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE), Aix Marseille Université, France. We are indebted to the curators of the Herbarium of Université de Montpellier, Caroline Loup, and Muséum national d'histoire naturelle in Paris, Dr Myriam Gaudeul, for their helps during the herbarium visit of M.D. We are also grateful to Saeed Javadi Anaghizi, technical assistant at the Central Laboratory of University of Shahid Beheshti, Tehran, for preparing SEM images of pollen grains. The costs of Scanning Electron Microscopy were granted by Iranian Science Elite Federation (ISEF) to H.A. The first author wishes also to thank the cultural service of the French Embassy in Tehran for their help and support in arranging the research stay in France. Finally, the linguistic editing of the text by Alison Rix (South Molton, UK) is much appreciated.

Declaration of interest statement

There is no conflict of interest

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Appendix:

Supplementary Internet Material: List of plant vouchers studied in this paper and the herbaria in which the vouchers are deposited

***Arthrocaulon macrostachyum* (Morice) K. Koch.** Greece: in Rhodo, Karpathos, Samos et Asia-Minore, auspice, 4-8.1886, W. Barbey 551, (MPU).

Arthrocaulon macrostachyum (Morici.) K. Koch. Morocco: Terrains marecageux, pres du canal de fuite de la station de pompage de l'île de Skrouna, dans Ile Chott Chergui, 22.4.1952, A. Dubuis, (MPU).

Arthrocaulon macrostachyum (Morici.) K. Koch. Pakistan: Baluchestan, ca. 40 km NW of Karachi, coastal areas near Ship Breaking Factory near in Gidani, 25°04'47''N, 66°42'27''E, sea level, 28.2.2003, H. Akhani 16536 (Hb. Akh.).

Arthrocaulon macrostachyum (Morici.) K. Koch. Pakistan: Sind, W of Karachi, mangroves and halophytic vegetation along the Arabian Sea coast, 24°50'50''N, 66°53'37''E, sea level, 28.2.2003, H. Akhani 16531 (Hb. Akh.).

Halocnemum strobilaceum (Pall.) M. Bieb. Iran: Bushehr 11 km NE of Borazjan towards Kazeroun, saline soils, c. 100 m, 20.11.1991, H. Akhani 7955 (Hb. Akh.).

Halocnemum strobilaceum (Pall.) M. Bieb. Turkey: Aksaray, 10 km E of Eskil towards southern saline shores of Tuz Gölü lake, high salty soils, 38°25'5''N, 33°29'52''E, 914 m, 28.8.2004, H. Akhani et al. 18004 (Hb. Akh.).

Halocnemum strobilaceum (Pall.) M. Bieb. Iran: Semnan, 67 km W Damghan in the road towards Cheshmeh Ali, high saline soils, 1822 m, 36°6'19''N, 53°47'27''E, 14.7.2001, H. Akhani and M. Salimian 15330 (Hb. Akh.).

Halocnemum strobilaceum (Pall.) M. Bieb. Iran: Semnan, Between Eivanakey and Semnan, 10 km W of Deh Namak, saline soils around the road, 35°16'6''N, 52°36'39''E, 821m, 16.10.2013, H. Akhani 24152 (Hb. Akh.).

Halopeplis amplexicaulis (Vahl) Ung.-Sternb. ex Ces., Pass. & Gibelli. Algeria: Southern edge of Sebkhia Ben Ziane, close to Ferry, Relizane Region, 15.5.1949, A. Dubuis, (MPU).

Halopeplis amplexicaulis (Vahl) Ces. & al. Spain: Alicante, Blche, Laguna del Hondo, 30SXH9730. Halonitrophilous therophytic communities, 23.6.1984, D. Sanchez-Mata & R. Gavilan 57 (MPU).

Halopeplis perfoliata (Forssk.) Asch. Iran: Hormozgan, Jask, saline wastelands along the road, 25°40'24''N, 57°49'3''E, ca. 10m, 27.11.2005, H. Akhani et al. 18337 (Hb. Akh.).

Halopeplis pygmaea (Pall.) Bunge ex Ung.-Sternb. Iran: Fars, N Tashk lake, high salty soils near Gomban, 29°48'N, 53°28'E, 1590 m, 20.9.2001, Akhani & Ghobadnejhad 15717 (Hb. Akh.).

Halopeplis pygmaea (Pall.) Bunge ex Ung.-Sternb. Iran: Semnan, Touran National Park, 50 km E of Biarjomand towards Ahmadabad, Kal Shur, saline soils around the river, 35°53'N, 56°19'E, 806m, 17.0.2013. H. Akhani 24170 (Hb. Akh.).

Halopeplis pygmaea (Pall.) Bunge ex Ung.-Sternb. Iran: Tehran, E of Heuze Soltan Lake, 850 m, 18.9.1987, Akhani 5824 (Hb. Akh.).

Halostachys belangeriana (Moq.) Botsch. Iran: Arak, 27 km after Delijan towards Esfahan Road, 4.8.2005, M. Dehghani and A.A. Dolatyari 353 (Hb. Akh.).

***Halostachys belangeriana* (Moq.) Botsch.** Iran: E Azarbaijan Province, Southern saline flats of Lake Urmia, 10 km NW of Tappeh Rash, 37°8'27"N, 45°45'17"E, 1297m, 27.6.2014, H. Akhani 24324 (Hb. Akh.).

***Halostachys belangeriana* (Moq.) Botsch.** Iran: Khorassan, Between Mashhad and Sarakhs, 18 km after Mazdavand to Sarakhs, 650 m, 16.8.1994, Akhani and Zangui 10055 (Hb. Akh.).

***Halostachys belangeriana* (Moq.) Botsch.** Iran: Khorassan, Rude Shur (salty river), 5 km S. Sabzevar, salty and sandy soils, 36°09'32"N, 57°38'22"E, 925 m, 20.7.2001, Akhani & Salimian 15434 (Hb. Akh.).

***Halostachys belangeriana* (Moq.) Botsch.** Iran: Semnan, Between Eivanakey and Semnan, 10 km W of Deh Namak, saline soils around the road, 35°16'6"N, 52°36'39"E, 821m, 16.10.2013, M. Dehghani 7118 (Hb. Akh.).

***Halostachys belangeriana* (Moq.) Botsch.** Iran: Tehran, E. of Hueze-Soltan Lake, 800 m, 18.9.1987, Akhani 4760 (Hb. Akh.).

***Halostachys belangeriana* (Moq.) Botsch.** Turkmenistan: Balkhan Province (= Krasnovodskayaoblasti), ca. 20 km NW of Nebet- Dagh, near Mollakara, salty and sandy substrate margin of Uzboy river, ca. sea level, 10.9.1994, Akhani 10086-T (Hb. Akh.).

***Kalidium capsicum* (L.) Ung -Sternb.**Iran: Gorgan, South of Golestan Natinal Park, 7 km W. of Mirza Baylu towards Ceshmeh Khan, 37°19'30"N, 56°11'30"E, 1200 m, 5.10.1995, Akhani 12120 (Hb. Akh.).

***Kalidium capsicum* (L.) Ung -Sternb.**Iran: Semnan, 23 km W. of Cheshmeh Ali towards Shurtangeh (salty valley), halophytic communities on salt flats around salty river dominated by *Tamarix*, 36°10'50"N, 53°53'51"E, 1733 m, 15.11.2002, Akhani 16500 (Hb. Akh.).

***Kalidium capsicum* (L.) Ung -Sternb.** Iran: Semnan, Touran National Park, 50 km E of Biarjomand towards Ahmadabad, Kal Shur, saline soils around the river, 35°53'N, 56°19'E, 806m, River water EC=43.3 ms/d, 17.0.2013, H. Akhani 24164 (Hb. Akh.).

***Kalidium wagenitzii*(Aellen) Freitag & G. Kadereit;** Turkey: Aksaray, 10 k E of Eskil towards southern saline shores of Tuz Gölü Lake, high saline soils, 38°25'5"N, 33°29'52"E, 914 m, 28.8.2004, H. Akhani et al. 18001 (Hb. Akh.).

***Microcnemum coralloides* (Loscos& J. Pardo) Buen subsp *anatolicum* Wagenitz;** Iran: East Azarbaijan Province, Eastern shores of Lake Urmia, saline wetland near mines located in 15 km SW of Azarshahr, partly dominated by *Juncus heldreichianus* and partly disturbed grazd land, 37°42'22"N, 45°50'37"E, 1307m, 26.6.2014, H. Akhani 24319 (Hb. Akh.).

***Microcnemum coralloides* (Loscos& J. Pardo) Buen subsp. *coralloides*;** Spain: Cfr. Series in confecta flantarum, Aragonia. Habitat in salsuginoni humidis, Velsiesi, regionis inferioris Aragonia (Sierra- baja), lecta in Govea la saladata juxta viam inter Castel-sera et Andorra, 6-9.1872 Socius Lores et Bernal, (MPU).

Salicornia iranica* Akhani subsp. *iranica Iran: Fars, N. Tashk lake, high salty soils near Gomban, 29°48'N, 23°28'E, 1590 m, 20.9.2001, Akhani & Ghobadnejhad 15721 (Hb. Akh.).

Salicornia iranica subsp. *rudshurensis* (Akhani) Chatrevoor & Akhani (ined.); Iran: Tehran, ca. 60 km W Tehran, Mardabad salt flats, 35°43'4"N, 50°44'24"E, 1169 m, 10.10.2013, Akhani 17319, (Hb. Akh.).

Salicornia persica Akhani; Iran: Esfahan, Varzaneh, Zayand-e– rud river bed, 32°25'32"N, 52°39'05"E, 1493 m, 16.9.2001, Akhani & Ghobadnejhad 15667 (Hb. Akh.).

Salicornia persica Akhani Iran: Esfahan, Varzaneh, Zayand-e– rud river bed, 32°25'32"N, 52°39'05"E, 1493 m, 16.9.2001, Akhani & Ghobadnejhad 15671 (Hb. Akh.).

Salicornia persica Akhani Iran: Esfahan, Varzaneh, Zayand-e– rud river bed, 32°25'32"N, 52°39'05"E, 1493 m, 16.9.2001, Akhani & Ghobadnejhad 15670, (Hb. Akh.).

Salicornia persica Akhani Iran: Fars, N Tashk lake, high salty soils near Gomban, 29°48'N, 23°28'E, 1590 m, 20.9.2001, Akhani & Ghobadnejhad 15720 (Hb. Akh.).

Salicornia persica subsp. *rudshurensis* Akhani; Iran: Tehran, ca. 60 km. W. Tehran, Mardabad salt flats, 35°43'40N, 50°44'24E, 1169 m., 24.10.2003, Akhani 17423, (Hb. Akh.)

Salicornia procumbens Sm. South England: Lime Regis, Sea level, 20.8.2006, H. Akhani 18494, (Hb. Akh.).

Salicornia sp.; Turkey Konya, W of Tuz lake, 11 km SE of Cihanbeyli towards Tereskan, Alkim factory (Alkim Alkali kymia), 33°33'13"N, 32°55'45"E, 945 m, 28.8.2004 H. Akhani, E. Dogan, M. Ekici, M. Ghasemkhani 18020 (Hb. Akh.).

Salicornia sp.; Turkey: Konya, W of Tuz lake, 11 km SE of Cihanbeyli towards Tereskan, Alkim factory (Alkim Alkali kymia), 33°33'13"N, 32°55'45"E, 945 m, 28.8.2004, H. Akhani et al. 18019 (Hb. Akh.).

Salicornia x tashkensis Akhani; Iran: Fars, N. Tashk lake, high salty soils near Gomban, 29°48'N, 23°28'E, 1590 m, 20.9.2001, Akhani & Ghobadnejhad 15722 (Hb. Akh.).

Sarcocornia perennis (Mill.) Scott; France: Province 17 Charente-Maritime, Fouras (Charente-Maritime), Plage de l'Espérance, 27.7.1960, H. Bouby 4951 (P05159478) (P).

Sarcocornia perennis (Mill.) Scott.; France: Salt marshes in Fouras (the area of lower Charente), 25.8.1867, A. Guillon 3895 (MPU).

Table 1. List of studied species and their distribution and their phytogeography or chorotype (ES=Euro-Siberian, IT=Irano-Turanian, M=Mediterranean, SS=Saharo-Sindian), and habitats

Species name	Life form	Distribution	Chorotype	Habitat
<i>Arthrocaulon macrostachyum</i> (Moric.) K. Koch.	Chamaephyte	Eurasia and northern Africa	SS, M	Hygrohalophyte
<i>Halocnemum strobilaceum</i> (Pall.) M. Bieb.	Chamaephyte	S Mediterranean, SW and C Asia	IT (ES, M)	Hygrohalophyte
<i>Halopeplis amplexicaulis</i> (Vahl) Ces. & al.	Annual	S Europe, N. Africa	M	Hygrohalophyte
<i>Halopeplis perfoliata</i> (Forssk.) Asch.	Hemicryptophyte	S Europe, N. Africa	SS, M	Hygrohalophyte
<i>Halopeplis pygmaea</i> (Pall.) Bunge ex Ung.-Sternb.	Annual	SW and C. Asia	IT	Hygrohalophyte
<i>Halostachys belangeriana</i> (Moq.) Botsch	Chamaephyte	Central and SW Asia, SE Europe	IT	Hygrohalophyte
<i>Kalidium caspicum</i> (L.) Ung - Sternb.	Chamaephyte	Eurasian	IT	Halophyte
<i>Kalidium wagenitzii</i> (Aellen) Freitag & G.Kadereit	Chamaephyte	Turkey	IT	Hygrohalophyte
<i>Microcnemum coralloides</i> (Loscos & J. Pardo) Buen subsp. <i>coralloides</i>	Annual	Spain	M	Hygrohalophyte
<i>Microcnemum coralloides</i> (Loscos & J. Pardo) Buen <i>anatolicum</i> Wagenitz	Annual	SW Asia	IT	Hygrohalophyte
<i>Salicornia procumbens</i> Sm.	Annual	Europe	ES	Hygrohalophyte
<i>Salicornia iranica</i> Akhani	Annual	Iran	IT	Hygrohalophyte
<i>Salicornia persica</i> Akhani	Annual	Iran, C. Asia, S. Arabia	IT	Hygrohalophyte
<i>Salicornia persica</i> subsp. <i>rudshurensis</i> Akhani	Annual	Iran	IT	Hygrohalophyte
<i>Salicornia</i> sp. 18019	Annual	Turkey	IT	Hygrohalophyte
<i>Salicornia x tashkensis</i> Akhani	Annual	Iran	IT	Hygrohalophyte
<i>Sarcocornia perennis</i> (Mill.) Scott	Chamaephyte	Europe, N. Africa	ES, M	Hygrohalophyte

Table 2. Plant taxa and pollen characters investigated in this paper: means and standard deviations based on 50 mature pollen grains for LM characters and 3-5 SEM observations for spinule traits.

Taxa	Voucher	Chord (μm)	Pore diameter (μm)	Pollen diameter (μm)	Exine thickness (μm)	Pore Number	Pollen area (μm^2)	Pore density on $100\mu\text{m}^2$	Pore area (μm^2)	Pore diameter/Pollen diameter	Chord/Pollen diameter	Spinul density on 2mm^2	Spinul number on operculum	Spinul density on $1\mu\text{m}^2\text{operculum}$
<i>Arthrocaulon macrostachyum</i> (Moric.) Piirainen & G.Kadereit	Dubuis 22.4.1952	6.25 \pm 0.5	2.72 \pm 0.3	24.30 \pm 1.5	2.27 \pm 0.2	36 \pm 2.6	1861 \pm 239	1.98 \pm 0.2	5.88 \pm 1.5	0.11 \pm 0.01	0.2576 \pm 0.02			
<i>Arthrocaulon macrostachyum</i> (Moric.) Piirainen & G.Kadereit	Akhani 16531	5.88 \pm 0.5	2.43 \pm 0.3	27.52 \pm 2	1.97 \pm 0.2	44 \pm 3.2	2391 \pm 358	1.87 \pm 0.3	4.69 \pm 1.1	0.09 \pm 0.01	0.2139 \pm 0.01	5.8 \pm 1	13 \pm 1.4	5
<i>Arthrocaulon macrostachyum</i> (Moric.) Piirainen & G.Kadereit	Akhani 16536	5.94 \pm 0.5	2.74 \pm 0.4	25.67 \pm 2	2.29 \pm 0.2	40 \pm 3	2081 \pm 327	1.98 \pm 0.3	6 \pm 1.7	0.11 \pm 0.01	0.2322 \pm 0.02			
<i>Arthrocaulon macrostachyum</i> (Moric.) Piirainen & G.Kadereit	Barbey 551	7.11 \pm 0.6	3.06 \pm 0.4	26.71 \pm 1.8	2.46 \pm 0.2	35 \pm 2.2	2250 \pm 309	1.58 \pm 0.2	7.45 \pm 1.7	0.11 \pm 0.01	0.2664 \pm 0.02			
<i>Halocnemum strobilaceum</i> (Pall.) M. Bieb.	Akhani & Salimian 15330	5.62 \pm 0.2	1.53 \pm 0.2	20.77 \pm 0.6	2.61 \pm 0.3	34 \pm 1.6	1356 \pm 83	2.55 \pm 0.2	1.86 \pm 0.5	0.07 \pm 0.01	0.2708 \pm 0.01			
<i>Halocnemum strobilaceum</i> (Pall.) M. Bieb.	Akhani et al. 18004	5.04 \pm 0.3	1.59 \pm 0.2	19.69 \pm 0.8	2.22 \pm 0.3	36 \pm 1.5	1219 \pm 96	3.01 \pm 0.2	2.1 \pm 0.5	0.08 \pm 0.01	0.2560 \pm 0.01			
<i>Halocnemum strobilaceum</i> (Pall.) M. Bieb.	Akhani 24152	6.08 \pm 0.3	2.75 \pm 0.3	23.24 \pm 1.7	2.03 \pm 0.2	36 \pm 2	1704 \pm 250	2.12 \pm 0.2	5.97 \pm 1.1	0.12 \pm 0.01	0.2623 \pm 0.01	16 \pm 0.8	15.3 \pm 3.1	8.8
<i>Halocnemum strobilaceum</i> (Pall.) M. Bieb.	Akhani 7955	5.27 \pm 0.4	1.50 \pm 0.2	19.18 \pm 0.9	2.28 \pm 0.3	34 \pm 1.7	1158 \pm 108	2.96 \pm 0.3	1.77 \pm 0.4	0.08 \pm 0.01	0.2746 \pm 0.01			
<i>Halopeplis amplexicaulis</i> (Vahl) Ces. & al.	Dubuis 15.5.1949	5.50 \pm 0.6	2.46 \pm 0.3	21.87 \pm 1.9	2.13 \pm 0.2	37 \pm 2.8	1513 \pm 278	2.54 \pm 0.5	4.75 \pm 1	0.11 \pm 0.01	0.2513 \pm 0.02			
<i>Halopeplis amplexicaulis</i> (Vahl) Ces. & al.	Sanchez-Mata & Gavilan 57	5.63 \pm 0.4	2.49 \pm 0.3	21.89 \pm 1.6	1.93 \pm 0.2	36 \pm 2.9	1513 \pm 221	2.44 \pm 0.3	4.87 \pm 1.2	0.11 \pm 0.01	0.2580 \pm 0.02			
<i>Halopeplis perfoliata</i> (Forssk.) Asch.	Dehghan i & Doulatyari 18337	5.45 \pm 0.7	2.76 \pm 0.4	21.36 \pm 2	1.83 \pm 0.2	37 \pm 4.7	1444 \pm 266	2.65 \pm 0.7	5.98 \pm 2.1	0.13 \pm 0.01	0.2552 \pm 0.02	8.8 \pm 1.5	30.5 \pm 3.8	7.3
<i>Halopeplis pygmaea</i> (Pall.) Bunge ex Ung.-Sternb.	Akhani & Ghobadnejhad 15717	6.45 \pm 0.3	2.1 \pm 0.2	21.61 \pm 0.6	2.97 \pm 0.1	31 \pm 1.1	1468 \pm 84	2.13 \pm 0.1	3.46 \pm 0.4	0.07 \pm 0.01	0.2983 \pm 0.01	14.3 \pm 1.3	37.5 \pm 2.6	6.8
<i>Halopeplis pygmaea</i> (Pall.) Bunge ex Ung.-Sternb.	Akhani 24170	6.77 \pm 0.4	2.84 \pm 0.3	25.72 \pm 1.7	2.35 \pm 0.2	35 \pm 2.3	2086 \pm 279	1.72 \pm 0.2	6.33 \pm 1.2	0.11 \pm 0.01	0.2639 \pm 0.02			
<i>Halopeplis pygmaea</i> (Pall.) Bunge ex Ung.-Sternb.	Akhani 5824	5.98 \pm 0.4	2.2 \pm 0.2	21.39 \pm 0.9	2.51 \pm 0.4	33 \pm 1.6	1439 \pm 119	2.33 \pm 0.2	3.8 \pm 0.6	0.07 \pm 0.01	0.2794 \pm 0.01			
<i>Halostachys belangeriana</i> (Moq.) Botsch	Akhani & Zangui 10055	6.23 \pm 0.3	1.82 \pm 0.2	23.53 \pm 1	2.70 \pm 0.3	35 \pm 1.9	1741 \pm 153	2.03 \pm 0.1	2.6 \pm 0.7	0.08 \pm 0.01	0.2649 \pm 1.01			
<i>Halostachys belangeriana</i> (Moq.) Botsch	Akhani 10086-T	5.53 \pm 0.4	2.65 \pm 0.3	23.51 \pm 1.4	2.14 \pm 0.2	40 \pm 2.6	1742 \pm 214	2.31 \pm 0.3	5.57 \pm 1.1	0.11 \pm 0.01	0.2356 \pm 0.02			
<i>Halostachys belangeriana</i> (Moq.) Botsch	Akhani & Salimian 15434	5.76 \pm 0.3	1.84 \pm 0.2	22.06 \pm 0.9	2.08 \pm 0.2	36 \pm 1.9	1531 \pm 123	2.35 \pm 0.2	2.68 \pm 0.7	0.08 \pm 0.01	0.2610 \pm 0.01	12.7 \pm 2.1	22.7 \pm 3.1	6.7
<i>Halostachys belangeriana</i> (Moq.) Botsch	Akhani 24324	6.25 \pm 0.3	2.97 \pm 0.2	23.35 \pm 0.9	2.18 \pm 0.2	35 \pm 1.8	1714 \pm 135	2.04 \pm 0.1	6.97 \pm 0.9	0.13 \pm 0.01	0.2681 \pm 0.01			
<i>Halostachys belangeriana</i> (Moq.) Botsch	Dehghan i &	5.80 \pm 0.3	1.74 \pm 0.3	22.71 \pm 0.8	2.57 \pm 0.3	37 \pm 1.7	1622 \pm 117	2.27 \pm 0.2	2.42 \pm 0.7	0.08 \pm 0.01	0.2553 \pm 0.01			

Botsch	Dolatyar i 353														
<i>Halostachys belangeriana</i> (Moq.) Botsch	Akhani 4760	5.63 ±0.3	1.80 ±0.2	21.89 ±0.6	2.39 ±0.3	36± 1.7	1505 ±82	2.42 ±0.2	2.57 ±0.7	0.08± 0.01	0.2573± 0.01				
<i>Halostachys belangeriana</i> (Moq.) Botsch	Dehghan i 7118	6.24 ±0.4	2.92 ±0.2	27.29 ±1.8	2.32 ±0.2	41± 2.4	2348 ±312	1.76 ±0.2	6.74 ±1.1	0.11± 0.01	0.2293± 0.01				
<i>Kalidium caspicum</i> (L.) Ung -Sternb.	Akhani 12120	5.57 ±0.3	2.1± 02	20.15 ±0.6	2.26 ±0.3	34± 1.6	1275 ±74	2.65 ±0.2	3.46 ±0.6	0.08± 0.01	0.2766± 0.01	10.3 ±1.3	12.5 ±1	6. 8	
<i>Kalidium caspicum</i> (L.) Ung -Sternb.	Akhani 16500	5.56 ±0.3	2.3± 0.2	20.15 ±0.6	2.26 ±0.2	34± 1.3	1276 ±83	2.66 ±0.2	4.15 ±0.7	0.08± 0.01	0.2759± 0.01				
<i>Kalidium caspicum</i> (L.) Ung -Sternb.	Akhani 24164	6.02 ±0.8	2.91 ±0.5	22.90 ±1.5	2.11 ±0.2	37± 9.8	1654 ±228	2.23 ±0.6	6.85 ±1.2	0.13± 0.01	0.2637± 0.04				
<i>Kalidium wagenitzii</i> (Aellen) Freitag & G.Kadereit	Akhani et al. 18001	5.34 ±0.3	2.20 ±0.2	18.16 ±1	1.82 ±0.2	32± 2	1039 ±118	3.07 ±0.3	3.85 ±0.8	0.12± 0.01	0.2948± 0.02	11.2 ±1.3	13.5 ±2.1	6. 3	
<i>Microcnemum coralloides</i> (Loscos & J. Pardo) Buen subsp. <i>coralloides</i>	Lores et Bernal 6-9.1872	6.74 ±0.6	2.40 ±0.2	25.91 ±1.9	2.12 ±0.2	36± 2.5	2120 ±317	1.73 ±0.3	4.56 ±0.9	0.09± 0.01	0.2604± 0.02±				
<i>Microcnemum coralloides</i> (Loscos & J. Pardo) Buen subsp. <i>anatolicum</i> Wagenitz	Akhani 24319	6.86 ±0.5	2.85 ±0.2	25.31 ±1.2	2.07 ±0.1	34± 2.6	2016 ±196	1.72 ±0.2	6.42 ±1	0.11± 0.01	0.2714± 0.02	14±1 .7	21.7 ±6.8	12. 1	
<i>Salicornia procumbens</i> Sm.	Akhani 18494	5.67 ±0.2	2.00 ±0.1	27.88 ±0.8	2.52 ±0.3	46± 1.5	2442 ±146	1.89 ±0.1	3.13 ±0.4	0.07± 0.01	0.2033± 0.01	10.8 ±1	29.5 ±3.1	6. 4	
<i>Salicornia iranica</i> Akhani	Akhani & Ghobadn ejhad 15721	5.46 ±0.4	1.87 ±0.2	24.81 ±1	2.40 ±0.3	43± 2.6	1935 ±139	2.21 ±0.2	2.76 ±0.6	0.08± 0.01	0.2201± 0.01	9.3± 1.7	17.3 ±1.8	4. 3	
<i>Salicornia persica</i> Akhani	Akhani & Ghobadn ejhad 15667	4.81 ±0.2	1.77 ±0.2	22.21 ±0.7	2.12 ±0.2	43± 2	1550 ±99	2.80 ±0.2	2.5± 0.2	0.08± 0.01	0.2166± 0.01				
<i>Salicornia persica</i> Akhani	Akhani & Ghobadn ezhad 15670	6.38 ±0.3	1.85 ±0.2	25.94 ±1	2.69 ±0.3	38± 1.6	2115 ±158	1.81 ±0.1	2.71 ±0.6	0.07± 0.01	0.2459± 0.01				
<i>Salicornia persica</i> Akhani	Akhani & Ghobadn ezhad 15671	5.41 ±0.3	1.92 ±0.2	22.97 ±0.9	3.17 ±4.5	40± 2.2	1659 ±127	2.41 ±0.2	2.92 ±0.5	0.08± 0.01	0.2356± 0.01				
<i>Salicornia persica</i> Akhani	Akhani & Ghobadn ezhad 15720	6.15 ±0.3	2.01 ±0.2	26.41 ±0.8	2.50 ±0.3	40± 1.8	2192 ±137	1.84 ±0.1	3.18 ±0.7	0.08± 0.01	0.2328± 0.01	7.2± 1.5	23.6 ±2.7	5. 9	
<i>Salicornia persica</i> subsp. <i>rudshurensis</i> Akhani	Akhani 17423	5.70 ±0.5	2.06 ±0.2	26.32 ±1.9	2.49 ±0.3	43± 2.4	2187 ±326	2.02 ±0.3	3.35 ±0.6	0.08± 0.01	0.2165± 0.01				
<i>Salicornia persica</i> subsp. <i>rudshurensis</i> Akhani	Akhani 17319	5.65 ±0.4	1.91 ±0.2	27.03 ±1	2.49 ±0.3	45± 1.9	2296 ±170	1.97 ±0.2	2.88 ±0.6	0.07± 0.01	0.2088± 0.01				
<i>Salicornia</i> sp. 18019	Akhani et al. 18019	5.06 ±0.3	1.77 ±0.2	23.97 ±0.9	2.22 ±0.3	44± 1.7	1806 ±134	2.47 ±0.2	2.49 ±0.7	0.07± 0.01	0.2109± 0.01				
<i>Salicornia</i> sp. 18020	Akhani et al. 18020	5.01 ±0.2	1.93 ±0.2	23.60 ±0.7	2.26 ±0.3	44± 1.8	1750 ±105	2.53 ±0.2	2.93 ±0.5	0.08± 0.01	0.2121± 0.01				
<i>Salicornia x tashkensis</i> Akhani	Akhani & Ghobadn ejhad 15722	5.85 ±0.6	2.00 ±0.1	25.11 ±1.4	2.38 ±0.4	40± 2.4	1986 ±233	2.06 ±0.3	3.13 ±0.4	0.08± 0.01	0.2326± 0.01				
<i>Sarcocornia perennis</i> (Mill.) Scott	Bouby 4951	5.59 ±0.4	2.86 ±0.4	27.62 ±2.5	2.31 ±0.2	46± 3.8	2414 ±415	1.97 ±0.3	8.27 ±1.6	0.10± 0.01	0.2032± 0.02	10±1 .4	21.7 ±2.5	5. 9	
<i>Sarcocornia perennis</i> (Mill.) Scott.	Guillon 3895	6.77 ±0.7	3.20 ±0.6	36.13 ±3.1	2.81 ±0.3	51± 7.7	4128 ±736	1.26 ±0.3	6.53 ±1.1	0.09± 0.01	0.1876± 0.02				

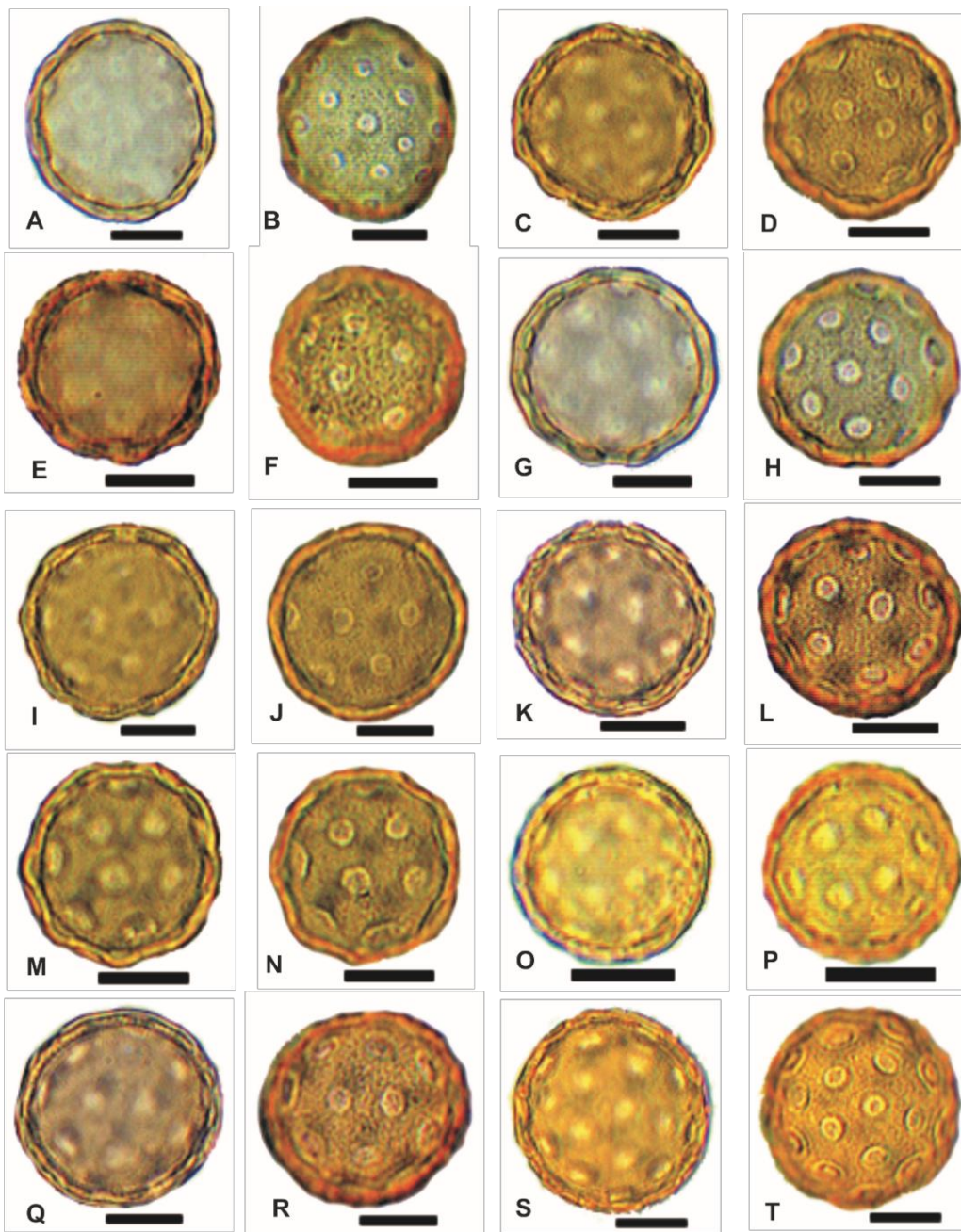


Fig. 1. Light microscope images of pollen grains of selected Salicornioideae taxa in two focal levels to show both exine structures and pore characteristics. Scale bar = 10 μ m. A, B. *Arthrocaulon macrostachyum* (Akhani 16531); C, D. *Halocnemum strobilaceum* (Akhani 24152); E, F. *Halopeplis amplexicaulis* (Sanchez- Mata & Gavilan 57); G, H. *Halopeplis perfoliata* (Dehghani & Doulatyari 18337); I, J. *Halopeplis pygmaea* (Akhani 24170); K, L. *Halostachys belangeriana* (Akhani 24324); M, N. *Kalidium capsicum* (Akhani 24164); O, P. *Kalidium wagenitzii* (Akhani et al. 18001); Q, R. *Microcnemum coralloides* (Akhani 24319); S, T. *Salicornia procumbens* (Akhani 18494)

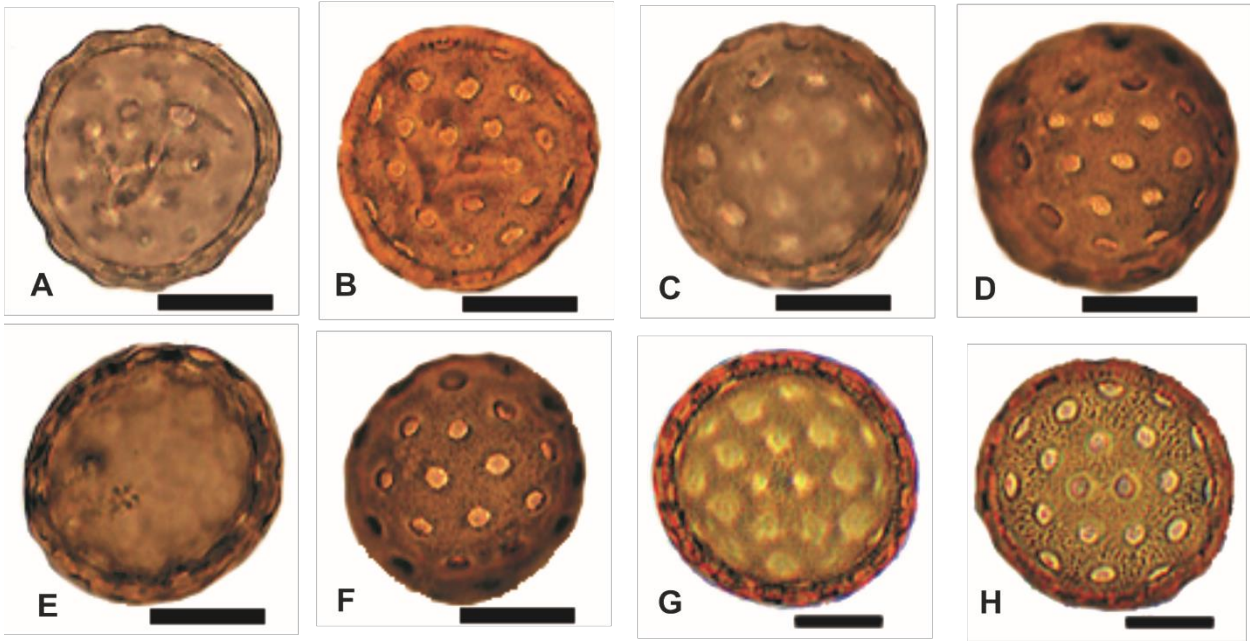


Fig. 2. Light microscope images of pollen grains of selected Salicornioideae taxa in two focal levels to show both exine structures and pore characteristics. Scale bar = 10 μm . A, B. *Salicornia iranica* (Akhani & Ghobadnejhad 15721); C, D. *Salicornia persica* (Akhani & Ghobadnejhad 15720); E, F. *Salicornia* sp (Akhani et al. 18019; G, H. *Sarcocornia perennis* (Bouby 4951)

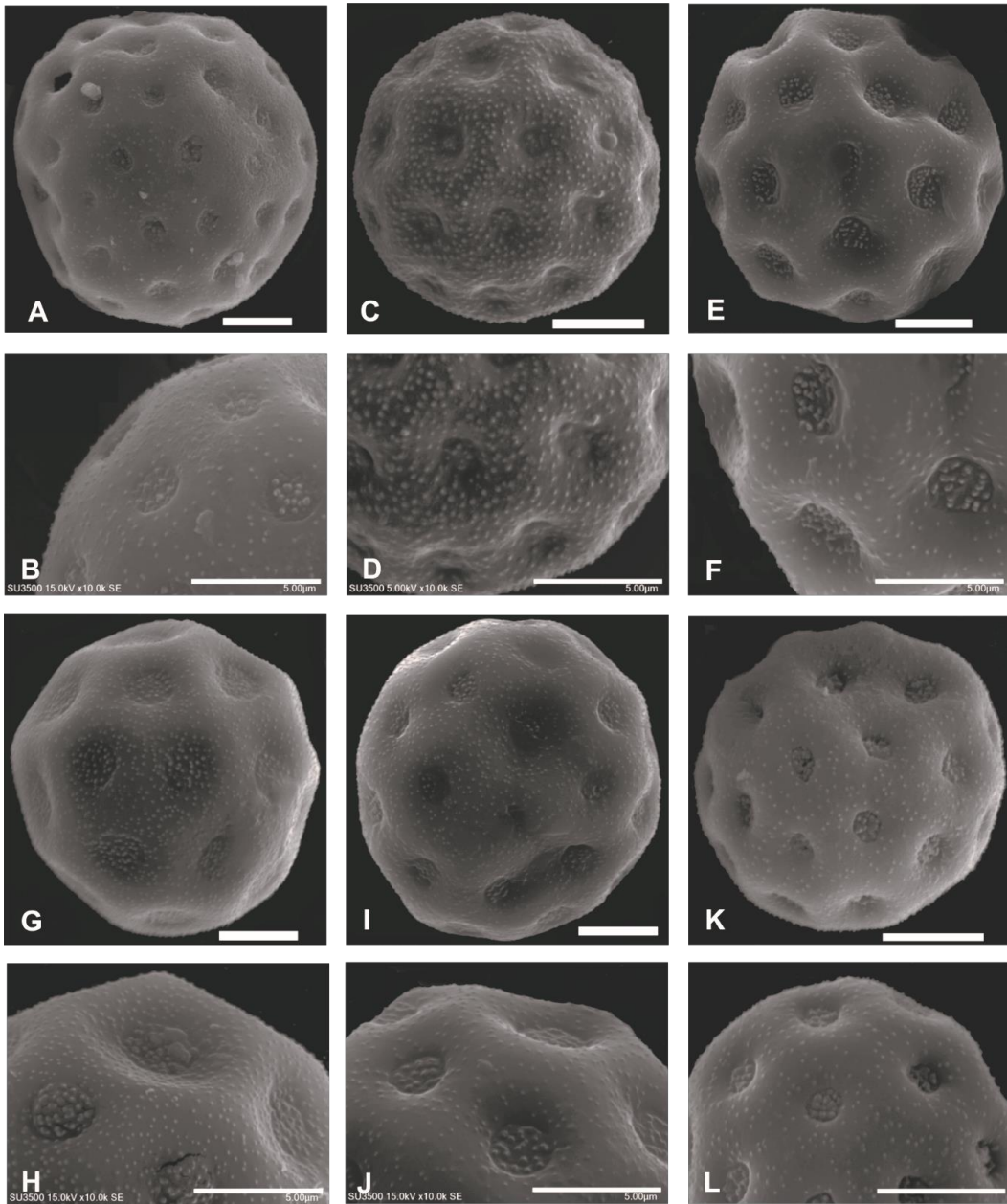


Fig. 3. SEM micrographs of selected pollen grains of Salicornioideae. Scale bar = 5 μ m. A, B. *Arthrocaulon macrostachyum* (Akhani 16531); C, D. *Halocnemum strobilaceum* (Akhani 24152); E, F. *Halopeplis perfoliata* (Dehghani & Doulatyari 18337); G, H. *Halopeplis pygmaea* (Akhani & Ghobadnejhad 15717); I, J. *Halostachis belangeriana* (Akhani & Salimian 15434); K, L. *Kalidium capsicum* (Akhani 12120)

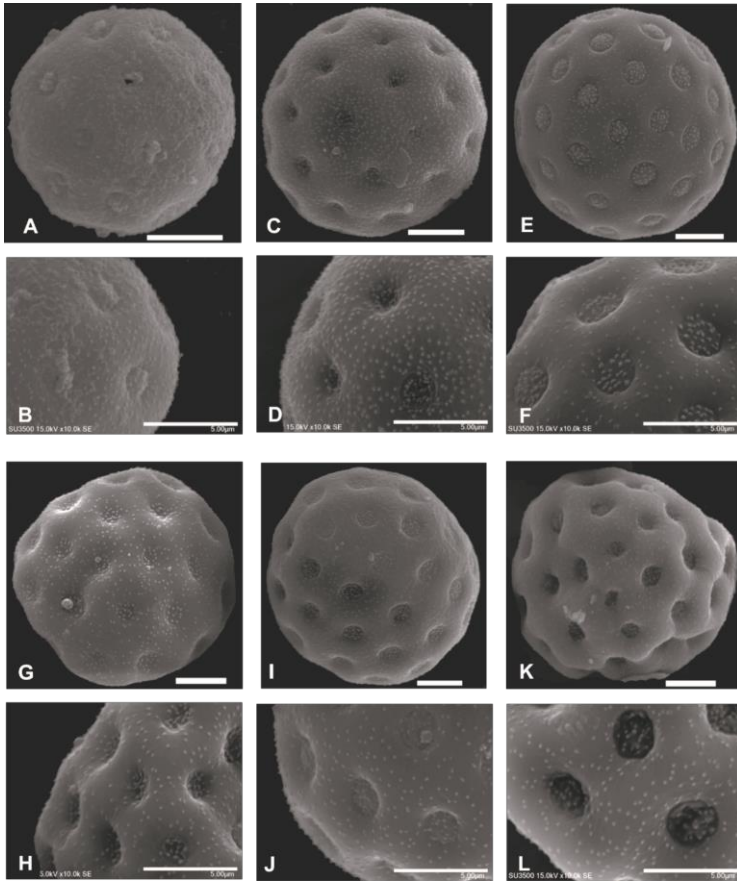


Fig. 4. SEM micrographs of selected pollen grains of Salicornioideae. Scale bar = 5 μ m. A, B. *Kalidium wagenitzii* (Akhani et al. 18001); C, D. *Microcnemum coralloides* (Akhani 24319); E, F. *Salicornia procumbens* (Akhani 18494); G, H. *Salicornia iranica* (Akhani & Ghobadnejhad 15721); I, J. *Salicornia persica* (Akhani & Ghobadnejhad 15720); K, L. *Sarcocornia perennis* (Bouby 4951)

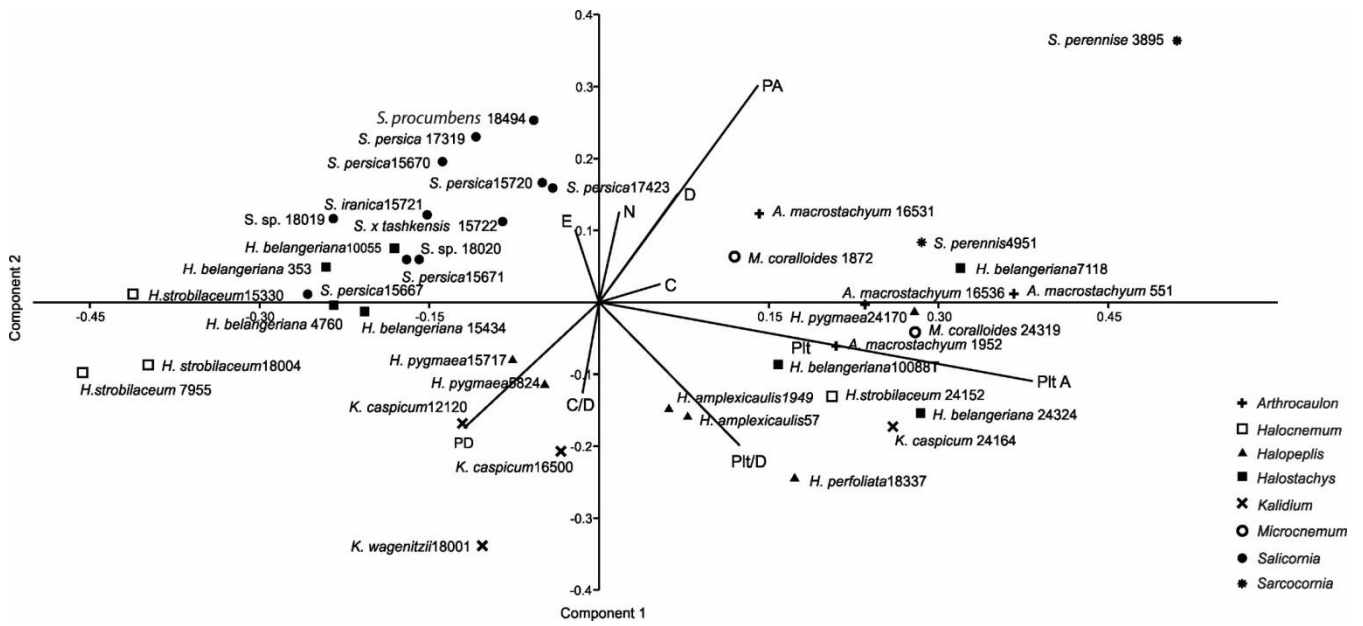


Fig. 5. Principal Components Analysis (PCA) biplot for pollen data of studied samples of Salicornioideae (Chenopodiaceae). PCA axes 1 and 2 explain respectively 67.99% and 27.11% of the total variance. C= chord, C/D= chord/pollen diameter, D= pollen diameter, E= exine, N= pore number, PA=pollen area, PD=pore density, Plt= pore diameter, PltA= pore area, Plt/D= pore diameter/ pollen diameter.