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P. Angelini, E. Bricchi, D. Gigante, S. Poponessi, A. Spina & R. Venanzoni

Pollen morphology of some species of *Amaranthaceae* s. lat. common in Italy

Abstract

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Comparative studies on the pollen grains biometry and morphology of the most common species of *Amaranthaceae* s. lat. (incl. *Chenopodiaceae*) relieved in the Italian territory were carried out by Light Microscope and Scanning Electron Microscope in order to compare similarities and differences among them. Many pollen characters like diameter, volume, exine thickness, number of pores, pore density, interpore distance, pore size were considered and analyzed from statistical points of view. Fisher's Least Significant Difference Test allowed clustering of groups and ordination analysis of taxa. Pollen analysis does not allow easy distinction of the pollen grains of the considered taxa. However, in spite of the many similarities shared by the two groups, some morphological and biometrical traits still allow the distinction of some taxa: interpore distance, exine thickness and above all microechinae density on pollen surface. These spinulous processes are more densely arranged on pollen from species of *Amaranthus* than from those formerly referred to *Chenopodiaceae*.
The results obtained support the inclusion of the former *Chenopodiaceae* into *Amaranthaceae.*

Key words: *Chenopodiaceae*, biometry, SEM, taxonomy.

Introduction

Chenopodiaceae Vent. and *Amaranthaceae* Juss. have long been considered two closely related families of the order *Caryophyllales* and they were subject to taxonomical revisions from the time they were first described to the present (Iamonico 2008, 2012, 2014; Kadereit & al. 2003, 2012). According to the Angiosperm Phylogeny Group (2003, 2009) one large family could be recognized, *Amaranthaceae s. lat.*

Concerning the pollen, several investigations were carried out on *Amaranthaceae s.lat.* (Alkhani & al. 2003; Iamonico 2009; McAndrews & Swanson 1967; Pinar & Inceoglu 1999; Riollet & Bonnefille 1976; Shepherd & al. 2005; Soliman 2006; Toderich & al. 2010; Tsukada 1967; Zare & Keshavarzi 2007). Despite of all these investigations many difficulties are still experienced in distinguishing the pollen of *Chenopodiaceae* from that of *Amaranthaceae*.

Both families shared many features, mostly derivated, such occurs in the case of pollen grains making a stenopalynologic group (Erdtman 1966) which feature rather similar pollen grains. Various authors have reported this group as an allergenic pollen producer: many members of the *Chenopodiaceae* family, as well as of the closely related *Amaranthaceae s. str.* family, are involved in inducing allergic diseases (Barderas & al 2002; Ianovici 2008). For the similarities of their pollen grains, this group is reported in aerobiological pollen monitoring in only one pollen type (Rodriguez De La Cruz & al. 2012).

The aim of the present work was to study and compare pollen characteristics of some *taxa* recorded in the Italian territory. The investigation is useful not only in Allergology and Aerobiology, but also in Palaeobotany and Palynology, because *Chenopodiaceae* and *Amaranthaceae* pollen grains are abundant in the air and the soil. Both *taxa* are wind-pollinated and their pollen grains are found far from the parental plants. They are well-preserved so their characteristic appearance leads to easy recognition in fossil samples.

Materials and methods

Pollen grains were collected in the Italian territory (Fig. 1) from the flower samples of 17 *taxa* belonging to *Amaranthaceae* family: *Amaranthus caudatus* L., *A. hybridus* L. (≡ *A. chlorostachys* Willd.), *A. graecizans* subsp. *sylvestris* (Vill.) Brenan., *A. retroflexus* L., *Atriplex halimus* L., *Bassia scoparia* (L.) Voss [≡ *Kochia scoparia* (L.) Schrad.], *Beta vulgaris* subsp. *cicla* (L.) Schübl. & G. Martens, (≡ *B. vulgaris* var. *cicla* L.), *B. vulgaris* var. *rubra* L., *B. vulgaris* var. *altissima* Döll (= *B. vulgaris* subsp. *vulgaris* L.), *Chenopodium album* L. *s.lat., Chenopodiastrum murale* (L.) S. Fuentes, Uotila & Borsch (≡ *C. murale* L.), *Dysphania ambrosioides* (L.) Mosyakin & Clemants (≡ *C. ambrosioides* L.), *Dysphania botrys* (L.) Mosyakin & Clemants (≡ C. *botrys* L.), *C. opulifolium* Schrad. ex W.D.J. Koch & Ziz, *Lipandra polysperma* (L.) S. Fuentes, Uotila & Borsh (≡ *C. polyspermum* L.), *Spinacia oleracea* L., *Suaeda vera* Forssk. ex J.F. Gmel [≡ *S. fruticosa* subsp. *vera* (J.F. Gmel.) Maire & Weiller] (Iamonico 2015).

The nomenclature according to the most recent taxonomic updates as reported in the database *anArchive*, an on-line synonymized list of botanical species names, developed to support the botanical data banking and vegetation analysis (Angelini & al. 2014, 2015; Gigante & al. 2012; Landucci & al. 2012; Lucarini & al. 2014; Pecoraro & al. 2014; Venanzoni & al. 2012).

For each of the 17 *taxa* investigated, 3 populations (more than 50 flowers per population) were examined. The collected pollen grains and the dried plants from which they were taken were stored in separate envelopes at the University of Perugia's Department of Chemistry, Biology and Biotechnology's Palynotheca and Herbarium PERU (www.anarchive.it) respectively.

A part of fresh pollen grains were stained with basic fuchsin on microscope slides. Comparative analysis of pollen morphology and measurement of several parameters were performed with Leica Dialux 20 Light Microscopy.

A part of the material was treated according to the acetolytic technique originally described by Erdtman (1960) and later modified slightly by Hideux (1972), mounted on

Fig. 1. Location map of the studied areas.

stubs and coated with gold (Angelini & al. 2008, 2009; Pagiotti & al. 2011). The observations and photos were made using SEM Stereoscan 90, Scanning Electron Microscope (Cambridge Instruments).

For each sample more than 50 grains were considered and the following parameters were measured or calculated: diameter, volume, exine thickness, number of pores, pores density, interpore distance, pores size (P os: max diameter; E os: min diameter).

In order to calculate the total number of pores for each grain, we considered the homogeneous distribution of pores on the pollen grain surface and the hexagonal area surrounding each pore (Fig. 2). Apothem of the hexagon is half of the sum of interpore distance plus mean pore diameter. Once the apotheme value is known, by mean simple geometrical formulas it is possible to know the value of the sides, of the height and of the hexagon area.

The calculation of the total area of pollen grains surface is very simple because grains are nearly spherical and diameter is noted.

Therefore, for each *taxon*, in order to obtain total number of pores, total area of pollen grain surface was divided by the area of one hexagon.

Data were analysed by one way ANOVA. A Fisher's *post hoc* test for LSD (Least Significant Difference) was performed for clustering of groups and ordination analysis of *taxa*. All statistical analyses were carried out using StatPlus Professional 2009 statistical software packages.

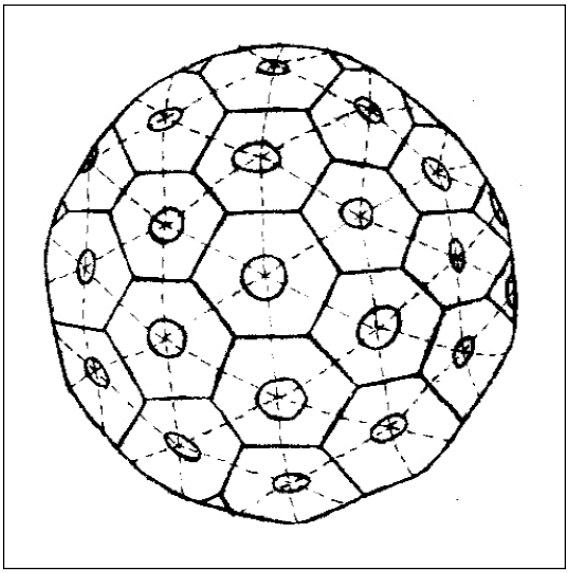

Fig. 2. Pores on pollen grain surface and hexagonal areas surrounding each pore.

Results

In Table (1) and Fig. (3) the examined characteristics of pollen morphology of the 17 *taxa* of the *Amaranthaceae* family are reported. Fisher's LSD allowed clustering of groups and ordination analysis of *taxa* (Fig. 3 a-h). Fig. (3 a, b) show that *Chenopodiastrum murale*, *Beta vulgaris* subsp. *cicla*, *B. vulgaris* var. *rubra*, *B. vulgaris* var. *altissima* have the smallest pollen grain with very similar size. The greatest pollens are those of *Bassia scoparia*, followed by *Spinacia oleracea*, *Chenopodium album s.lat.* and *Suaeda vera*. Volume values of the pollen of these species are not overlapping. The other *taxa* have similar sizes and are grouped in common clusters.

Fig. (3 c) shows the exine thickness histograms. Pollen grains of *Suaeda vera* have the thickest exine (2.88 µm) but these values are similar (not statistically different) to *Bassia scoparia*, *Atriplex halimus*, *Chenopodium album s.lat.* and *Spinacia oleracea*. Pollen grains of *Amaranthus graecizans* and *A. hybridus* have the thinnest exine (1.54 µm), but *A. retroflexus* and *A. caudatus* have an exine thickness similar to the pollen of other species.

Fig. (3 d) shows the number of pore histograms. Pollen of *Amaranthus* genus (*Amaranthus retroflexus, A. graecizans* and *A. caudatus*) have less than 70 pores, but pollen grains of *Amaranthus hybridus* show a very high value with 132 pores.

Pore density on 100 μm^2 is reported in Fig. (3 e). *Chenopodiastrum murale* pollen grains show the highest value (6.88), followed by the "B" cluster of *Dysphania ambrosioides, Amaranthus hybridus, Atriplex halimus* and *Lipandra polysperma* (5.60 - 5.96). *Amaranthus retroflexus* and *A. graecizans* show the smallest values (2.20 - 2.60).

Table 1. Comparison of pollen characteristics [mean(min-max)±st. dev.] of the investigated species.*

	Diameters (µm) .	Volumes (µm3)	Exine thickness (µm)	Pores number	Pore density	Interpore distance (µm)	E os (porus min diameter) (µm)	P os (porus max diameter) (µm)
A.c.	24.67(20.02-27.72) ±2.22	8038 (4199-11147) ±2034.38	1.88(1.54-2.77) ±0.45	69(48-97) ±14.65	3.84(2-5) ±0.80	3.78(3.08-4.62) ±0.61	1.88 (1.54-2.31) ±0.28	1.92 (1.54-2.77) ±0.40
A.g.	25.75(21.56-30.80) ±2.29	9138(5245-15291) ±2452.92	1.54(1.54-1.54) ±0	51(37-73) ±12.32	2.60(2-5) ±0.76	3.94(3.08-6.16) ±0.87	2.91 (2.31-3.08) ±0.31	2.98 (1.54-3.08) ±0.32
A.r.	26.36(21.56-29.26) ±1.88	9728(5245-13110) ±1958.78	1.74(1.54-2.31) ±0.34	50(34-65) ±7.73	2.20(2-4) ±0.50	4.35(3.08-6.16) ±0.66	2.87 (2.01-3.08) ±0.35	2.82 (1.54-3.08) ±0.43
A.h.	26.15(22.33-30.03) ±1.97	9511(5827-14172) ±2149.71	2.69(2.00-3.08) ±0.30	113(91-144) ±17.7	5.76(4-12) ±1.69	2.74(1.54-3.54) ±0.44	1.95 (1.54-2.31) ±0.28	1.98 (1.54-2.77) ±0.30
A.hy.	26.30(23.10-27.72) ±1.25	9585(6451-11147) ±1324.95	1.54(1.54-1.54) ±0	132(99-190) ±23.48	5.92(5-9) ±1.29	1.66(1.54-2.31) ±0.29	2.71 (1.85-3.08) ±0.45	2.76 (1.85-3.08) ±0.44
B.s.	35.05(32.34-36.96) ±1.42	23003(17701-32255) ±3346.9	2.7(1.85-3.08) ±0.35	119(100-133) ±9.71	3.00(2-4) ±0.12	3.04(2.77-3.08) ±0.10	3.07(2.77-3.08) ±0.06	3.08(3.07-3.09) ±0.01
B.v.c.	19.71(18.48-20.02) ±0.63	4020(3303-4199) ±365.96	1.77(1.54-2.31) ±0.35	53(44-67) ±6.11	4.24(4-6) ±0.52	2.52(2.00-3.08) ±0.32	2.73 (2.31-3.08) ±0.34	2.67 (2.31-3.08) ±0.34
B.v.r.	20.08(18.48-21.56) ±0.54	4247(3303-5245) ±349.56	2.02(1.54-2.77) ±0.41	48 (40-58) ±5.85	3.76(3-5) ±0.60	2.78(2.31-3.08) ±0.32	2.82(2.31-3.39) ±0.33	2.78(2.31-3.08) ±0.32
B.v.a.	20.08(18.48-21.56) ±0.86	4257(3303-5245) ±548.85	1.86(1.54-2.31) ±0.34	42(35-49) ±4.53	3.20(3-4) ±0.41	3.08(2.77-3.85) ±0.22	2.82(2.31-3.08) ±0.22	2.90(2.31-3.08) ±0.25
C.a.	28.71(26.18-33.88) ±2.03	12561(9390-20352) ±2817.03	2.61(2.31-3.08) ±0.36	137(105-188) ±25.81	5.24(4-8) ±1.23	2.78(2.00-3.08) ±0.38	2.00(1.54-2.77) ±0.39	1.95(1.54-2.77) ±0.37
C.m.	18.60(15.40-20.02) ±1.47	3429(1911-4199) ±758.71	1.61(1.51-2.31) ±0.19	78(54-99) ±14.03	6.88(4-9) ±0.79	2.38(1.54-3.08) ±0.53	1.69(1.54-2.77) ±0.28	1.73(1.54-2.31) ±0.29
D.a.	26.30(24.64-27.72) ±0.99	9562(7829-11147) ±1071.01	2.09(1.54-3.08) ±0.43	129(106-161) ±17.44	5.96(5-8) ±0.84	2.27(1.54-3.08) ±0.34	2.22(1.85-2.77) ±0.29	2.07(1.85-2.77) ±0.26
D.b.	23.72(21.56-27.72) ±1.54	6982(4829-11147) ±1498.90	1.73(1.54-2.31) ±0.34	76(54-97) ±11.87	4.28(3-7) ±0.89	2.97(2.00-3.54) ±0.32	2.20(1.00-3.08) ±0.57	2.17(1.54-3.08) ±0.57
C.o.	22.53(2156-24.64 0.92	6226(5245-7829) ±779.15	1.80(1.54-2.62) ±0.40	76(53-97) ±14.70	4.72(3-7) ±0.79	2.90(2.31-3.08) ±0.32	2.04(1.54-2.77) ±0.49	1.95(1.54-3.08) ±0.50
L.p.	23.73(21.56-26.18) ±1.45	7072(5245-9390) ±1280.32	2.05(1.54-2.77) ±0.47	97(63-147) ±21.68	5.60(4-10) ±1.32	2.85(1.69-3.85) ±0.48	1.78(1.54-2.00) ±0.16	1.78(1.54-2.31) ±0.25
S.o.	32.85(30.03-36.96) ±1.88	19033(15291-26422) ±2867.4	2.44(1.85-3.08) ±0.36	141(118-171) ±15.51	4.16(3-5) ±0.47	3.16(2.93-3.85) ±0.23	2.13(1.85-2.77) ±0.26	2.10(1.85-2.62) ±0.25
S.v.	27.66(26.64-29.26) ±1.54	11178(7829-13110) ±1792.10	2.88(2.62-3.08) ±0.17	123(101-158) ±16.15	5.12(4-7) ±0.67	2.81(2.31-3.08) ±0.32	1.97(1.54-2.62) ±0.28	1.88(1.54-2.31) ±0.25

Amaranthus caudatus* (A.c.**), *A. graecizans* subsp. *sylvestris* (**A.g.**), *A. retroflexus* (**A.r.**), *Atriplex halimus* (**A.h.**), *A. hybridus* (**A.hy.**), *Bassia scoparia* (**B.s.**), *Beta vulgaris* L. subsp. *cicla* (**B.v.c.**), *Beta vulgaris* var. *rubra* (**B.v.r.**), *Beta vulgaris* var. *altissima* (**B.v.a.**), *Chenopodium album s.lat.* (**C.a.**), *Chenopodiastrum murale* (**C.m.**), *Dysphania ambrosioides* (**D.a.**), *Dysphania botrys* (**D.b.**), *Chenopodium opulifolium* (**C.o.**), *Lipandra polysperma* (**L.p.**), *Spinacia oleracea* (**S.o.**), *Suaeda vera* (**S.v.**).

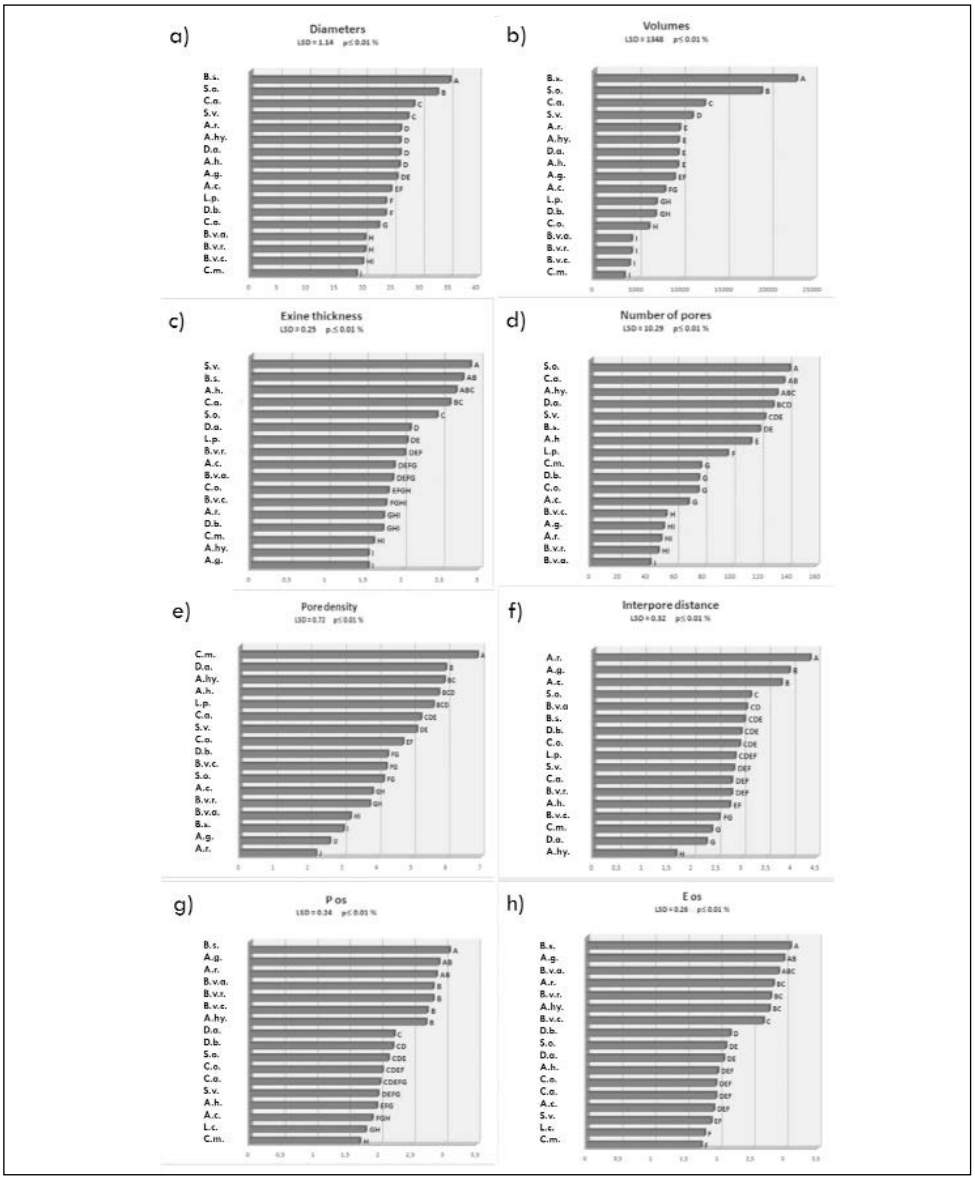

Fig. 3. Characteristics of pollen grains of *Amaranthus caudatus* (**A.c.)**, *A. graecizans* subsp. *sylvestris* (**A.g.**), *A. retroflexus* (**A.r.**), *A. hybridus* (**A.hy.**), *Atriplex halimus* (**A.h.**), *Bassia scoparia* (**B.s.**), *Beta vulgaris* L. subsp. *cicla* (**B.v.c.**), *B. vulgaris* var. *rubra* (**B.v.r.**), *B. vulgaris* var. *altissima* (**B.v.a.**), *Chenopodium album s.lat.* (**C.a.**), *Chenopodiastrum murale* (**C.m.**), *Dysphania ambrosioides* (**D.a.**), *D. botrys* (**D.b.**), *Chenopodium opulifolium* (**C.o.**), *Lipandra polysperma* (**L.p.**), *Spinacia oleracea* (**S.o.**), *Suaeda vera* (**S.v.**): a) Mean diameters, b) Mean volumes, c) Mean exine thickness, d) Mean number of pores, e) Mean pore density, f) Mean interpore distance, g) Mean P os, h) Mean E os.
Different capital letters on the right side of each histogram indicate LSD ($p \leq 0.01$) among the pollen grains of each species, while common capital letters indicate similarity

The data reported in Fig. (3 f) relative to interpore distances are in inverse proportion to those reported in Fig. (3 e) (pore density on 100 μm^2). Pollen of the *Amaranthus* genus (*Amaranthus retroflexus, A. graecizans* subsp. *sylvestris* and *A. caudatus*) have the greatest interpore distances (3.78 - 4.36 μm), but pollen grains of *Amaranthus hybridus* show the smallest value with 1.66 μm.

In Fig. (3 g) and Fig. (3 h) P os and E os pore sizes are reported, respectively. Values of P os (from 1.69 to 3.07) are similar to those of E os (from 1.73 to 3.08) confirming that pores are more or less circular. *Bassia scoparia* shows the highest value, while *Chenopodiastrum murale* pollen grains have the smallest pores. All investigated *taxa* have radially symmetrical spheroidal polypantoporate pollen with circular perimeter (Figs 4-20). The exine is tectate at mesoporia where *tectum* is supported by simple, not branched *columellae*; *tectum* disappears near pores where exine is directly connected with nexine. In the poral areas, *columellae* not supporting *tectum* become *bacula* or *echinae*. In Fig. (13), 4 exine in cross sections, clearly shows *bacula* or little *echinae* (spines) emerging from nexine and protruding out of the pores making a sort of fragmented *operculum*. The examined *taxa* have different levels of pore depth and convexness of mesoporial exine. Also the number of spines on the pore membrane and the density of the perforations and echinae on pollen surfaces are characteristic (Fig. 4-20).

Discussion and conclusions

Pollen analysis of 17 *taxa* of *Amaranthaceae s. str.* and *Chenopodiaceae* does not allow the clear distinction of the pollen grains of the two groups. However, three important parameters can be pointed out: the first two are biometrical parameters, the third one is morphological.

The first biometrical parameter is interpore distance: there is a great difference among *Amaranthus retroflexus*, *A. graecizans*, *A. caudatus* and the other species of *Amaranthaceae*. These three species have the greatest interpore distances. On the other hand, *A. hybridus* shows the shortest interpore distance (1.66 μm).

The second biometrical parameter is exine thickness that is smaller in *Amaranthus*, except for *A. caudatus* that shows an exine thickness greater than other *taxa* such as *Beta vulgaris var. altissima*, *Chenopodium opulifolium*, *B. vulgaris* subsp. *cicla*, *Dysphania botrys* and *Chenopodiastrum murale*.

The third, morphological, parameter is more helpful to distinguish pollen of *Amaranthus*. It is the microechinae on pollen surface: these spinulous processes are more densely arranged on pollen from the *Amaranthus* species than from those formerly referred to *Chenopodiaceae.*

In conclusion, the outcomes of our study support the inclusion of the former *Chenopodiaceae* into *Amaranthaceae*. However, in spite of the many similarities shared by the two groups, some morphological and biometrical traits still allow some *taxa* to be distinguished.

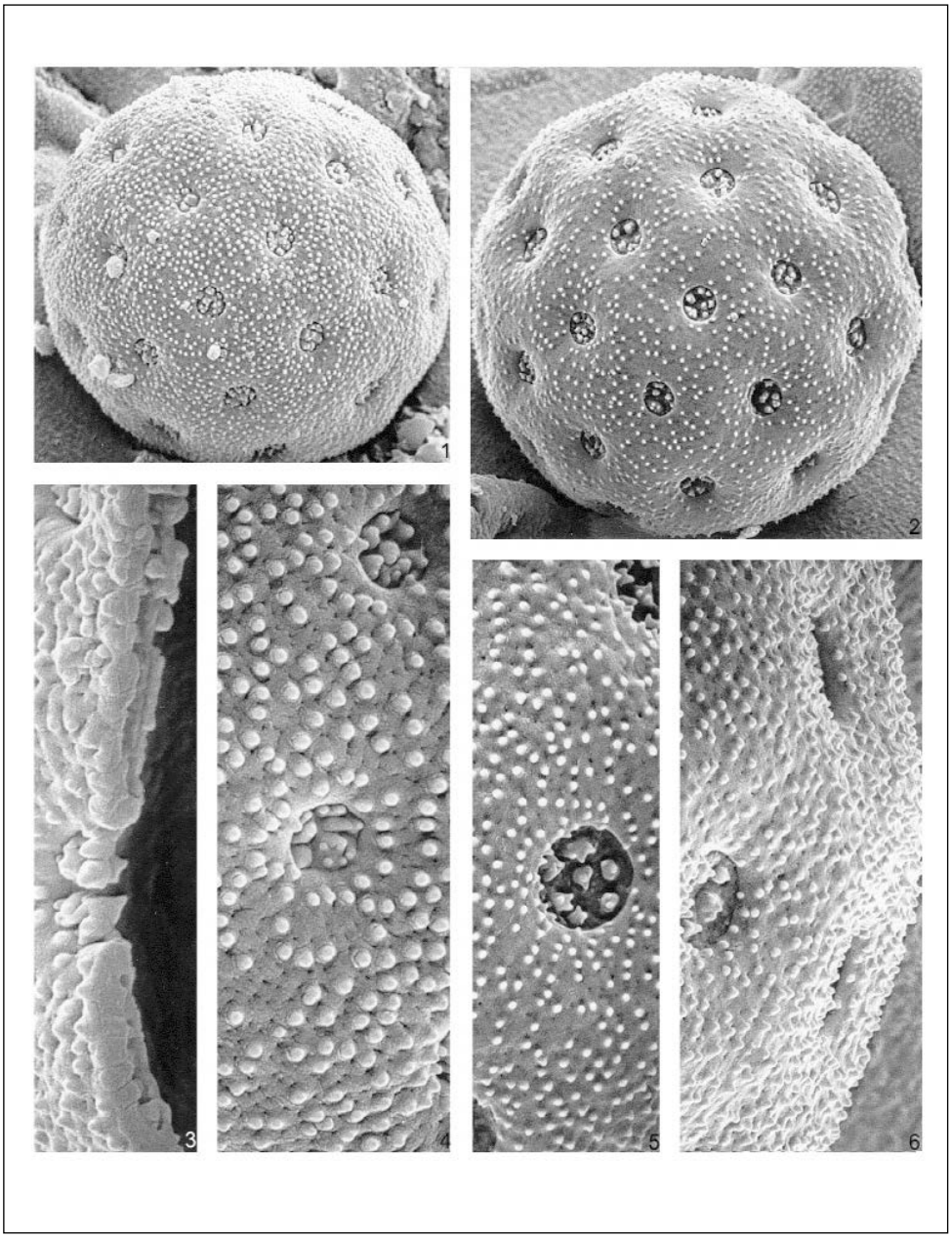

Fig. 4. *Amaranthus caudatus* L.
1-2: Pollen grains at different magnifications (1: × 2900; 2: × 3300)
3: Exine section (× 11200)
4: Exine surface with pores, perforations and microechinae (× 10600)
5: Exine surface with perforations, microechinae and pores with evident inner microechinae (× 8200)
6: Exine surface with pores, perforations and microechinae (× 8200)

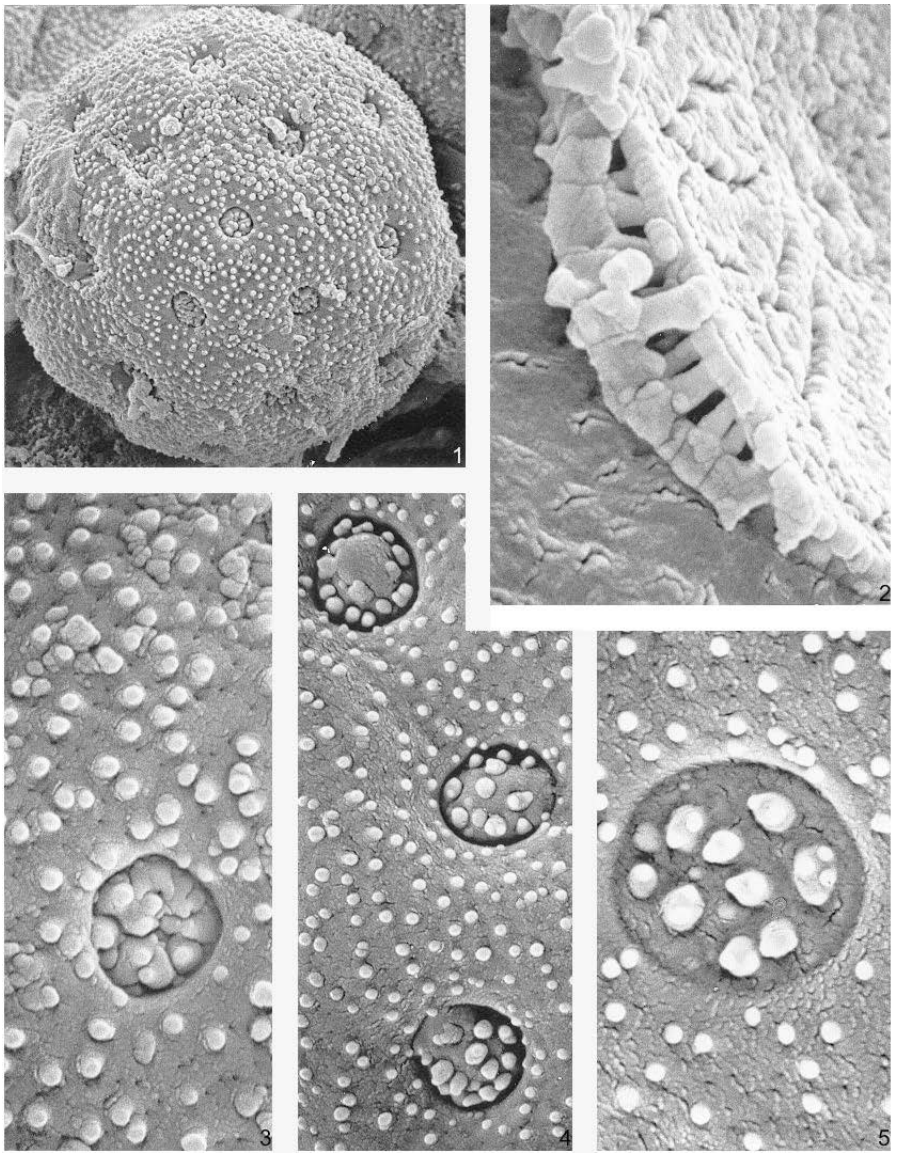

Fig. 5. *Amaranthus graecizans* subsp. *sylvestris* (Vill.) Brenan
1: Pollen grain (× 3400)
2: Exine section at interporium showing tectum, columellae and nexine (× 11200)
3: Exine surface with perforations, microechinae and one pore (× 14100)
4: Exine surface with perforations, microechinae and three pores (× 8000)
5: Detail of a pore with evident inner microechinae forming a fragmented operculum (× 14100)

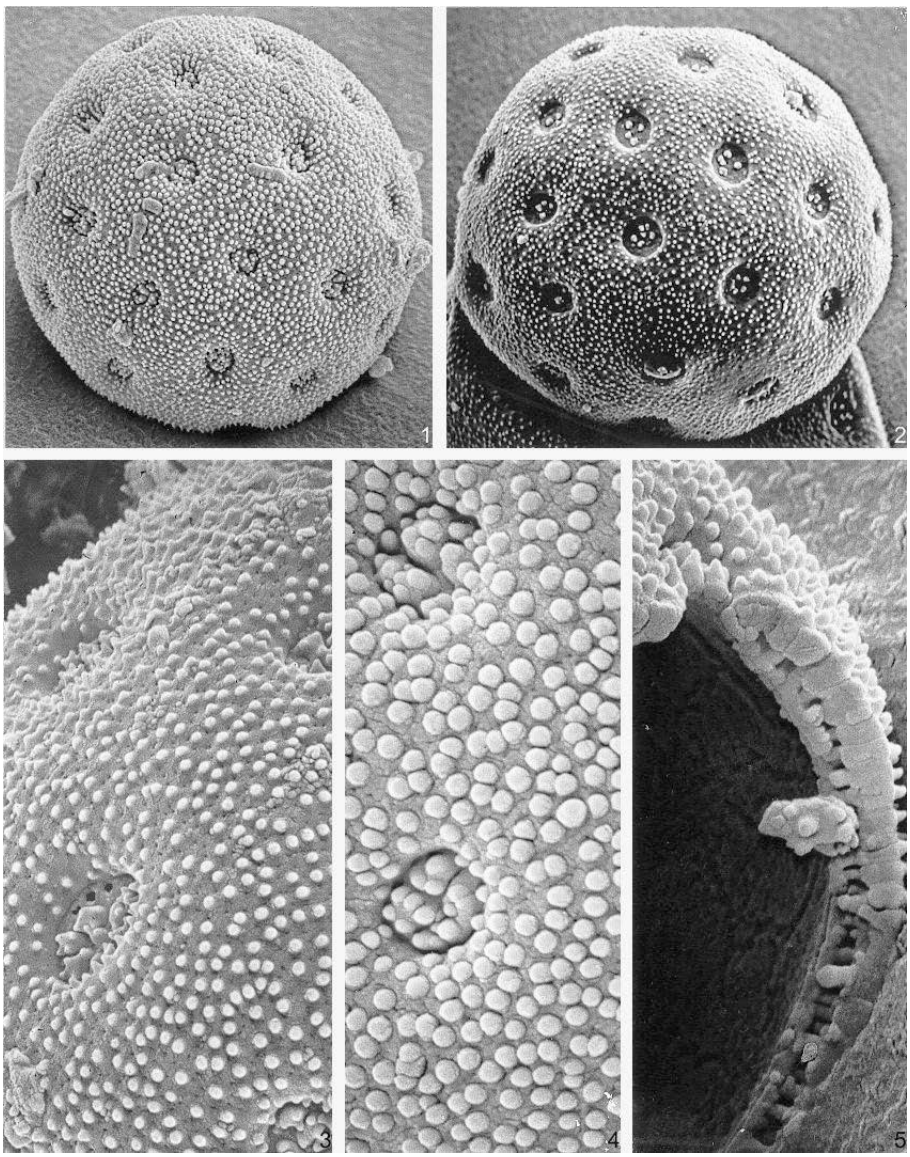

Fig. 6. *Amaranthus retroflexus* L.
1-2: Pollen grains at different magnifications (1: × 2500; 2: × 2600)
3-4: Exine surfaces showing numerous microechinae (3: × 8600; 4: × 11000)
5: Exine section (× 11300)

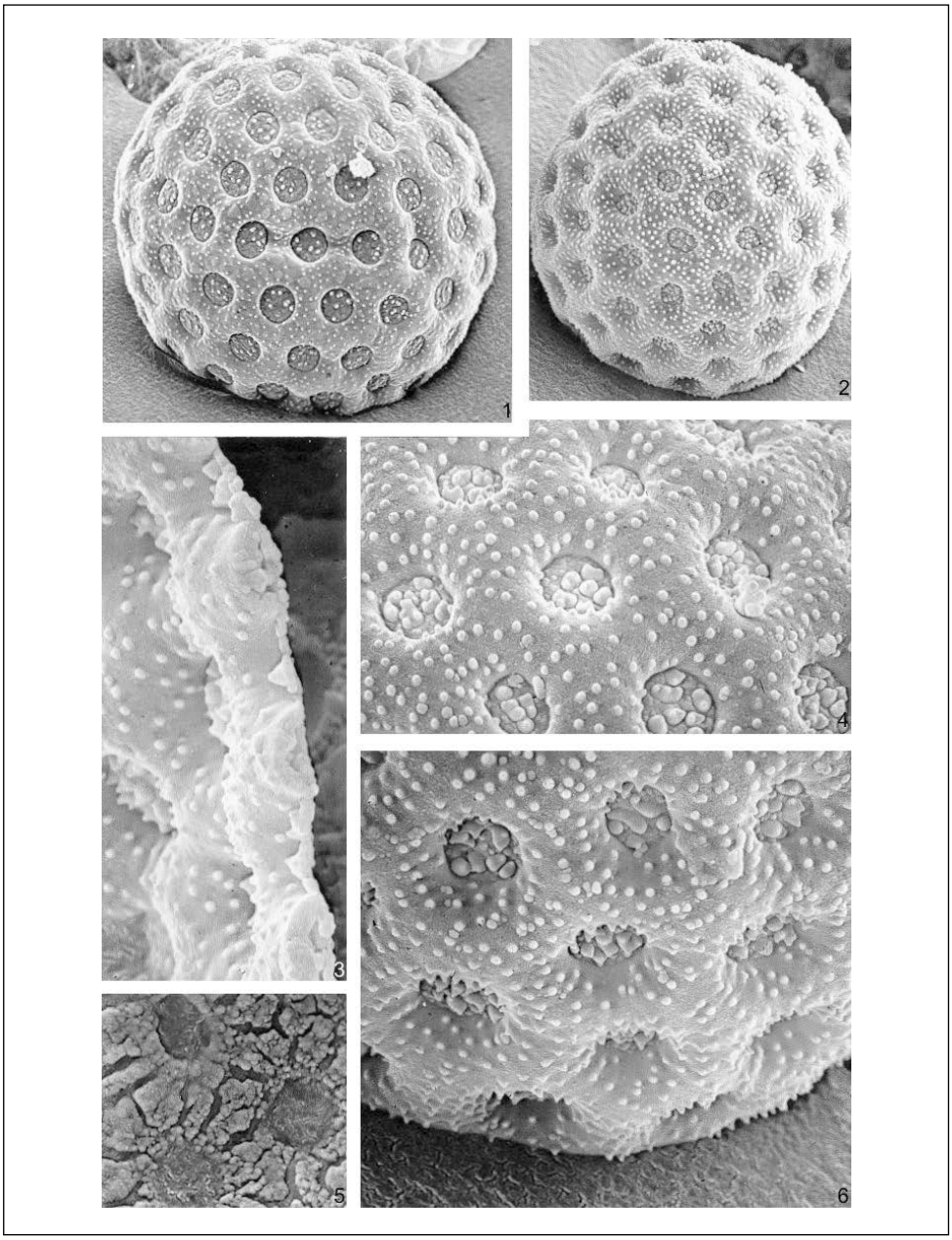

Fig. 7. *Amaranthus hybridus* L.
1-2: Pollen grains at different magnifications (1: × 2600; 2: × 2100)
3: Exine section showing three pores and three interporia (× 9700)
4: Exine surface with perforations, microechinae and pores with inner microechinae (x 8500)
5: Inner part of pollen grain wall with three pores on the nexinic layer (× 7100)
6: Exine surface with pores, perforations and microechinae (× 8000)

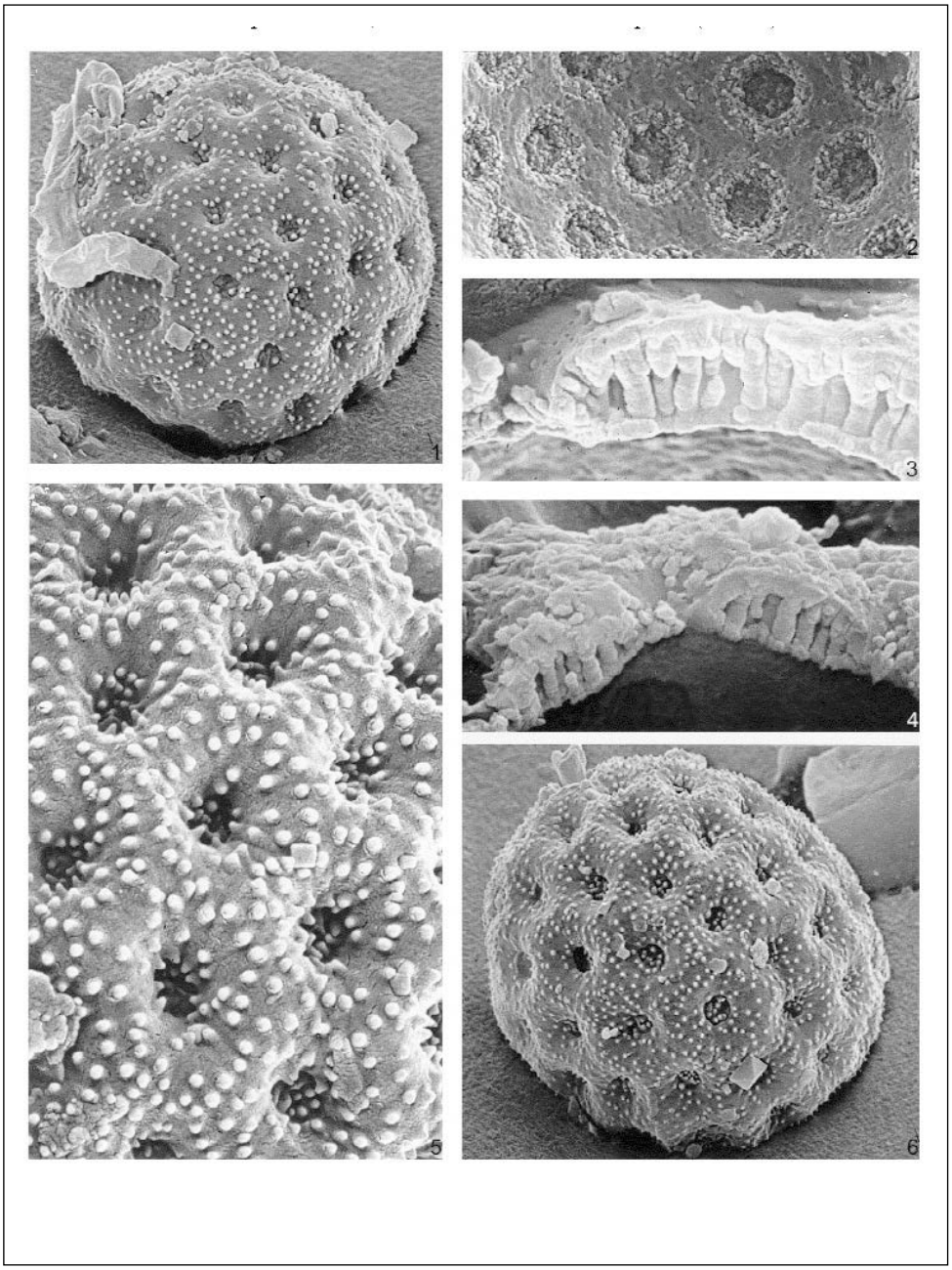

Fig. 8. *Atriplex halimus* L.
Fig. 1-6: Pollen grains at different magnifications (1: × 2800; 6: × 3000)
2: Inner part of pollen grain wall with numerous pores on the nexinic layer (× 5100)
3-4: Exine sections showing tectum, columellae and nexine (3: × 12200; 4: × 9300)
5: Exine surface with perforations, microechinae and pore depth (× 9000)

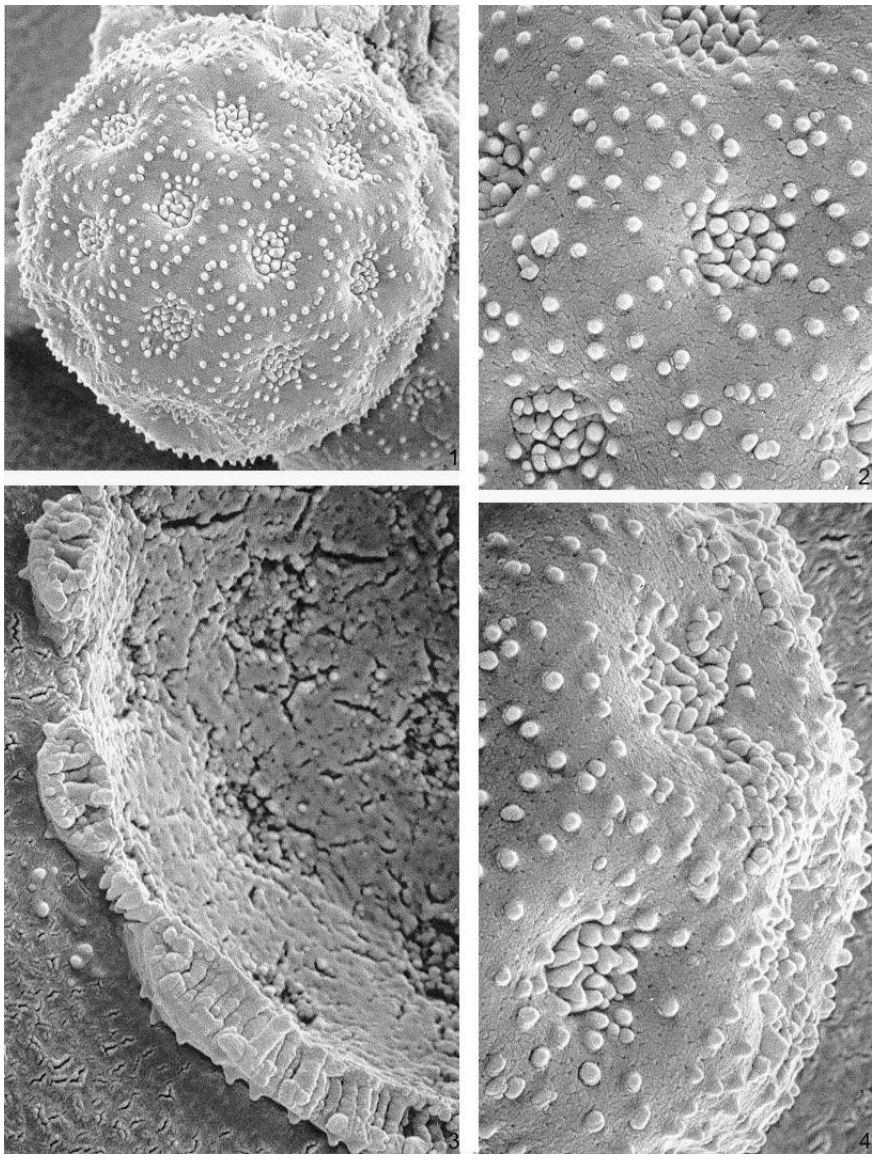

Fig. 9. *Beta vulgaris* var. *altissima* Döll
1: Pollen grain (× 4200)
2: Exine surface with pores, perforations and microechinae (× 9300)
3: Exine section showing tectum, columellae and inner part of nexine layer (× 8800)
4: Tangential view of exine surface with perforations, microechinae and pores with evident inner microechinae forming fragmented opercula (× 10400)

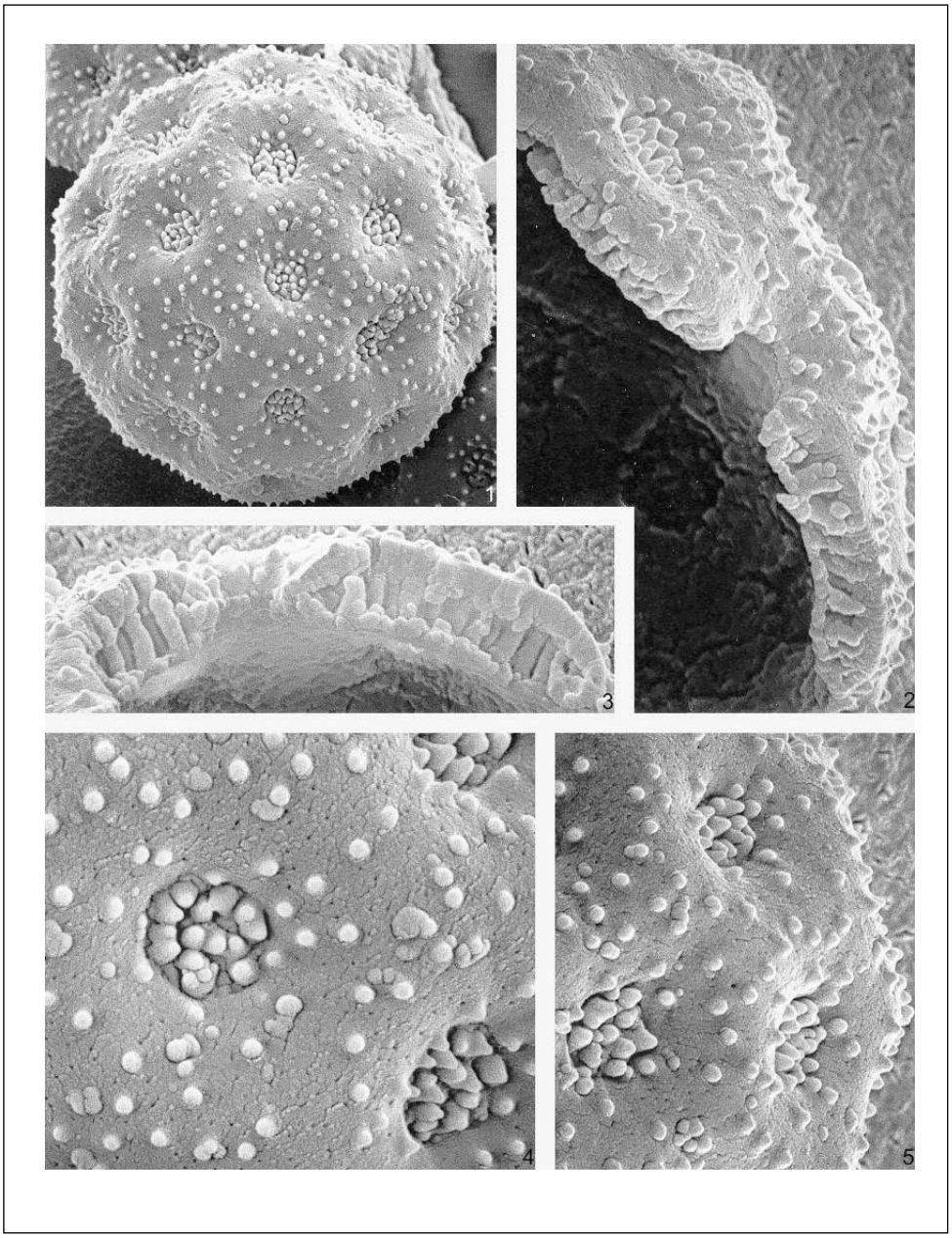

Fig. 10. *Beta vulgaris* subsp. *cicla* (L.) Schübl. & G.Martens
1: Pollen grain (× 4600)
2-3: Exine sections showing tectum, columellae and nexine (2: × 10000; 3: × 11200)
4: Exine surface with perforations, microechinae and pores with evident inner microechinae (× 14600)
5: Tangential view of exine surface showing the microechinae shape (× 10300)

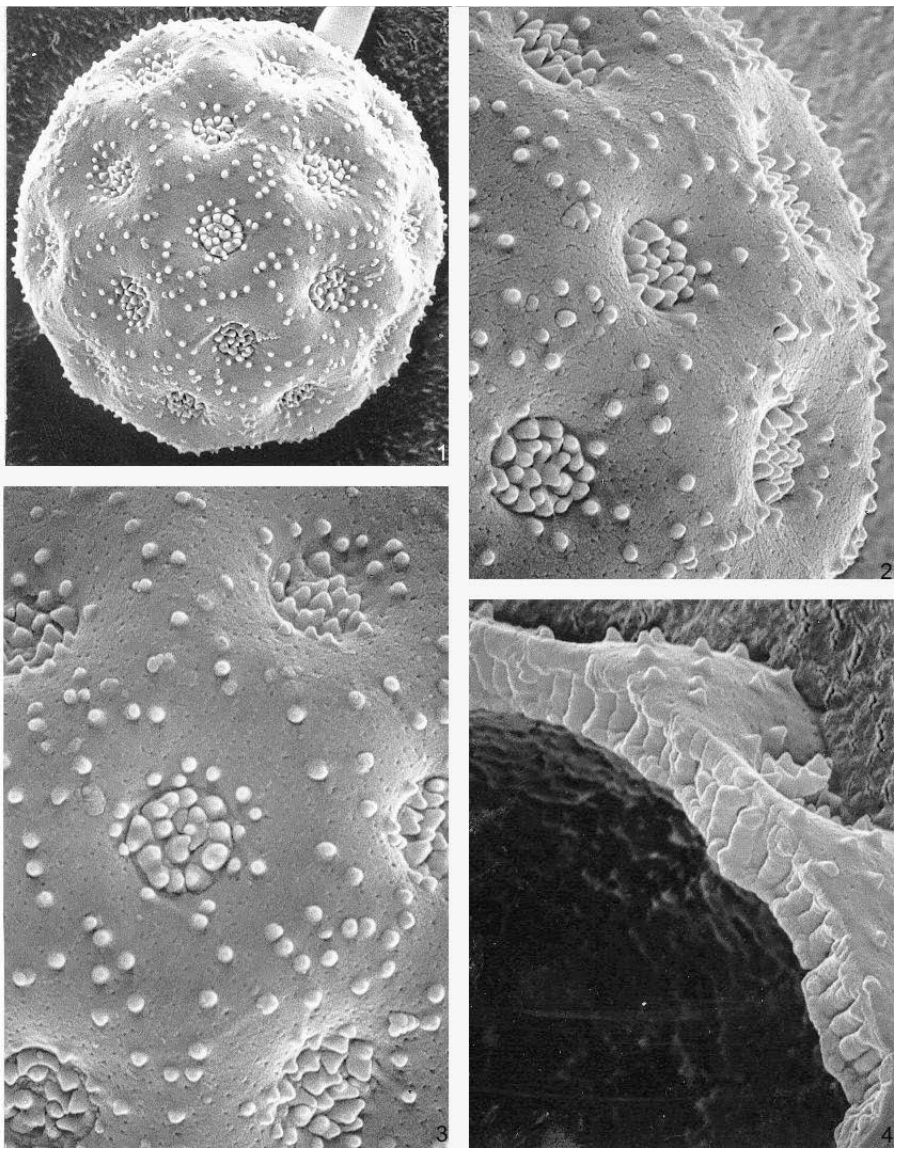

Fig. 11. *Beta vulgaris* var. *rubra* L.
1: Pollen grain (× 4470)
2: Tangential view of exine surface showing the microechinae shape (× 10000)
3: Exine surface with perforations, rare microechinae and pores with evident inner microechinae forming fragmented opercula (× 10700)
4: Exine section showing tectum, columellae and nexine (× 12300)

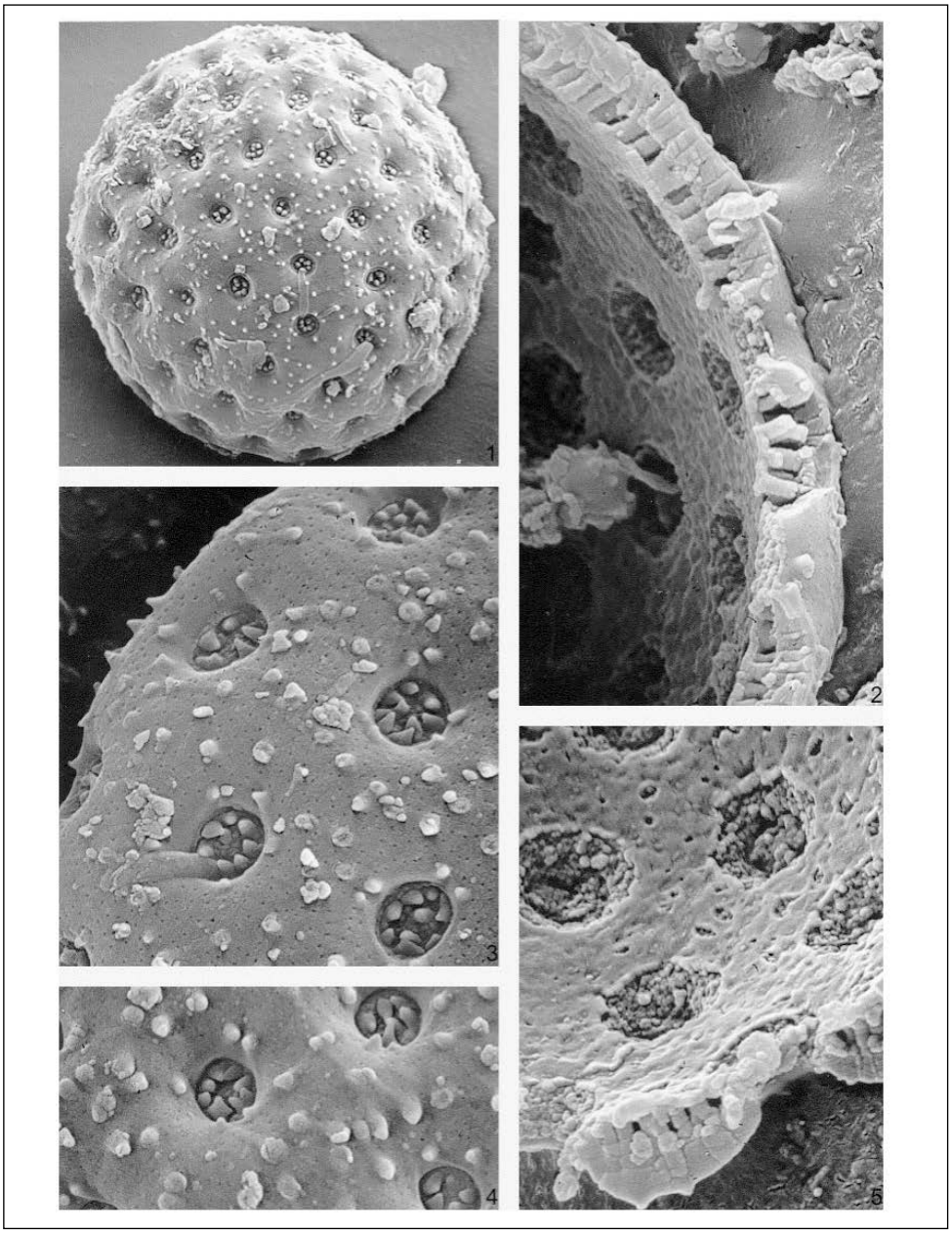

Fig. 12. *Chenopodium album* L. *s.lat.*
1: Pollen grain (× 2400)
2-5: Exine sections showing tectum, columellae and the inner part of pollen grain wall with pores on the nexinic layer (2: × 8100; 5: × 8300)
3- 4: Exine surfaces with perforations, microechinae and pores with inner microechinae (3: × 8500; 4: x 8300)

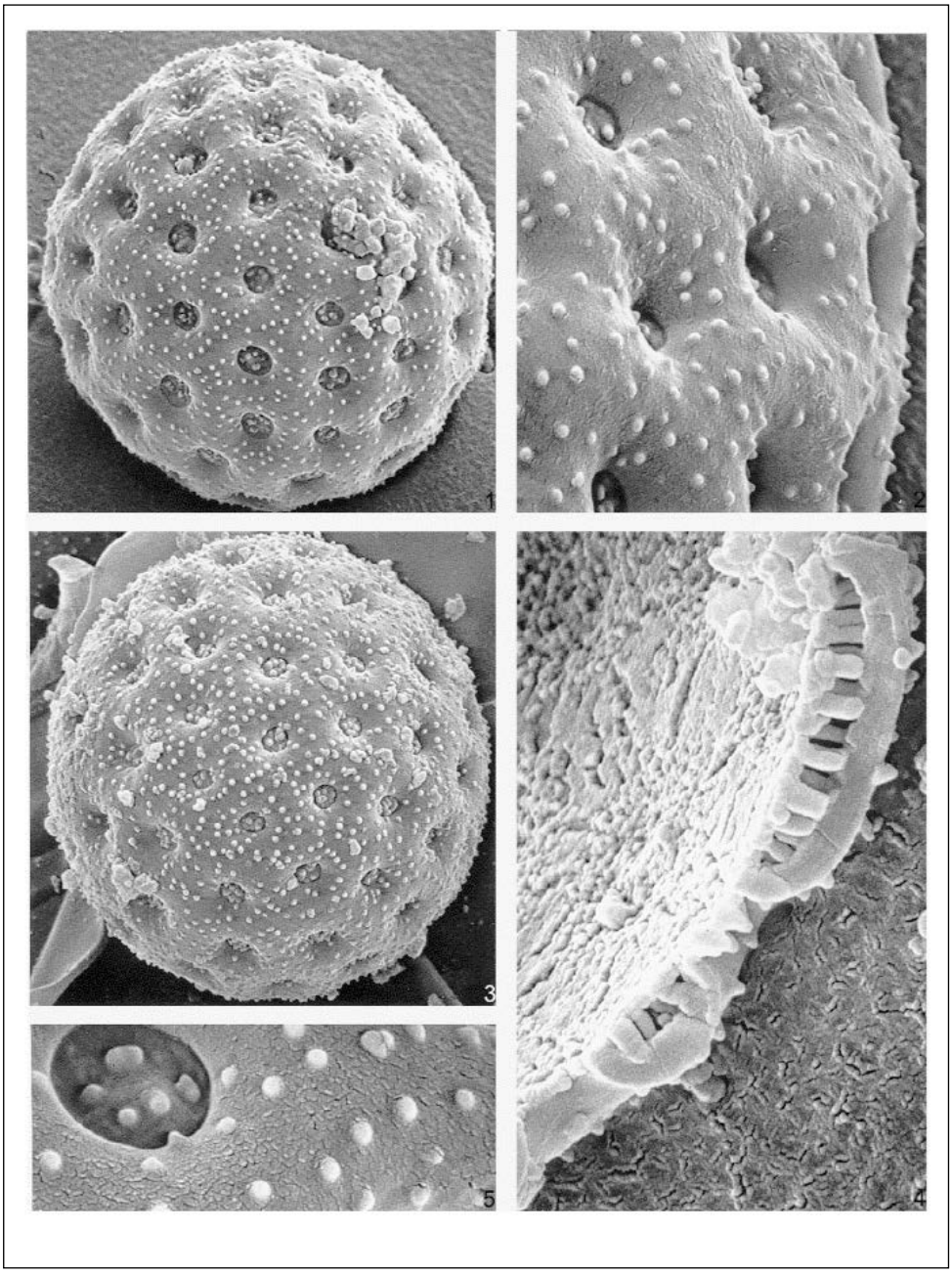

Fig. 13. *Dysphania ambrosioides* (L.) Mosyakin & Clemants
1-3: Pollen grains (× 2900)
2: Tangential view of exine surface with microechinae and pore depth (× 8300)
4: Exine section showing tectum, columellae and the inner part of the nexinic layer (× 12200)
5: Detail of microechinae on a pore and on interporial surface (× 13500)

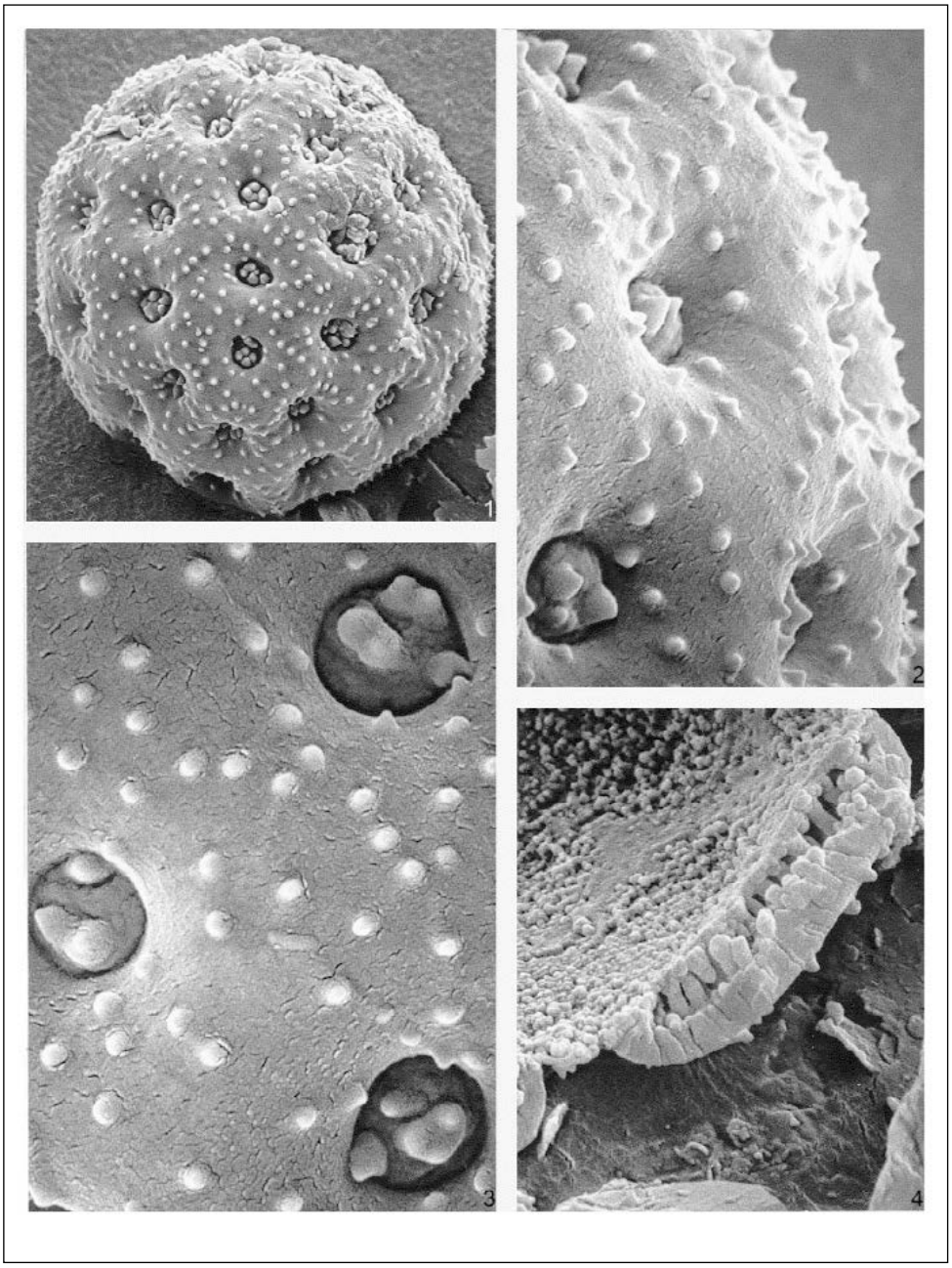

Fig. 14. *Dysphania botrys* (L.) Mosyakin & Clemants
1: Pollen grain (× 3300)
2: Tangential view of exine surface showing the microechinae shape and some pores (× 12000)
3: Exine surface with microechinae and pores with rare inner microechinae (× 14300)
4: Exine section showing tectum, columellae and the inner part of the nexinic layer (× 10700)

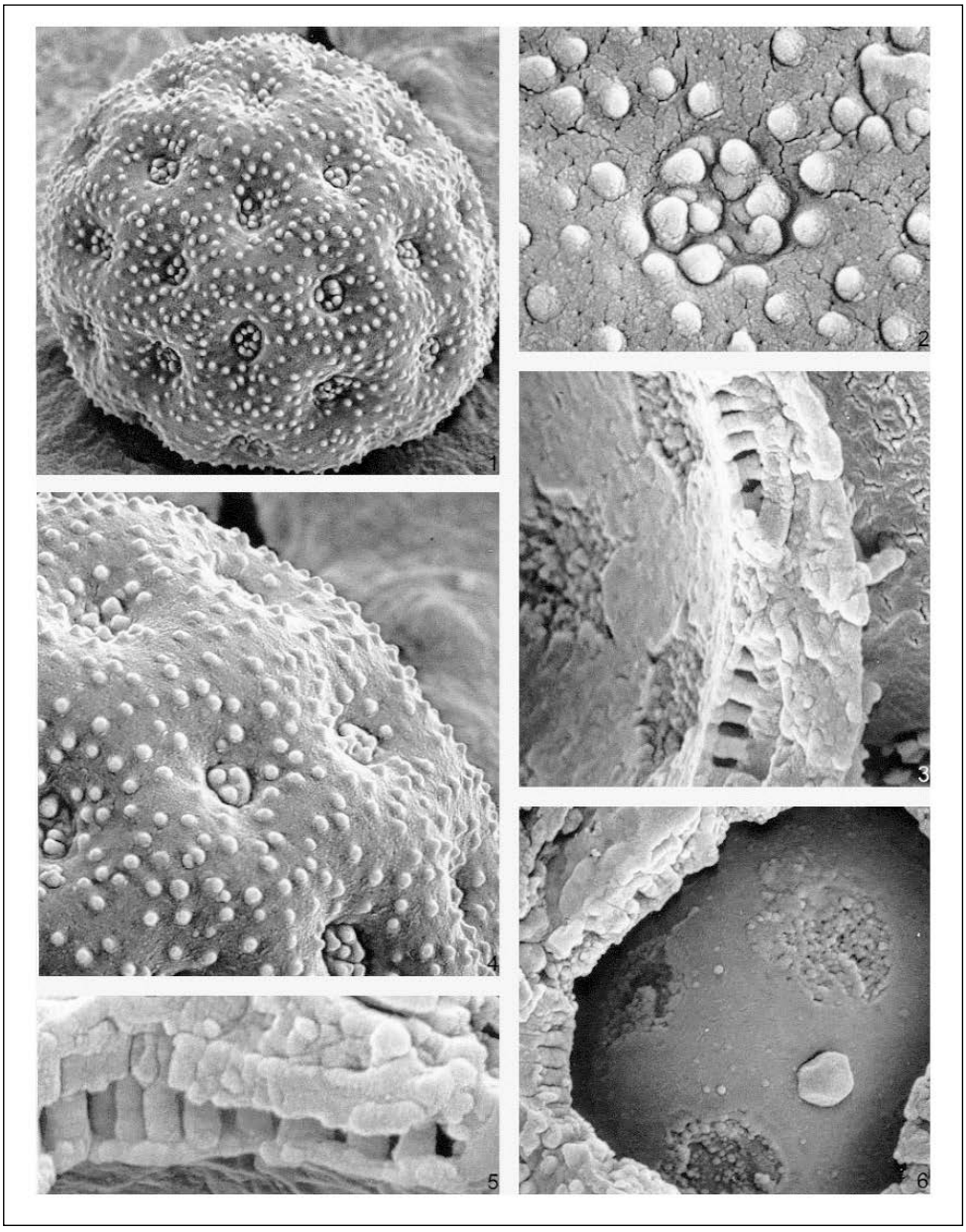

Fig. 15. *Chenopodiastrum murale* (L.) S. Fuentes, Uotila & Borsch
1: Pollen grain (× 3900)
2: Microechinae on a pore and on interporial surface (× 15800)
3-6: Exine sections showing tectum, columellae and the inner part of the nexinic layer (3: × 10700; 6: × 8900)
4: Tangential view of exine surface with microechinae and pores (× 7900)
5: Interporial exine section showing tectum, columellae and nexine (× 20100)

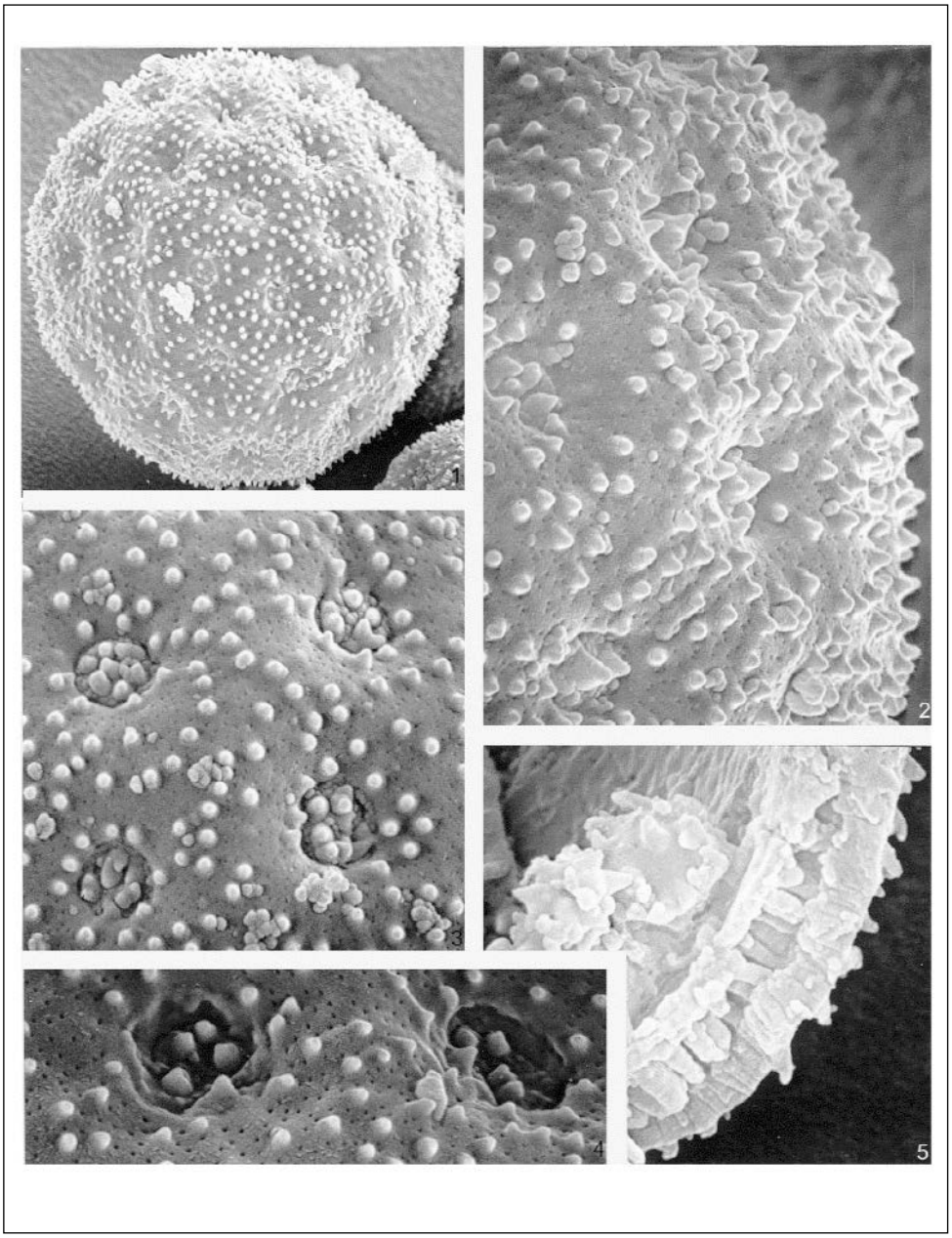

Fig. 16. *Chenopodium opulifolium* Schrad. ex W.D.J.Koch & Ziz
1: Pollen grain (× 3400)
2: Tangential view of exine surface showing the microechinae shape (× 11400)
3-4: Exine surfaces with perforations, microechinae and pores with evident inner microechinae forming fragmented opercula (3: × 9300; 4: × 11700)
4: Exine section showing tectum, columellae and nexine (× 15000)

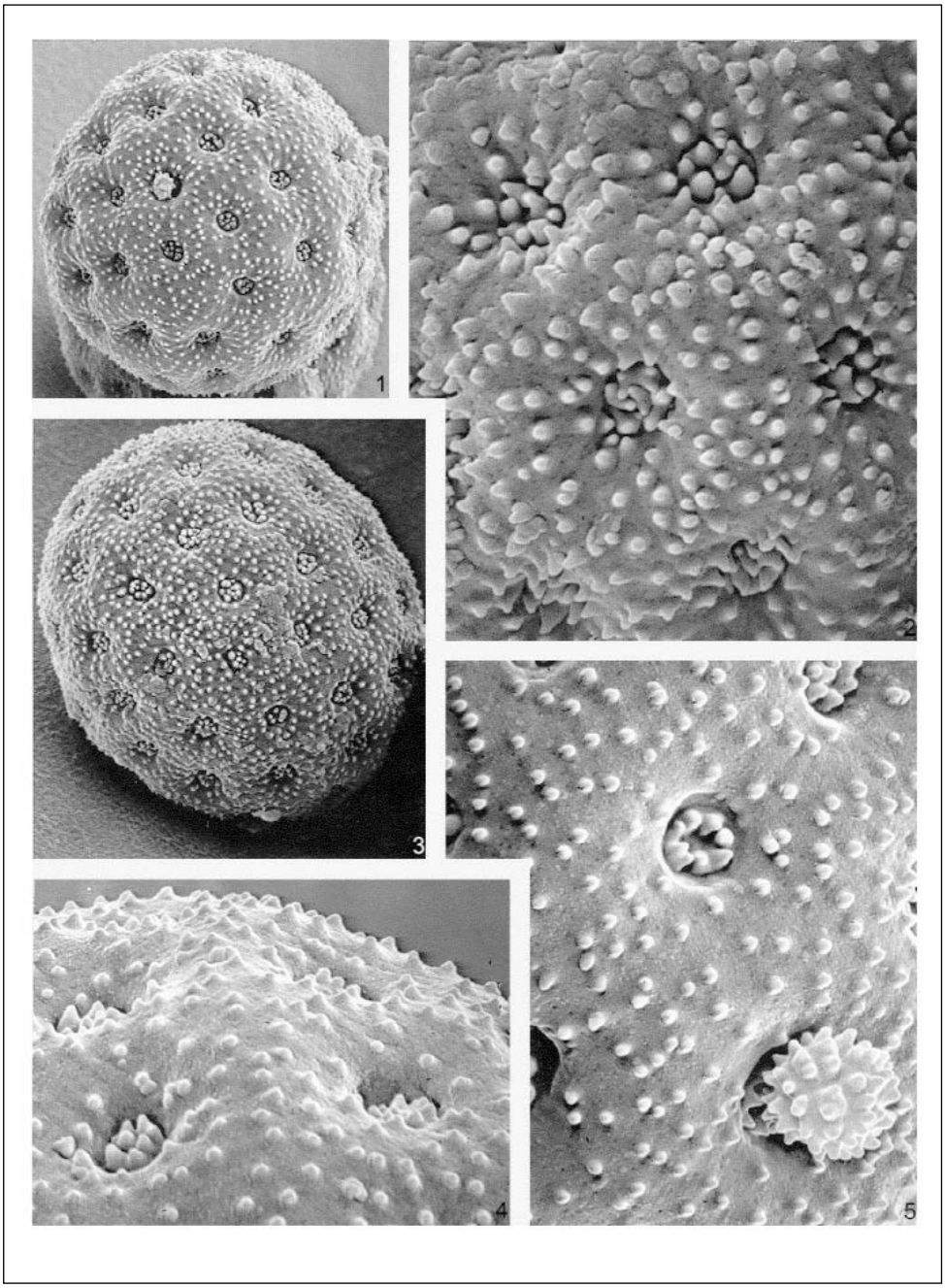

Fig. 17. *Lipandra polysperma* (L.) S. Fuentes, Uotila & Borsh
1-3: Pollen grains at different magnifications (1: × 2100; 3: × 2400)
2-4: Exine surfaces with pores, perforations and microechinae (2: × 9000; 4: × 8400)
5: Exine surface with perforations, microechinae, pores and one "Ubish body" (× 8200)

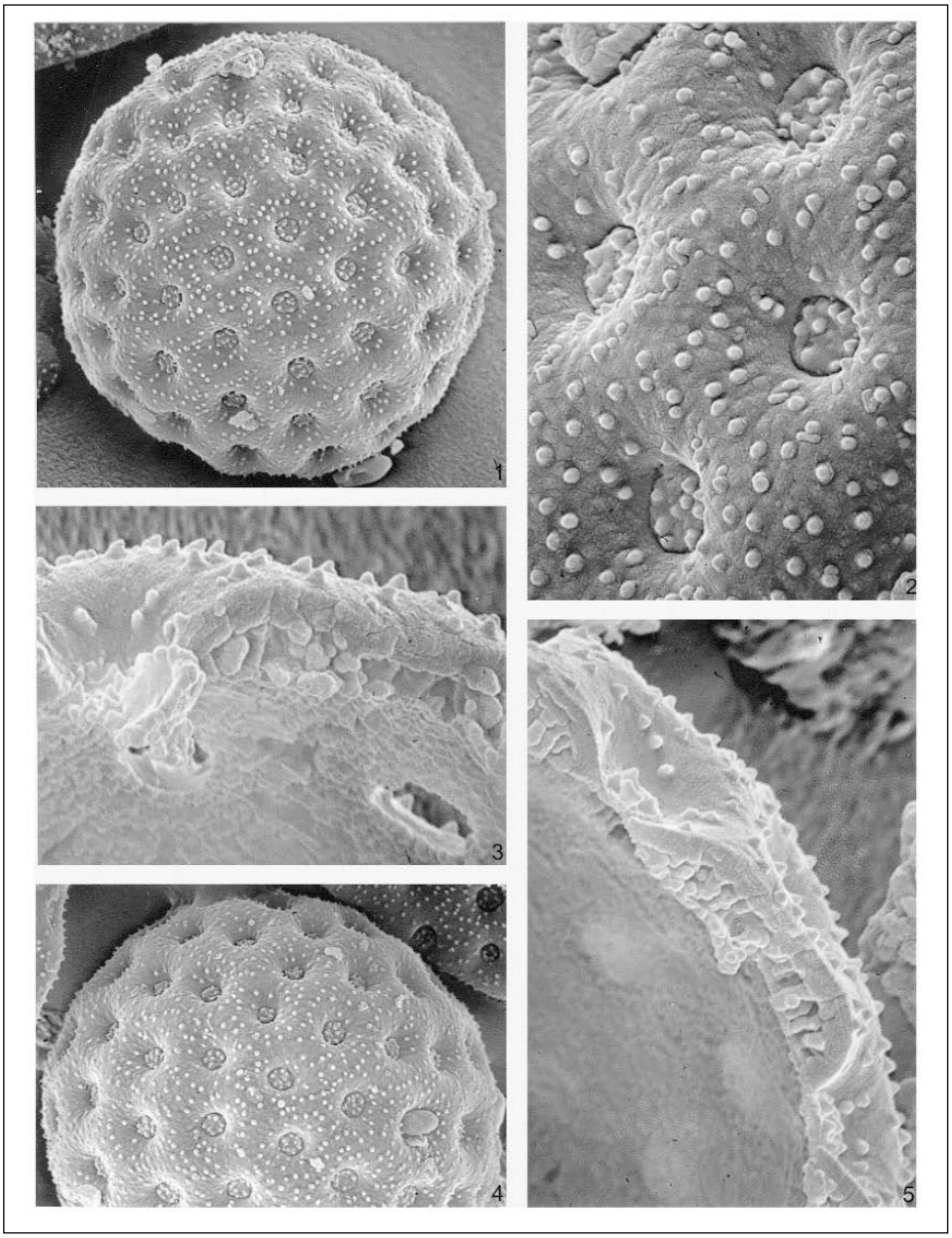

Fig. 18. *Bassia scoparia* (L.) Voss
1: Pollen grain (× 2400)
2: Exine surface with pores and microechinae (× 8200)
3-5: Exine section showing tectum, columellae and the inner part of the nexinic layer (3: × 9400; 5: × 8100)
4: Part of a pollen grain (× 2400)

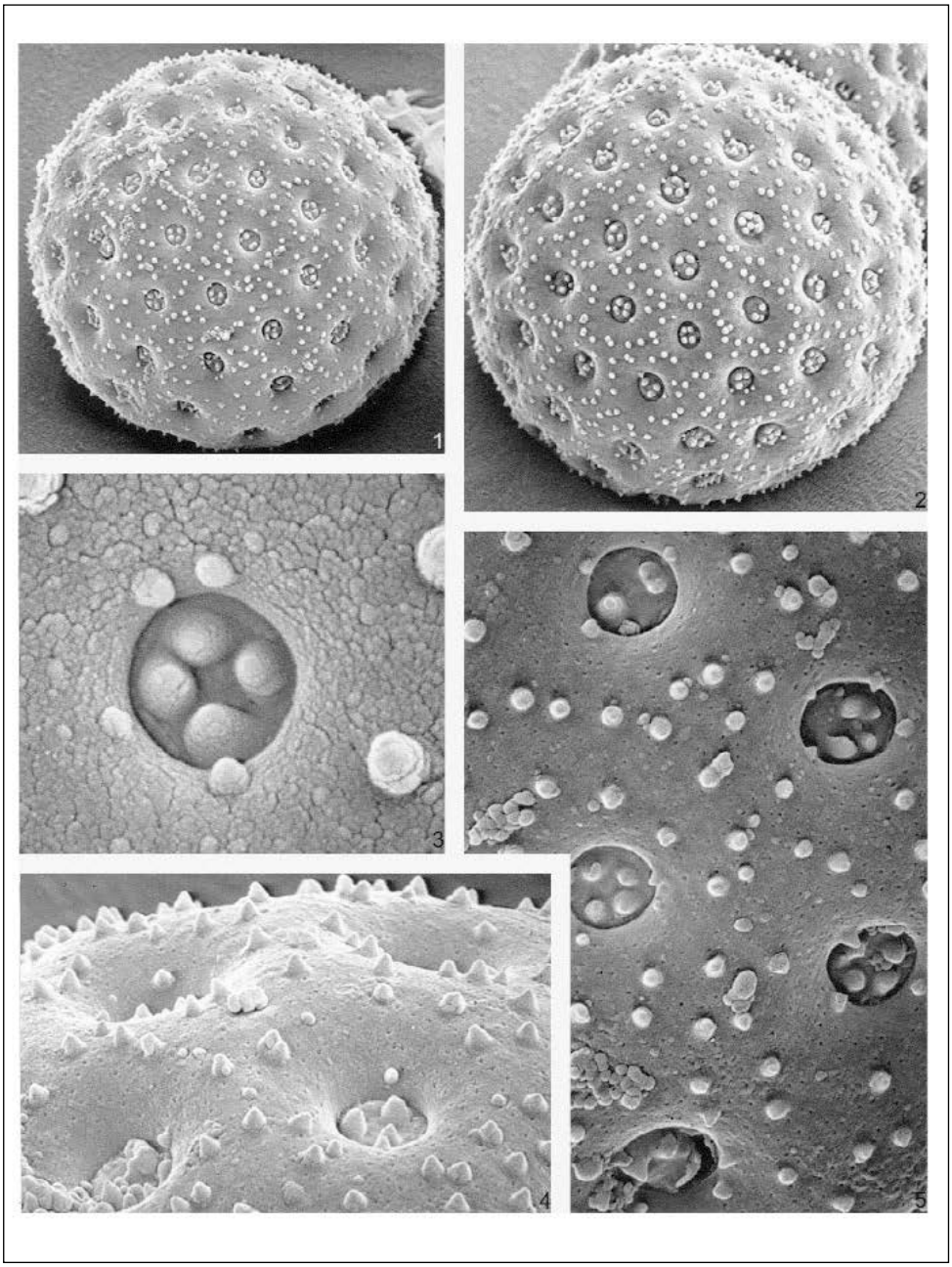

Fig. 19. *Spinacia oleracea* L.
1-2: Pollen grains at different magnifications (1: × 2000; 2: × 2300)
3: Detail of a pore with four inner microechinae (× 17300)
4: Exine surface with pores, perforations and rare microechinae (× 8300)
5: Tangential view of exine surface showing the microechinae shape (× 8300)

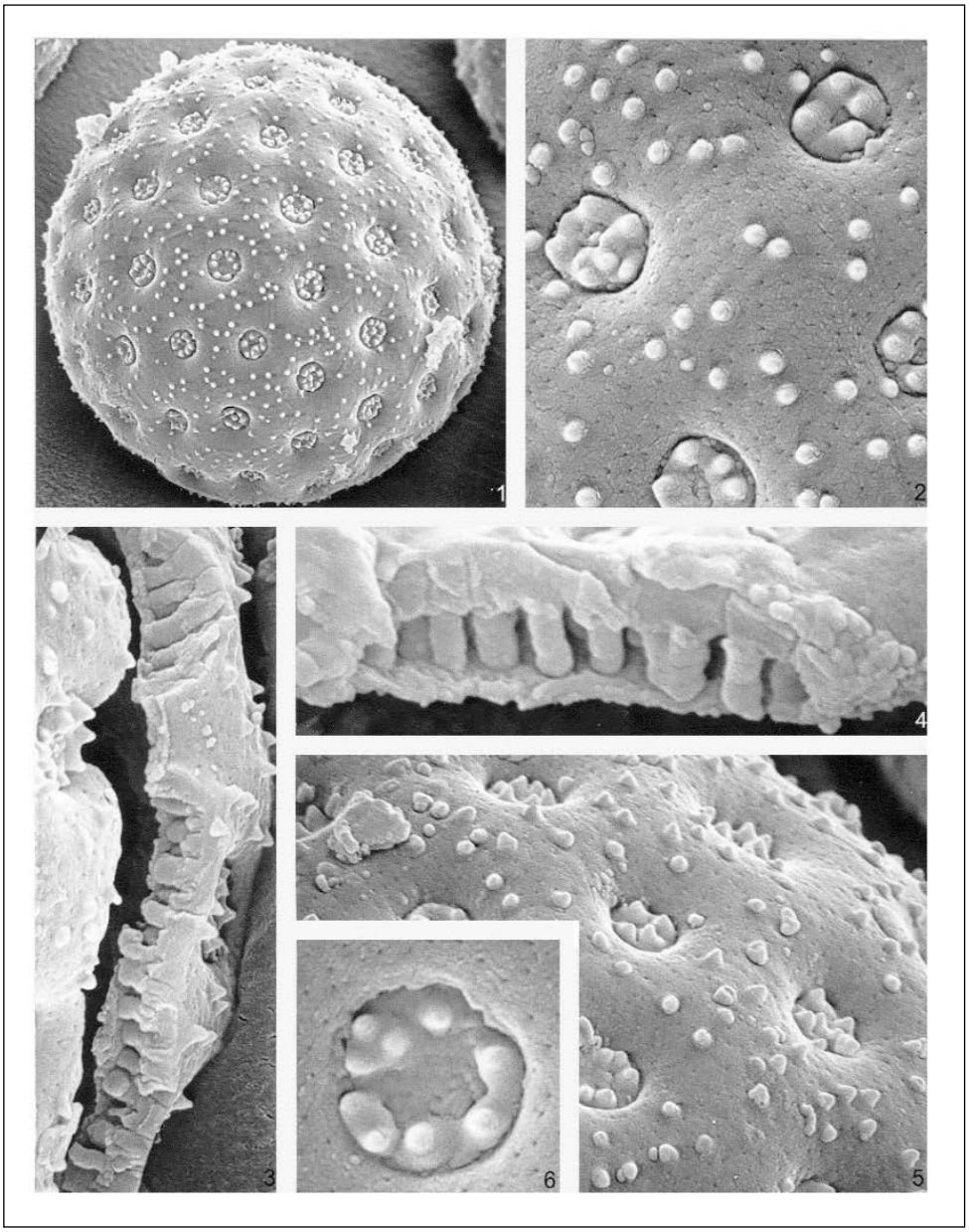

Fig. 20. *Suaeda vera* Forssk. ex J.F. Gmel
1: Pollen grain (× 2700)
2: Exine surface with perforations, microechinae and pores with evident inner microechinae forming fragmented opercula (× 11400)
3-4: Exine sections showing tectum, columellae and nexine (3: × 10900; 4: × 18400)
5: Tangential view of exine surface showing the microechinae shape (× 8700)
6: Detail of a pore with inner microechinae (× 15700)

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Addresses of the authors:
Paola Angelini[1], Emma Bricchi[1], Daniela Gigante[1], Silvia Poponessi[2], Amalia Spina[3] & Roberto Venanzoni[1]
[1]Department of Chemistry, Biology and Biotechnology, University of Perugia, Borgo XX Giugno 74 - 06121 Perugia, Italy. E-mail: paola.angelini@unipg.it
[2]Department of Earth, Environment and Life Sciences, University of Genova, Corso Dogali 1M, 16136 Genova, Italy.
[3]Dept. of Physics and Geology, University of Perugia, Via Pascoli 1 - 06123 Perugia, Italy