Loredana Rizzi Longo & Laura Feoli Chiapella

# Pollen morphology and taxonomy of *Genista* sect. *Spartioides* (*Genisteae*, *Fabaceae*)

**Abstract**

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A pollen analysis was carried out on 138 samples from 19 taxa of *Genista* sect. *Spartioides*. The taxa were compared in terms of quantitative and qualitative characters, examined by LM and SEM. The combined analysis of the pollen characters allows to notice some differences among the species. The western and eastern taxa of the section appear distinguishable. Among the western ones, a grouping is highlighted including *G. cinerea* (various subspecies), *G. majorica* and *G. ramosissima*, which corresponds to ser. *Spartioides* of subsect. *Spartioides*. The other series of the subsection, ser. *Floridae* Cantó, Rivas-Martínez, Greinwald & van Rensen, is not homogeneous: *G. obtusiramea* emerges as the most distinct species of the whole section; *G. cinerascens*, described by Gibbs (1966) as a variety of *G. cinerea*, differs from *G. cinerea* s.l.; the Moroccan populations of *G. florida* (ascribed to subsp. *maroccana*) differ from the Iberic ones. Subsect. *Chamaespartum* Cantó, Rivas-Martínez, Greinwald & van Rensen proves to be heterogeneous as well. *G. pilosa*, the only widely distributed species of the section, is more similar to the western taxa, and acts as a trait d'union with the eastern ones. Among the eastern taxa, the pollen analysis supports the distinction of the two examined subspecies of *G. pulchella* (*pulchella* and *villarsiana*), and of the two varieties of *G. albida* (*albida* and *godetii*); *G. involucrata*, belonging to *G. albida* aggr., emerges as even more dissimilar. From the comparison of the data obtained in the present study with those formerly obtained on the taxa of *G. sericea* aggr., the specific rank of *G. sakellariadis, G. halacsyi, G. subcapitata* and *G. millii* is endorsed. The pollen analysis of the whole section is thus completed.

*Key words*: *Genista*, Mediterranean region, pollen analysis, systematics.

## Introduction

*Genista* L. subgen. *Genista* comprises about sixty taxa arranged by Gibbs (1966) in four sections: *Genista*, *Spartioides* Spach, *Erinacoides* Spach and *Scorpioides* Spach.

Sect. *Spartioides* is the largest of the subgenus; it includes non-spiny shrubs with alternate branching, simple leaves with pulvinules sometimes prominent, and three vascular traces (Pellegrin 1908), broadly ovate standard, usually with sericeous hairs, pubescent keel, a narrowly oblong and several-seeded legume, with sericeous to lanate hairs (Gibbs 1966).

The species of this section occur mostly in the Mediterranean region. Two main distribution centres may be singled out: a western centre (S Spain and NW Africa), and an eastern one (Balkan Peninsula and Anatolia); only *Genista pilosa* is widely distributed in western and central Europe (Gibbs 1966).

Sect. *Spartioides* is heterogeneous on the basis of morphological and phytochemical characters (Cantó & al. 1997), as well as karyological (Cusma Velari & al. 2003, 2009) and molecular data (Pardo & al. 2004). Cantó & al. (1997) suggested to divide the section in two subsections: subsect. *Chamaespartum* (Spach) Cantó, Rivas-Martínez, Greinwald & van Rensen (with *Genista pilosa, G. teretifolia* and *G. pseudopilosa*) and subsect. *Spartioides*, with all the other taxa. Within subsect. *Spartioides*, these authors have established two series: ser. *Spartioides* (which includes *G. ramosissima*, *G. cinerea* and *G. majorica*) and ser. *Floridae* Cantó, Rivas-Martínez, Greinwald & van Rensen, which comprehends *G. florida*, *G. cinerascens* and *G. obtusiramea*.

In the present study, a detailed pollen analysis of *Genista* sect. *Spartioides* is carried out by LM and SEM. The pollen analysis was undertaken in order to contribute to the knowledge of the pollen morphology of the taxa of the section and to clarify the systematic correlations among them. This paper presents a pollen analysis of the western Mediterranean taxa of the section, of *Genista albida* aggr., *G. pulchella* and *G. pilosa*. Data obtained with the present study are compared with those already published concerning the taxa of *G. sericea* aggr. (Rizzi Longo & Feoli Chiapella 1993). With this research the pollen analysis of the whole section will be completed.

Other sections of *Genista* have been already studied by the authors: *Voglera* (Gaertn., Mey. & Schreb.) Spach (Feoli Chiapella 1983), *Spartocarpus* Spach (Rizzi Longo & Feoli Chiapella 1994), *Cephalospartum* Spach emend. P. Gibbs (Rizzi Longo & al. 2006), *Acanthospartum* Spach and *Fasselospartum* P. Gibbs (Rizzi Longo & Feoli Chiapella 2007).

*Examined taxa*

The western species of sect. *Spartioides* are: *Genista ramosissima* (Desf.) Poir. in Lam., *G. cinerea* (Vill.) DC. in Lam. & DC., *G. majorica* Cantó & M. J. Sánchez, *G. florida* L., *G. cinerascens* Lange, *G. obtusiramea* J. Gay ex Spach, *G. teretifolia* Willk. and *G. pseudopilosa* Coss. (Cantó & al. 1997).

*Genista ramosissima*, the type species of the section, is found in SE Spain and in the northern regions of Algeria and Morocco; *G. majorica* is endemic to Mallorca; *G. cinerascens* is spread in the central and western parts of the Iberian Peninsula; *G. obtusiramea* is endemic to the north-eastern part of the Iberian Peninsula; *G. teretifolia* is endemic to a small area of N Iberian Peninsula; *G. pseudopilosa* grows in the south-eastern provinces of Spain, in Morocco and Algeria (Maire 1987, Cantó & Sánchez 1988, Cantó & al. 1997, Talavera 1999).

*Genista florida* is found in the Iberian Peninsula, in SW France and in Morocco; subsp. *maroccana* (Ball) Cantó & al. (= *G. florida* var. *maroccana* Ball) is endemic to Great Atlas in Morocco (Raynaud 1979; Maire 1987; Cantó & al. 1997).

The *Genista cinerea* aggr. includes *G. cinerea* and *G. majorica*. *G. cinerea* is subdivided into a number of endemic vicariant subspecies: subsp. *cinerea* (SE France and the neighbouring area in Italy); subsp. *ausetana* O. Bolòs & Vigo [= *G. ausetana* (O. Bolòs & Vigo) Talavera], distributed in NE Spain and S France; subsp. *valentina* (Willd. ex Spreng.) Rivas Mart. [= *G. valentina* (Willd. ex Spreng.) Steud.], endemic to E Spain; subsp. *murcica* (Coss.) Cantó & M. J. Sánchez (SE Spain); subsp. *speciosa* Rivas Goday & T. Losa ex Rivas Mart. & al., in S Spain and NW Africa (Cantó & Sánchez 1988; Greuter & al. 1989; Cantó & al. 1997).

The eastern taxa of the section belong to *Genista albida* aggr. and *G. sericea* aggr. (Greuter & al. 1989).

The *Genista albida* aggr. includes *G. albida* Willd., distributed in Anatolia, Caucasia, Syria, Krym, Romania, with var. *albida* and var. *godetii* (Spach) Boiss., and *G. involucrata* Spach, endemic to southern and central Anatolia (Săvulescu 1957, Gibbs 1966, 1970, Mouterde 1978-84, Greuter & al. 1989).

*Genista pulchella* Vis. (= *G. villarsii* Clementi) is distributed both in the eastern and in the western part of the Mediterranean region; it is an orophyte S European with a disjunct distribution from S France to the eastern Adriatic coast (Hayek 1924/27; Gibbs 1966; Greuter & al. 1989). Conti (2007) subdivides *G. pulchella* into three subspecies: subsp. *pulchella*, distributed in the western part of the Balkan Peninsula (Croatia, Bosnia and Hercegovina, Montenegro, and Albania), subsp. *villarsiana* (Jord.) F. Conti, endemic to southern France, and the new described subsp. *aquilana* F. Conti & Manzi, endemic to a small zone of central Apennines (National Park of Gran Sasso-Monti della Laga).

*Genista pilosa* L. is spread in western and central Europe, extending to S Sweden, central Italy and Macedonia (Gibbs 1966).

**Materials and methods**

Pollen grains from 138 samples of the taxa of *Genista* sect. *Spartioides* were examined, using dried material. The geographical origin of the studied populations, scattered within the respective distributional ranges of the taxa, is reported in Fig. 1-3.

The following groups of characters were taken into account:

- *quantitative characters by LM*: length of the polar axis (P), equatorial diameter (E), length of the colpus, equatorial breadth of the colpus, equatorial breadth of the mesocolpium, all in equatorial view; distance between the apices of two ectocolpi in polar view;
- *qualitative characters by LM:* outline in equatorial and polar view; shape of the colpi in equatorial view;
- *qualitative and quantitative characters by SEM:* exine ornamentation at mesocolpium, at apocolpium and at the rim of the apertures; aperture membrane; density of the exine perforations in the interapertural zone at equatorial level.

For light microscopy (LM), the material was acetolysed according to Erdtman (1960). The measurements were made by filar ocular micrometer mounted on a Nikon Optiphot within a standard period after preparation of the slide (4 hours), in order to avoid any alteration in dimensions (Van Campo 1966, Hanks & Fairbrothers 1976, Rizzi Longo 1986). Thirty pollen grains were considered for each sample, since the average values of the quantitative characters stabilize after 20-25 measures (Rizzi Longo 1986). Thirty grains were observed for each sample also for the qualitative characters.

For SEM, acetolysed anthers were dehydrated in acetone, dried according to the critical point technique (Anderson 1951). The pollen was coated with gold-palladium and examined with a Philips 500 SEM. Thirty pollen grains were observed for each sample to study the exine pattern; ten counts of the number of the perforations in a standard area (10 $\mu m^2$) were carried out at x 5000 for each sample.

The taxa were compared in terms of average value of the quantitative characters and in terms of average frequency of the qualitative character states. The comparison was carried out by analyzing all the characters together, using the Euclidean distance. Single linkage clustering was applied to obtain a hierarchical classification (Sneath & Sokal 1973) and an eigenanalysis was applied to the distance matrix to order the taxa (Lagonegro & Feoli 1981). To link the taxa according to maximum

Fig. 1. Geographical origin of the examined populations of some taxa of *Genista* sect. *Spartioides*:
● *Genista pilosa* ○ *G. pseudopilosa* ♦ *G. ramosissima* ▲ *G. obtusiramea* ◊ *G. teretifolia*
△ *G. cinerascens* ■ *G. pulchella* ssp. *pulchella* □ *G. pulchella* ssp. *villarsiana.*

affinity, a minimum spanning tree (Gower & Ross 1969) was constructed. The computer programs used for classification and ordination are described in Podani (1994).

The nomenclature of the taxa follows Gibbs (1966), Greuter & al. (1989), Cantó & al. (1997), and Conti (2007). For pollen terminology see Punt & al. (1994).

## Results

### *Description of pollen grains*

The pollen grains of *Genista* sect. *Spartioides* are single, isopolar, radially symmetric, small to medium-sized (sensu Erdtmann 1952), with a perforate suprareticulate tectum (Plates 1-5). The aper-

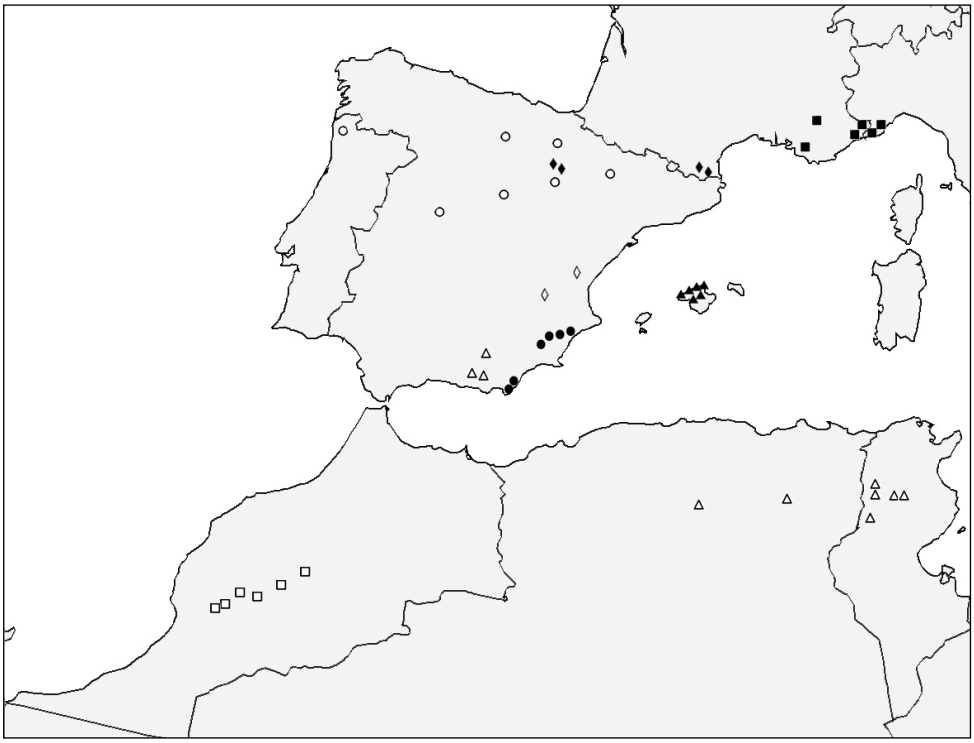

Fig. 2. Geographical origin of the examined populations of the taxa of *Genista cinerea* aggr. and of *G. florida*: ■ G. *cinerea* ssp. *cinerea* ♦ *G. cinerea* ssp. *ausetana* ◊ *G. cinerea* ssp. *valentina* ● *G. cinerea* ssp. *murcica* △ *G. cinerea* ssp. *speciosa* ▲ *G. majorica* ○ *G. florida* (Europe) □ *G. florida* ssp. *maroccana.*

tures are three furrows located in the equatorial region (3-zonocolpate grains). Sometimes the colpi break in their central part forming a long and rather undefined endoaperture, often resulting in a longitudinal interruption (3-zonocolporate with a long ectoaperture and a diffuse lolongate endoaperture, corresponding to tricolporoidate grains after Erdtman 1952). Such apertures were already observed in other sections of *Genista*: *Spartocarpus* (Rizzi Longo & Feoli Chiapella 1994), *Cephalospartum* (Rizzi Longo & al. 2006), *Acanthospartum* and *Fasselospartum* (Rizzi Longo & Feoli Chiapella 2007).

*Quantitative pollen characters (LM)*

Table 1A presents the means and standard deviations of all the quantitative characters considered by LM and of the ratios in the taxa of the section examined in this study.

The grains of the western species *Genista obtusiramea* differ from those of all the other taxa of the section because of their size, their average values being the highest for the length of the polar axis (36.1 µm), the equatorial diameter (32.6 µm), the length of the colpus (29,8 µm) and the breadth of the mesocolpium (25.4 µm), and the lowest for the mean apocolpium index (0.10).

The other western taxa usually present grains with lower mean values than the eastern ones for

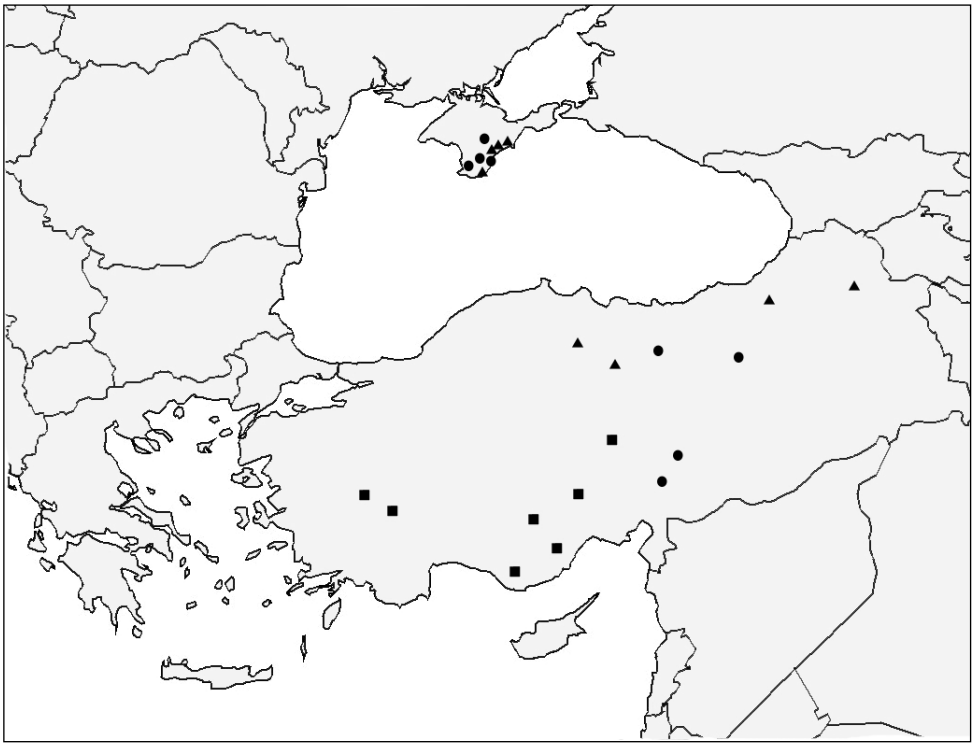

Fig. 3. Geographical origin of the examined populations of the taxa of *Genista albida* aggr.*:*
▲*G. albida* var. *albida* ● *G. albida* var. *godetii* ■ *G. involucrata.*

the length of the polar axis (respectively 23.7-27.3 and 27.4-30.2 μm). Also the length of the colpus in the western taxa is smaller than in the eastern ones (respectively 17.7-22.1 and 23.5-25.6 μm). Among the western taxa, *Genista florida* is the species with the smallest grains, while *G. cinerascens* shows higher values for the length of the polar axis (30.0 μm) and the length of the colpus (24.7 μm), although in the only examined population.

Among the eastern taxa, *Genista involucrata* is the species with the largest grains.

*Genista pilosa*, the only widely distributed species, displays grains with values similar to those of the western taxa.

The taxa of the section usually present prolato-spheroidal grains, with a mean P/E ratio which varies between 1.03 in *Genista pseudopilosa* and 1.14 in *G. pulchella* subsp. *pulchella*; *G. cinerea* subsp. *murcica* shows oblato-spheroidal grains. *G pulchella* subsp. *villarsiana*, *G. florida*, *G. albida* var. *godetii* and *G. cinerea* subsp. *valentina* have subprolate grains, with a mean P/E ratio varying between 1.18 and 1.23.

*Qualitative pollen characters (LM)*

Table 1B shows the average frequency of qualitative character states by LM in the taxa of the section examined in this study (see also Plate 1).

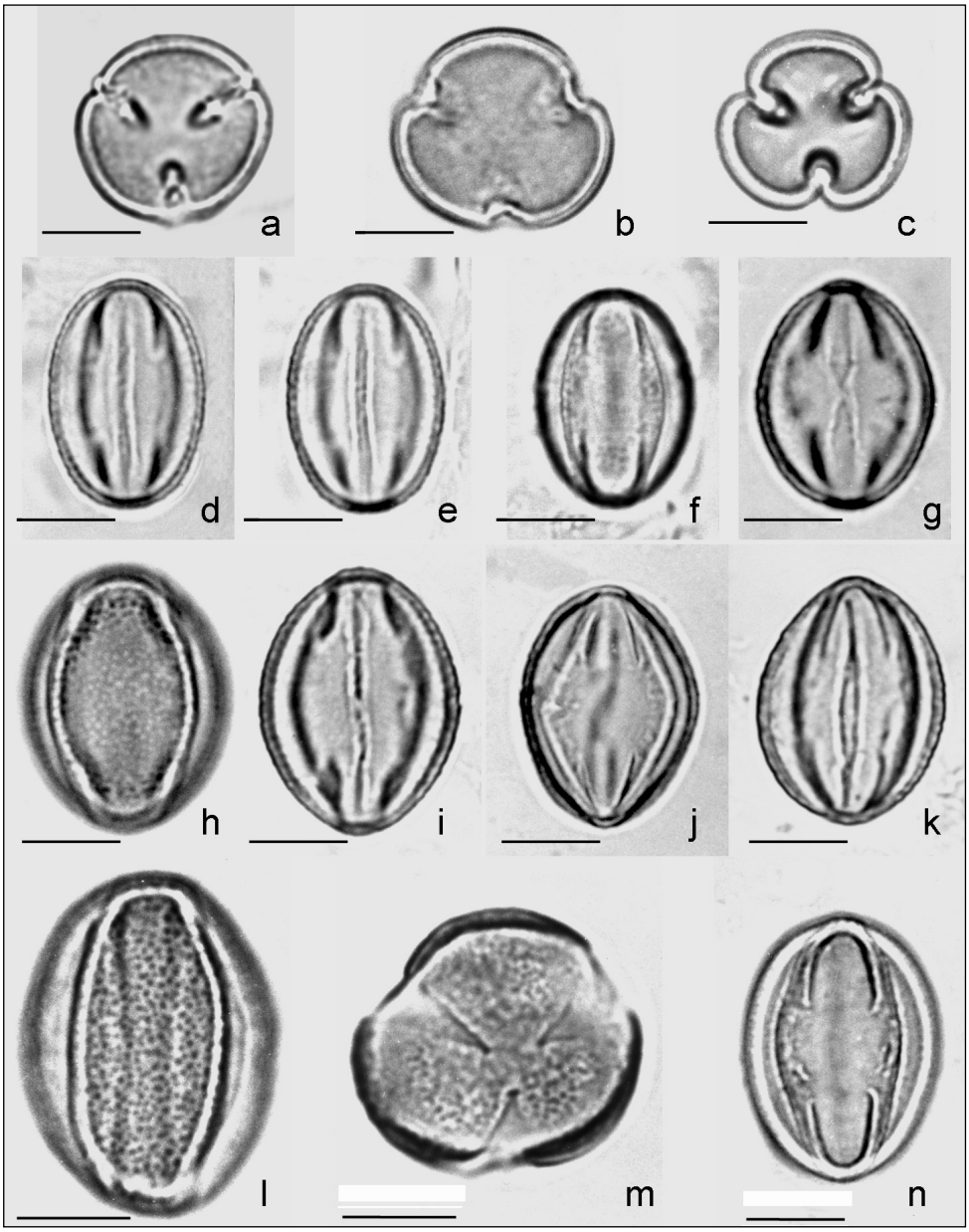


Plate 1. LM micrographs of pollen grains of *Genista* sect. *Spartioides*.
(a-c) Optical cross-section in polar view: (a) *G. florida* (Europe), (b) *G. majorica*, (c) *G. pulchella* ssp. *pulchella*. (d) Optical cross-section in equatorial view, *G. florida* (Europe). (e, g, i, k) Colpus in direct view, equatorial view: (e) *G. florida* (Europe), (g) *G. florida* ssp. *maroccana*, (i) *G. cinerea* ssp. *valentina*, (k) *G. teretifolia*. (f, j, n) Colpi in profile view, equatorial view: (f) *G. florida* (Europe), (j) *G. teretifolia*, (n) *G. cinerea* ssp. *cinerea*. (h, l) Low focus, equatorial view: (h) *G. cinerea* ssp. *valentina*, (l) *G. pulchella* ssp. *pulchella*. (m) Low focus, polar view, *G. cinerea* ssp. *ausetana*. – Scale bar – 10 μm.

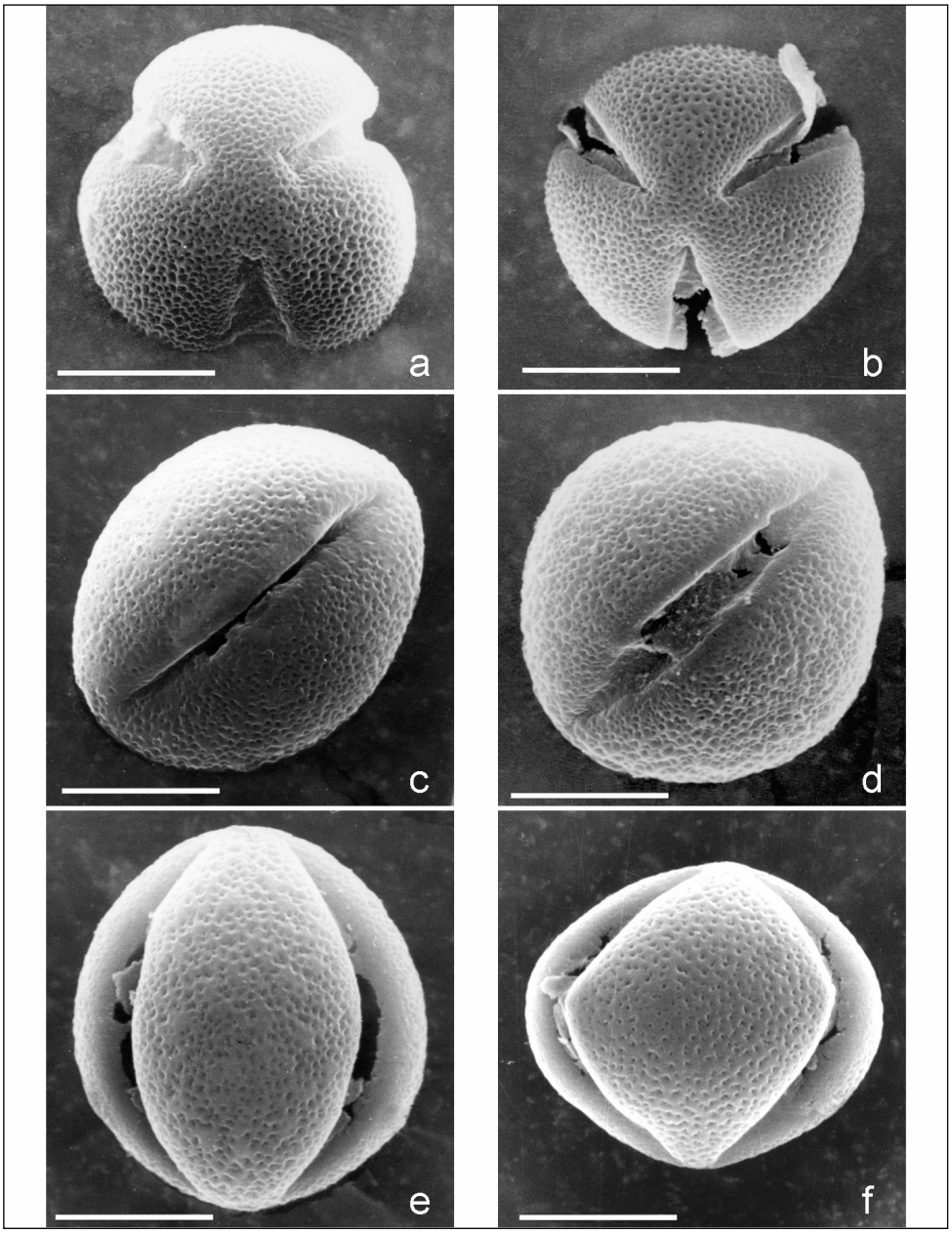


Plate 2. SEM micrographs of *Genista* sect. *Spartioides*: **a-b**, polar view; **c-f**, equatorial view. (a) Subcircular outline, *G. albida* var. *albida*. (b) Subtriangular outline, *G. pilosa*. (c) Narrowly elliptic outline, rectangular furrow in direct view, *G. albida* var. *godetii.* (d) Broadly elliptic outline, boat-shaped furrow in direct view, *G. pulchella* ssp. *villarsiana.* (e) Narrowly elliptic outline, curved furrows in profile view, *G. cinerea* ssp. *speciosa.* (f) Subrhomboidal outline, angular furrows in profile view, *G. cinerea* ssp. *murcica.* – Scale bar – 10 μm.

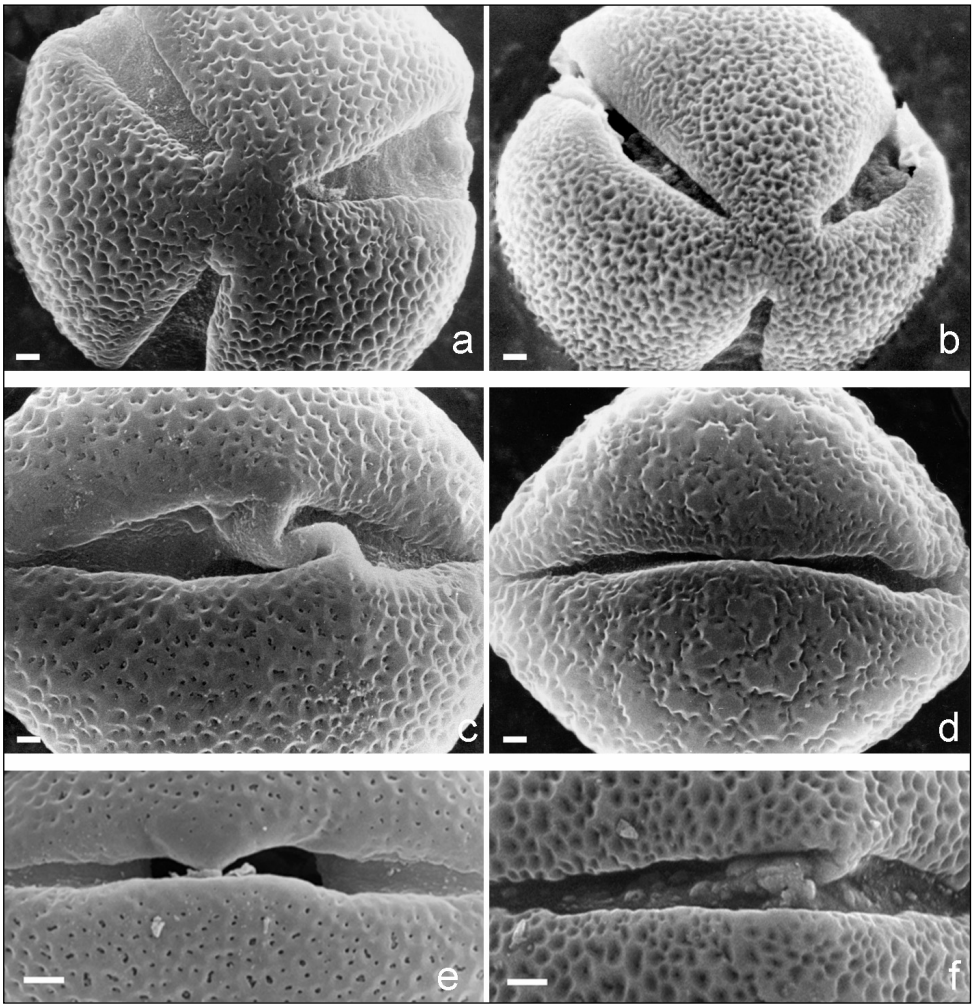


Plate 3. SEM micrographs of *Genista* sect. *Spartioides*: **a-b**, polar view; **c-f**, equatorial view. (a-b) Tectum ornamentation at apocolpium: (a) Pattern similar to mesocolpium, *G. albida* var. *albida*. (b) Lower reticulum, tectum more densely perforate, *G. pilosa.* (c-f) Tectum ornamentation at furrow rim: (c) Trend to disappearing reticulum, *G. involucrata*. (d) Lower reticulum, tectum more densely perforate, *G. albida* var. *godetii*. (e) Trend to disappearing reticulum, smooth colpus membrane, *G. ramosissima*. (f) Microverrucate colpus membrane, *G. pseudopilosa*. – Scale bar – 1 μm.

The pollen grains present generally an ellipsoid form in equatorial view. The outline is in most cases broadly elliptic. Almost all taxa show a certain frequency of narrowly elliptic and subrhomboidal grains, while only *G. cinerea* subsp. *cinerea*, *G. pulchella* subsp. *villarsiana* and *G. involucrata* have a small frequency of rhomboidal grains.

The outline in polar view is in most cases more frequently circular. A high frequency of subcircular grains may be observed in *G. pseudopilosa, G. pilosa* and *G. florida* subsp. *maroccana*,

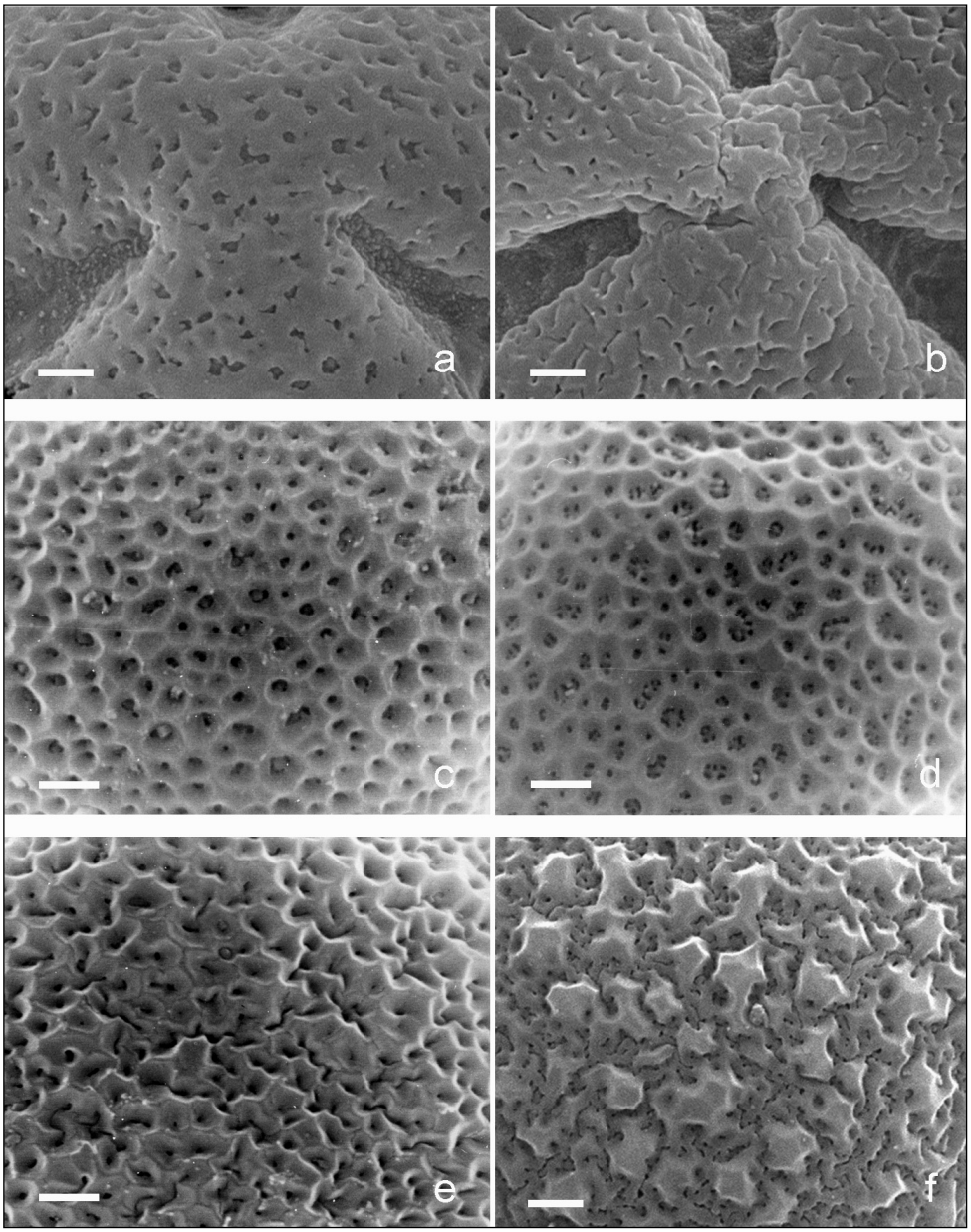


Plate 4. SEM micrographs of *Genista* sect. *Spartioides*: **a-b**, polar view; **c-f**, equatorial view. (a-b) Tectum at apocolpium: (a) Perforate as at mesocolpium, granulate colpus membrane, *G. obtusiramea*. (b) Less densely perforate, *G. albida* var. *godetii.* (c-f) Tectum ornamentation at mesocolpium: (c) Homogeneously supramicroreticulate perforate, lumina with one circular perforation, *G. sericea* var. *sericea*. (d) Lumina with several separated perforations, *G. pilosa*. (e) Angular muri, some lumina with joined perforations, *G. cinerascens*. (f) Several unperforate areas, *G. pseudopilosa*. – Scale bar – 1 μm.

subtriangular in *G. obtusiramea*, *G. pilosa* and *G. cinerea* subsp. *cinerea*. The taxa show a certain variability in the apertural types: colpate pollen grains prevail in most taxa; colpi with diffuse endoaperture are more frequent in *G. pilosa*, *G. cinerea* subsp. *murcica* and *G. pulchella* subsp. *villarsiana*.

The most frequent shape of the furrows in direct view is rectangular in most taxa. Equatorially constricted colpi are less frequently found; boat-shaped furrows are observed with a lower frequency. The rims of the colpi are most frequently wavy in the eastern taxa; in the western taxa the furrows with straight rim are more frequent, except in *G. majorica*, *G. pseudopilosa*, *G. florida* subsp. *maroccana* and *G. obtusiramea*. The colpi in profile view are mostly curved; angular furrows in profile view clearly prevail in *G. cinerascens* and *G. pulchella* subsp. *pulchella*. When viewed in profile, a thickening of the apertural region towards the poles can be observed; it is more frequently longer, in some cases shorter and less frequently equal to half of the colpus.

*Ultrasculptural exine characters (SEM)*

Table 1C shows the average frequency of the qualitative character states by SEM of the exine ornamentation and the average number of the perforations in a standard area (10 μm$^2$) of the mesocolpium at equatorial level (see also Plates 2-4).

In the examined taxa of the section, the tectum at the interapertural zone is supramicroreticulate perforate, with some small unperforate and more rised areas. Fossulate areas have been rarely observed. The muri are more frequently blunt in almost all taxa. Small perforations of the tectum, with or without inclusions, are present on the bottom of the lumina. The number of the perforations per 10 μm$^2$ varies from 22 in *G. cinerea* subsp. *cinerea* and *G. pulchella* subsp. *villarsiana* to 34 in *G. florida* (Europe). Often, only one circular perforation (or less frequently irregular) can be observed; sometimes, many small perforations are present on the bottom of the lumina, either separated or confluent. At the apocolpium, the reticulum usually extends unchanged up to the poles, but in some cases lowers. The supratectal reticulum mostly tends to disappear towards the rim of the colpi in the equatorial region, especially near the aperture, and the density of the perforations of the tectum usually decreases. The aperture membrane is often granulate, but may be also smooth (particularly in *G. obtusiramea*) or micro-verrucate, less frequently verrucate.

*Ultrastructural exine characters (TEM)*

In a former study (Ghirardelli & al. 1994), the ultrastructure of the exine of two taxa representative of the sect. *Spartioides*, *Genista pilosa* and *G. sericea*, was examined by TEM in the frame of an analysis of 15 species representative of all the sections of *Genista.* In both species, the exine shows four layers: tectum, columellar layer, foot layer and endexine (Plate 5). The tectum, interrupted by perforations, has a supratectal reticulum. In comparison with other taxa of *Genista*, the exine in *G. pilosa* and *G. sericea* is not very thick (0.77 and 0.70 μm, respectively). The ectexine (tectum, columellar layer and foot-layer) is thicker in *G. pilosa* (0.71 μm) than in *G. sericea* (0.62 μm); the endexine is slightly thicker in *G. sericea* (0.07 μm).

*Numerical analysis*

Fig. 4 represents the dendrogram of the taxa of *Genista* sect. *Spartioides* examined in this study, based on quantitative pollen characters by LM. In the data processing, *G. cinerea* subsp. *valentina* and *G. cinerascens* were not considered, as only one or two populations were examined for both species. Two main clusters can be highligthed, the former (I) comprehending the taxa distributed in the western

Table 1. Pollen characters in *Genista* sect. *Spartioides*. Means and standard deviations (µm) of quantitative characters (LM) and average frequencies of qualitative character states (LM, SEM) are given.

| | G.obtusiramea | G.cinerascens | G. cinerea ssp. cinerea | G. cinerea ssp. speciosa | G. cinerea ssp. ausetana | G. cinerea ssp. murcica | G. cinerea ssp. valentina | G. majorica |
|---|---|---|---|---|---|---|---|---|
| **A) QUANTITATIVE POLLEN CHARACTERS (LM)** | | | | | | | | |
| **in equatorial view** | | | | | | | | |
| polar axis length (P) | 36,1 ± 1,88 | 30,0 ± 1,20 | 26,1 ± 1,11 | 25,7 ± 1,32 | 25,9 ± 1,85 | 25,3 ± 1,27 | 27,3 ± 0,38 | 24,7 ± 0,45 |
| equatorial diameter (E) | 32,6 ± 2,40 | 27,2 ± 1,05 | 24,0 ± 1,47 | 23,6 ± 1,90 | 25,1 ± 1,32 | 25,4 ± 1,15 | 22,2 ± 0,98 | 23,6 ± 0,71 |
| colpus length | 29,8 ± 2,10 | 24,7 ± 1,41 | 21,3 ± 0,83 | 20,8 ± 2,16 | 20,1 ± 1,01 | 18,9 ± 1,71 | 22,1 ± 0,28 | 21,3 ± 0,59 |
| equatorial colpus breadth | 3,9 ± 0,52 | 2,5 ± 0,20 | 2,4 ± 0,12 | 2,7 ± 0,25 | 2,5 ± 0,17 | 2,9 ± 0,28 | 2,5 ± 0,03 | 2,3 ± 0,23 |
| equatorial mesocolpium breadth | 25,4 ± 2,33 | 18,8 ± 1,35 | 16,4 ± 2,51 | 16,8 ± 2,50 | 18,0 ± 2,02 | 18,0 ± 1,13 | 13,6 ± 0,44 | 17,9 ± 1,04 |
| **in polar view** | | | | | | | | |
| distance between the apices of two ectocolpi | 3,1 ± 0,63 | 3,9 ± 0,48 | 3,1 ± 0,60 | 3,2 ± 0,62 | 3,3 ± 1,14 | 4,1 ± 0,38 | 3,1 ± 0,34 | 3,9 ± 0,42 |
| P/E ratio | 1,11 ± 0,14 | 1,10 ± 0,01 | 1,09 ± 0,09 | 1,10 ± 0,13 | 1,03 ± 0,07 | 0,99 ± 0,04 | 1,23 ± 0,05 | 1,05 ± 0,02 |
| apocolpium index | 0,10 ± 0,02 | 0,14 ± 0,03 | 0,13 ± 0,03 | 0,14 ± 0,04 | 0,13 ± 0,02 | 0,16 ± 0,05 | 0,14 ± 0,04 | 0,17 ± 0,04 |
| **B) QUALITATIVE POLLEN CHARACTERS (LM)** | | | | | | | | |
| **outline in equatorial view** | | | | | | | | |
| narrowly elliptic | 15 | 10 | 15 | 30 | 20 | 6 | 25 | 35 |
| broadly elliptic | 75 | 57 | 40 | 50 | 45 | 55 | 75 | 45 |
| subrhomboidal | 10 | 33 | 30 | 20 | 35 | 39 | - | 20 |
| rhomboidal | - | - | 15 | - | - | - | - | - |
| **outline in polar view** | | | | | | | | |
| circular | 5 | 97 | 31 | 23 | 56 | 61 | 72 | 9 |
| subcircular | 29 | - | 19 | 34 | 8 | 9 | - | 60 |
| 3-lobate | - | - | 1 | 2 | - | - | - | - |
| subtriangular | 62 | 3 | 49 | 39 | 34 | 30 | 28 | 24 |
| triangular | 4 | - | - | 2 | 2 | - | - | 7 |
| **apertures in equatorial view** | | | | | | | | |
| colpi | 75 | 75 | 80 | 80 | 85 | 38 | 85 | 78 |
| colpi with diffuse endoaperture | 25 | 25 | 20 | 20 | 15 | 62 | 15 | 22 |
| *in direct view* | | | | | | | | |
| rectangular | 38 | 77 | 67 | 77 | 71 | 76 | 73 | 52 |
| boat-shaped | 25 | 11 | 11 | 8 | 12 | 11 | 12 | 13 |
| equatorially constricted | 37 | 12 | 22 | 15 | 17 | 13 | 15 | 35 |
| straigth rim | 48 | 83 | 59 | 54 | 61 | 59 | 68 | 27 |
| wavy rim | 52 | 14 | 41 | 46 | 39 | 41 | 32 | 73 |
| *in profile view* | | | | | | | | |
| curved | 42 | 30 | 67 | 72 | 94 | 69 | 58 | 59 |
| angular | 58 | 70 | 33 | 28 | 6 | 31 | 42 | 41 |
| long thickening towards the poles | 20 | 83 | 71 | 49 | 86 | 60 | 85 | 32 |
| medium length thickening towards the poles | 25 | 12 | 12 | 25 | 8 | 33 | 10 | 30 |
| short thickening towards the poles | 55 | 5 | 17 | 26 | 6 | 7 | 5 | 38 |
| **C) ULTRASCULPTURAL EXINE CHARACTERS (SEM)** | | | | | | | | |
| **tectum ornamentation at mesocolpium** | | | | | | | | |
| homogeneously supramicroreticulate perforate | 92 | 85 | 78 | 89 | 88 | 87 | 71 | 84 |
| percentage of unperforate areas | 7 | 5 | 21 | 8 | 10 | 6 | 20 | 14 |
| percentage of fossulate areas | 1 | 10 | 1 | 3 | 2 | 7 | 9 | 2 |
| *muri* | | | | | | | | |
| angular | 37 | 40 | 30 | 43 | 30 | 36 | 20 | 33 |
| blunt | 63 | 60 | 70 | 57 | 70 | 64 | 80 | 67 |
| *lumina* | | | | | | | | |
| with one circular perforation | 38 | 60 | 38 | 66 | 40 | 44 | 50 | 35 |
| with one irregular-shaped perforation | 56 | 30 | 52 | 27 | 50 | 43 | 35 | 54 |
| with several separated perforations | 2 | - | 2 | 2 | 5 | 5 | 5 | 1 |
| with several joined perforations | 4 | 10 | 8 | 5 | 5 | 8 | 10 | 10 |
| **density of perforations (n°/10 µm²)** | 23 | 29 | 22 | 27 | 24 | 32 | 25 | 29 |
| **tectum ornamentation at apocolpium** | | | | | | | | |
| pattern similar to mesocolpium | 96 | 80 | 96 | 70 | 95 | 94 | 95 | 95 |
| with lower reticulum | 4 | 20 | 4 | 30 | 5 | 6 | 5 | 5 |
| perforate as at mesocolpium | 95 | 80 | 92 | 73 | 88 | 90 | 90 | 67 |
| less densely perforate | 4 | 19 | 7 | 25 | 10 | 7 | 10 | 25 |
| more densely perforate | 1 | 1 | 1 | 2 | 2 | 3 | - | 8 |
| **tectum ornamentation at furrow rim** | | | | | | | | |
| pattern similar to mesocolpium | 51 | 15 | 12 | 10 | 10 | 16 | 20 | 12 |
| with lower reticulum | 13 | 23 | 13 | 20 | 30 | 13 | 10 | 25 |
| with trend to disappearing reticulum | 36 | 62 | 75 | 70 | 60 | 71 | 70 | 63 |
| with disappeared reticulum | - | - | - | - | - | - | - | - |
| less densely perforate | 89 | 88 | 90 | 92 | 80 | 90 | 90 | 90 |
| more densely perforate | 11 | 12 | 10 | 8 | 20 | 10 | 10 | 10 |
| **colpus membrane** | | | | | | | | |
| smooth | 67 | 40 | 30 | 28 | 30 | 34 | 35 | 28 |
| granulate | 24 | 40 | 62 | 64 | 50 | 46 | 51 | 52 |
| microverrucate | 9 | 20 | 8 | 8 | 20 | 18 | 14 | 18 |
| verrucate | - | - | - | - | - | 2 | - | 2 |

Table 1. continued.

| G.ramosissima | G.pseudopilosa | G. teretifolia | G. florida | G. florida ssp. maroccana | G. pilosa | G. pulchella ssp. pulchella | G. pulchella ssp. villarsiana | G. albida var. albida | G. albida var. godetii | G.involucrata |
|---|---|---|---|---|---|---|---|---|---|---|
| 26,3 ± 1,48 | 24,8 ± 2,10 | 23,8 ± 0,75 | 23,7 ± 0,77 | 24,3 ± 1,42 | 25,0 ± 0,65 | 27,4 ± 2,62 | 28,5 ± 1,99 | 28,2 ± 1,62 | 29,7 ± 1,68 | 30,2 ± 1,98 |
| 24,7 ± 1,71 | 24,1 ± 2,33 | 22,3 ± 1,19 | 20,1 ± 2,23 | 22,8 ± 1,39 | 22,5 ± 0,87 | 24,1 ± 1,87 | 24,2 ± 1,66 | 25,3 ± 2,05 | 24,9 ± 2,21 | 27,9 ± 1,38 |
| 21,2 ± 1,79 | 20,2 ± 2,01 | 18,1 ± 1,82 | 17,7 ± 0,85 | 19,9 ± 1,19 | 22,0 ± 0,65 | 23,5 ± 2,43 | 24,9 ± 2,00 | 23,9 ± 2,67 | 25,4 ± 2,09 | 25,6 ± 2,76 |
| 2,7 ± 0,22 | 2,5 ± 0,22 | 2,9 ± 0,20 | 2,6 ± 0,77 | 2,5 ± 0,21 | 2,3 ± 0,47 | 2,9 ± 0,19 | 2,6 ± 0,98 | 2,8 ± 0,64 | 2,7 ± 0,19 | 2,9 ± 0,16 |
| 17,9 ± 2,22 | 18,3 ± 1,99 | 15,3 ± 1,55 | 12,7 ± 1,80 | 17,0 ± 1,88 | 14,8 ± 1,95 | 16,4 ± 2,33 | 17,1 ± 1,64 | 18,0 ± 1,36 | 16,5 ± 1,73 | 20,0 ± 1,32 |
| 3,8 ± 0,50 | 3,9 ± 0,54 | 2,7 ± 0,96 | 3,4 ± 0,92 | 3,6 ± 0,88 | 4,9 ± 0,85 | 4,1 ± 0,63 | 4,3 ± 0,54 | 4,3 ± 0,62 | 4,3 ± 0,25 | 4,5 ± 0,62 |
| 1,07 ± 0,09 | 1,03 ± 0,06 | 1,07 ± 0,04 | 1,19 ± 0,17 | 1,07 ± 0,07 | 1,11 ± 0,03 | 1,14 ± 0,13 | 1,18 ± 0,12 | 1,12 ± 0,07 | 1,20 ± 0,12 | 1,08 ± 0,06 |
| 0,16 ± 0,01 | 0,16 ± 0,03 | 0,12 ± 0,03 | 0,17 ± 0,05 | 0,16 ± 0,04 | 0,22 ± 0,09 | 0,17 ± 0,03 | 0,18 ± 0,02 | 0,17 ± 0,02 | 0,17 ± 0,02 | 0,16 ± 0,02 |
| 25 | 9 | 12 | - | 30 | 13 | 17 | 30 | 30 | 28 | 27 |
| 45 | 55 | 50 | 70 | 53 | 74 | 50 | 57 | 69 | 67 | 43 |
| 30 | 36 | 38 | 30 | 17 | 13 | 33 | 8 | 1 | 5 | 27 |
| - | - | - | - | - | - | - | 5 | - | - | 3 |
| 28 | 6 | 49 | 78 | 12 | 10 | 24 | 38 | 50 | 35 | 39 |
| 38 | 64 | 26 | 1 | 54 | 26 | 11 | 18 | 12 | 34 | 16 |
| - | - | 3 | - | 6 | 9 | 16 | 10 | 10 | 8 | 2 |
| 34 | 27 | 21 | 21 | 21 | 55 | 32 | 24 | 24 | 17 | 29 |
| - | 3 | 1 | - | 7 | - | 17 | 10 | 4 | 6 | 14 |
| 73 | 81 | 77 | 78 | 71 | 32 | 70 | 41 | 72 | 73 | 71 |
| 27 | 19 | 23 | 22 | 29 | 68 | 30 | 59 | 28 | 27 | 29 |
| 68 | 42 | 79 | 79 | 46 | 42 | 52 | 52 | 40 | 45 | 55 |
| 13 | 13 | 11 | 7 | 6 | 11 | 4 | 7 | 6 | 8 | 10 |
| 19 | 45 | 10 | 14 | 48 | 47 | 44 | 41 | 54 | 47 | 35 |
| 51 | 40 | 69 | 81 | 46 | 51 | 42 | 45 | 49 | 45 | 47 |
| 49 | 60 | 31 | 19 | 54 | 49 | 58 | 55 | 51 | 55 | 53 |
| 73 | 51 | 81 | 73 | 42 | 75 | 38 | 45 | 49 | 45 | 79 |
| 27 | 49 | 19 | 27 | 58 | 25 | 62 | 55 | 51 | 55 | 21 |
| 50 | 19 | 71 | 87 | 27 | 59 | 34 | 29 | 30 | 37 | 46 |
| 27 | 37 | 21 | 12 | 29 | 30 | 26 | 28 | 26 | 21 | 22 |
| 23 | 44 | 8 | 1 | 44 | 11 | 40 | 43 | 44 | 42 | 32 |
| 86 | 86 | 87 | 95 | 96 | 86 | 91 | 78 | 80 | 80 | 89 |
| 10 | 12 | 12 | 4 | 3 | 13 | 8 | 21 | 12 | 17 | 9 |
| 4 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 2 |
| 40 | 38 | 40 | 55 | 40 | 40 | 48 | 36 | 43 | 37 | 42 |
| 60 | 62 | 60 | 45 | 60 | 60 | 52 | 64 | 57 | 63 | 58 |
| 61 | 62 | 56 | 72 | 83 | 49 | 78 | 78 | 63 | 78 | 74 |
| 24 | 31 | 22 | 13 | 10 | 21 | 12 | 12 | 25 | 13 | 14 |
| 7 | 2 | 12 | 4 | 3 | 16 | 4 | 3 | 3 | 1 | 3 |
| 8 | 5 | 10 | 11 | 4 | 14 | 6 | 7 | 9 | 8 | 9 |
| 34 | 24 | 28 | 34 | 25 | 31 | 24 | 22 | 23 | 26 | 24 |
| 94 | 94 | 83 | 94 | 90 | 97 | 89 | 92 | 94 | 88 | 71 |
| 6 | 6 | 17 | 6 | 10 | 3 | 11 | 8 | 6 | 12 | 29 |
| 90 | 93 | 83 | 80 | 60 | 88 | 90 | 91 | 93 | 90 | 78 |
| 8 | 5 | 17 | 18 | 40 | 9 | 10 | 9 | 6 | 10 | 22 |
| 2 | 2 | - | 2 | - | 3 | - | - | 1 | - | - |
| 14 | 31 | 30 | 16 | 10 | 11 | 49 | 36 | 23 | 25 | 13 |
| 34 | 10 | 33 | 16 | 5 | 15 | 3 | 2 | 4 | 2 | 2 |
| 52 | 59 | 37 | 68 | 85 | 74 | 46 | 60 | 73 | 73 | 85 |
| - | - | - | - | - | - | 2 | 2 | - | - | - |
| 70 | 94 | 90 | 80 | 95 | 93 | 98 | 97 | 97 | 98 | 96 |
| 30 | 6 | 10 | 20 | 5 | 7 | 2 | 3 | 3 | 2 | 4 |
| 34 | 40 | 17 | 24 | 37 | 22 | 19 | 22 | 25 | 17 | 18 |
| 44 | 46 | 63 | 48 | 41 | 63 | 50 | 53 | 47 | 33 | 53 |
| 22 | 14 | 20 | 28 | 22 | 11 | 27 | 24 | 25 | 42 | 28 |
| - | - | - | - | - | 4 | 4 | 1 | 3 | 8 | 1 |

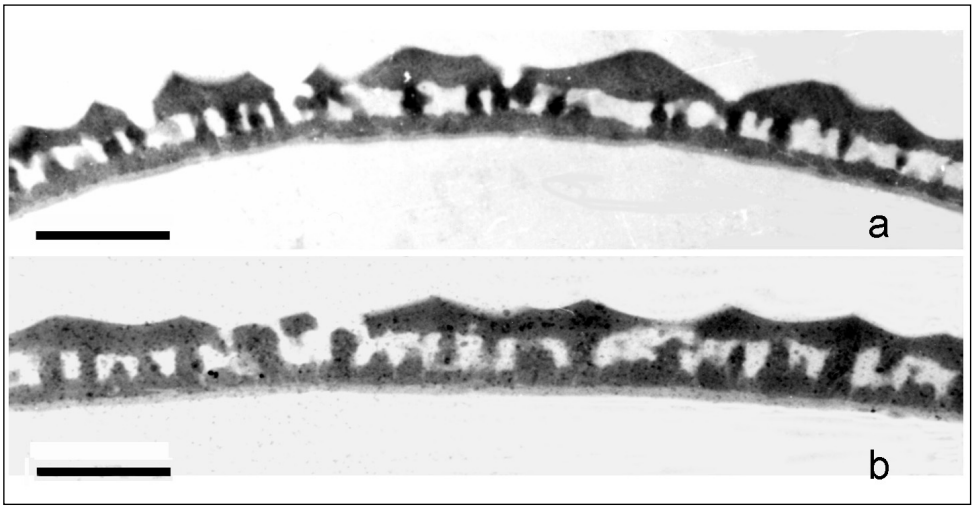


Plate 5. TEM micrographs of the exine of *Genista* sect. *Spartioides* in the interapertural zone at equatorial level.
(a) *G. pilosa*. (b) *G. sericea* var. *sericea*. – Scale bar – 1 µm.

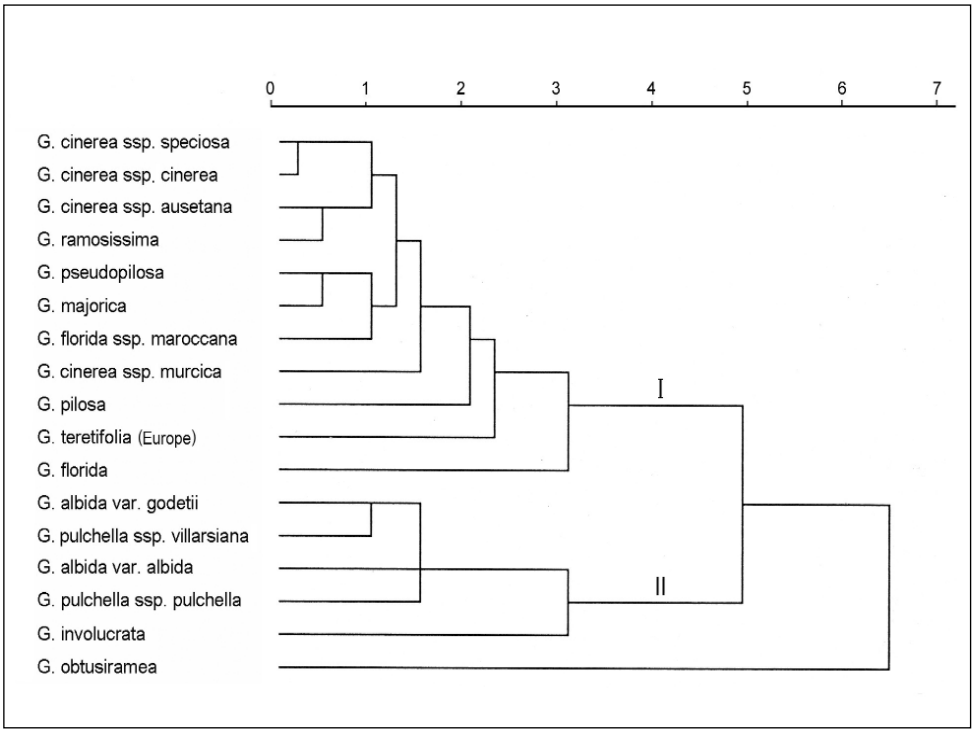


Fig. 4. Dendrogram of the examined taxa of *Genista* sect. *Spartioides* based on pollen characters.

Mediterranean region and *G. pilosa* (central-western European), the latter (II) including the taxa distributed in the eastern Mediterranean region. *G. obtusiramea* is linked at a higher level of distance.

Fig. 5 represents the ordination and the overimposed minimum spanning tree of all the taxa of sect. *Spartioides* (including those of *G. sericea* aggr. formerly studied in Rizzi Longo & Feoli Chiapella 1993) based on quantitative characters measured by LM. The western Mediterranean taxa of the section are placed in the inferior part of the graphic, on the right side. A rather high affinity can be noticed among *G. ramosissima*, *G. majorica*, *G. pseudopilosa*, *G. cinerea* subsp. *cinerea*, subsp. *speciosa*, subsp. *ausetana*, and subsp. *murcica*, while *G. florida* subsp. *maroccana*, *G. teretifolia* and *G. florida* (Europe) result progressively more distant. The eastern Mediterranean taxa, including those of *G. sericea* aggr., and *G. pilosa* are set on the upper and left sides of the graphic. A fairly good affinity is found among the two subspecies of *G. pulchella* (*pulchella* and *villarsiana*), the two varieties of *G. albida* (*albida* and *godetii*) and some taxa of *G. sericea* aggr. (*G. halacsyi*, *G. subcapitata* and *G. sakellariadis*); *G. involucrata* and *G. millii* are more distant. The taxa belonging to *G. sericea* aggr. are thus very scattered in the graphic, particularly *G. sericea* var. *sericea* and *G. millii*. Like in the dendrogram, also in the ordination *G. obtusiramea* is isolated from all the taxa of the section, placing on the lower left side of the graphic, and is linked with *G. millii*, although with a very low affinity. It is worth noting that *G. pilosa*, which fell within the western species in the dendrogram, presents in the ordination the greatest affinity with the eastern taxa, but acts as trait d'union with the western taxa linking with *G. cinerea* var. *cinerea*.

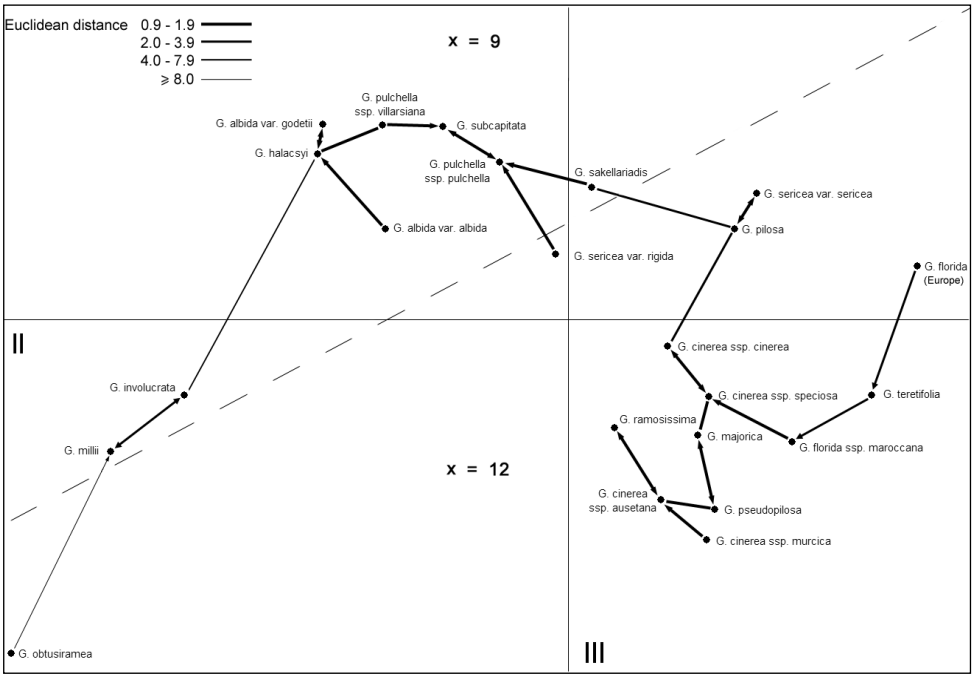


Fig. 5. Ordination of all the taxa of *Genista* sect. *Spartioides* on the basis of pollen characters; the minimum spanning tree, which links the taxa according to maximum affinity, is overimposed.

## Discussion

### *Pollen analysis*

*Genista obtusiramea* emerges as clearly distinguishable from all the taxa of sect. *Spartioides* for several pollen characters: quantitative by LM, displaying the highest values for most examined characters, qualitative by LM (in particular, a high frequency of grains with subtriangular outline in polar view), and qualitative by SEM (especially, a high frequency of smooth colpus membrane).

The taxa distributed in the western Mediterranean region, except *Genista obtusiramea* and, to a lesser extent, *G. cinerascens*, clearly differ from those distributed in the East for quantitative pollen characters, in particular for the smaller length of the polar axis and of the colpus. Within the western taxa, *G. majorica*, the subspecies of *G. cinerea*, *G. ramosissima* and *G. pseudopilosa* form a grouping rather homogeneous on the basis of pollen characters, mostly quantitative. *G. florida* and *G. teretifolia* present the smallest grains. *G. cinerascens* displays larger grains, though only one population was examined. The European populations of *G. florida* differ from the Moroccan ones (subsp. *maroccana*) for several characters, both quantitative (equatorial breadth of mesocolpium and P/E ratio) and qualitative by LM (outline in polar view, shape of the apertures both in direct and in profile view).

Within the eastern taxa, the two varieties of *Genista albida* (*albida* and *godetii*) differ for some quantitative characters (length of polar axis, length of colpus and P/E ratio) and some qualitative ones by SEM. *G. involucrata* appears the most distinguishable species, showing grains with the highest values for all quantitative characters and displaying some qualitative differences, particularly by SEM. The two subspecies of *G. pulchella* (*pulchella* and *villarsiana*) differ, though slightly, for some quantitative characters, the frequency of apertural types and the tectum ornamentation. From the comparison with the already examined taxa of *G. sericea* aggr. (Rizzi Longo & Feoli Chiapella 1993), *G. millii* appears the most distinguishable species; *G. halacsyi*, *G. subcapitata* and *G. sakellariadis* prove to be distinct, and affine to *G. albida* and *G. pulchella*. *G. sericea* clearly differs from the other eastern taxa; the two varieties (*sericea* and *rigida*) appear distinct on the basis of pollen characters.

*Genista pilosa*, the only widely distributed species of the section, is more similar to western taxa for the size of the pollen grains, but acts as a trait d'union with the eastern taxa, particularly with *G. sericea*.

### *Comparison with other biotaxonomical data*

Sect. *Spartioides* is heterogeneous as to morphological and phytochemical (alkaloids and isoflavonoids) characters (Cantò & al. 1997). Some taxa (as *Genista cinerea*) are mostly retamoid-like (or ephedroid-like) erect shrubs, 0.4 to 1.5 m tall, with numerous, flexuous branches growing from the base (nanophanerophytes); other are smaller subshrubs, 0.1 to 0.35 m tall, much branched at the base, prostrate, decumbent or forming hummocks (chamaephytes). While western taxa display both morphotypes, eastern ones are prostrate subshrubs, often tending to form hummocks.

The karyological data concerning the section are numerous. All data concerning the western taxa and *Genista pilosa* are reported in Cusma Velari & al. (2003). Most species display the chromosome number $2n = 48$ (*G. ramosissima*, *G. majorica*, *G. teretifolia*, all the subspecies of *G. cinerea*, often *G. florida* and *G. obtusiramea*), which is traced back to the basic number $x = 12$ by most authors (among others, Sañudo 1979, Goldblatt 1981, Cusma Velari & al. 2003); all the above mentioned taxa are therefore tetraploid. *G. pilosa* and *G. cinerascens* are in most cases diploid with $2n = 24$; the

exaploid number 2*n* = 72 was rarely releved in *G. cinerascens* and *G. obtusiramea*. A tendency towards descending aneuploidy was found in *G. pilosa* (also 2*n* = 22, 44) and in *G. florida* (2*n* = 46, too). Among the eastern taxa, *G. involucrata*, *G. albida*, *G. halacsyi*, *G. subcapitata* and the subspecies of *G. pulchella* present all the chromosome number 2n = 18, *G. sakellariadis* and *G. millii* 2*n* = 36, which may all be traced back to the basic number *x* = 9. Among the eastern taxa, only *G. sericea* displays 2n = 48, with x = 12. Sect. *Spartioides* is thus heterogeneous from a karyological point of view, presenting two basic numbers (*x* = 9 and *x* = 12) (Cusma Velari & al. 1996, 2009).

The species of the section do not form a monophyletic group also considering the molecular data obtained from the analysis of nrDNA (ITS region) and cpDNA (*trn*L-*trn*F IGS) by Pardo & al. (2004); these authors examined almost exclusively the taxa distributed in the western Mediterranean region. Some groups are highlighted: the first includes *G. ramosissima*, *G. majorica*, *G. cinerea* subsp. *cinerea*, subsp. *ausetana*, subsp. *speciosa* and subsp. *valentina*; the second comprehends two clades, the former with *G. pseudopilosa* and *G. teretifolia*, the latter with *G. florida* s.l.; the third includes *G. cinerascens* and *G. obtusiramea*. *G. pilosa* is close to the first group on the basis of the data of the ITS region, but is isolated from all the other taxa of the section on the basis of the data of *trn*L-*trn*F IGS. Among the eastern taxa, a partial analysis, relative to cpDNA, was carried out only on *Genista sericea*, which clusters with the taxa of *G. cinerea* aggr.

**Conclusions**

The morphological and biometrical analysis of the pollen grains of *Genista* sect. *Spartioides* confirms the main characters already described in various taxa of *Genista*. The qualitative characters, particularly by SEM, are seldom discriminant among the taxa; only the frequency of the character states may prove useful in order to distinguish them. Sometimes, the taxa are more distinguishable on the basis of quantitative characters by LM (as e.g. *G. obtusiramea*), other times on the basis of qualitative characters by LM (as e.g. *G. pilosa* and *G. cinerea* subsp. *murcica*) and by SEM (as e.g. *G. obtusiramea*). The comprehensive analysis of the pollen characters allows to point out some differences among the taxa of the section.

The western taxa of sect. *Spartioides* appear distinguishable from the eastern ones on palynological ground. Western and eastern taxa differ also on the basis of karyological data showing basically different chromosome basic numbers.

Among the western taxa, the group of *Genista cinerea*, including *G. majorica*, *G. ramosissima* and the various subspecies of *G. cinerea*, is identified on the basis of pollen characters, as well as morphological and phytochemical characters, and molecular and karyological data previously obtained. This grouping corresponds to ser. *Spartioides* of subsect. *Spartioides* described by Cantó & al. (1997).

The other series of the subsection (ser. *Floridae*), by contrast, does not result homogeneous on palynological ground; *Genista obtusiramea* and, to a lesser extent, *G. cinerascens* present the largest grains, while *G. florida* displays the smallest ones. Also the molecular data separate *G. obtusiramea* and *G. cinerascens* from *G. florida*. *G. obtusiramea* emerges as the most distinct species of the whole section. It is worth noting that *G. cinerascens*, which was described by Gibbs (1966) as a variety of *G. cinerea*, differs from the taxa of *G. cinerea* group both for pollen characters and for phytochemical and molecular data. Moreover, pollen analysis endorses the segregation of subsp. *maroccana* from the Iberic populations of *G. florida.*

Subsect. *Chamaespartum*, as well, described by Cantó & al. (1997), proves to be heterogeneous on the basis of pollen characters: *Genista pseudopilosa* is close to the taxa of *G. cinerea* group, *G. teretifolia* to *G. florida*. On the other hand, *G. pseudopilosa* and *G. teretifolia* are similar for molecular data. G. *pilosa*, which is the most isolated species of the section for molecular data, differs from the western taxa of the section for pollen characters, linking with the eastern species.

Among the eastern taxa of the section, the two examined subspecies of *Genista pulchella* (*pulchella* and *villarsiana*), recently described by Conti (2007), are confirmed also on the basis of pollen characters.

The two varieties of *Genista albida* (*albida* and *godetii*), mentioned by Gibbs (1966) but not by Gibbs (1970) and Greuter & al. (1989), differ for pollen characters. *G. involucrata*, belonging to *G. albida* aggr., is remarkably distinguishable from *G. albida* and from most eastern species of the section.

Among the taxa attributed to *Genista sericea* aggr. by Greuter & al. (1989), particularly *G. millii* and, to a lesser extent, *G. halacsyi*, *G. subcapitata* and *G. sakellariadis* emerge as distinct on the basis of pollen characters. The pollen differences, as well as morphological characters and karyological data (different basic chromosome numbers and different level of ploidy) endorse the specific rank of *G. sakellariadis*, *G. halacsyi*, *G. subcapitata* and *G. millii*, clearing the doubts advanced in turn by Gibbs (1966) and Strid (1986). The pollen differences support also the subdivision of *G. sericea* into two taxa (var. *sericea* and var. *rigida*), whose taxonomic rank deserves further studies.

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Address of the authors:
Loredana Rizzi Longo & Laura Feoli Chiapella,
Dipartimento di Scienze della Vita, Università di Trieste, Via L. Giorgieri 10,
I-34127 Trieste, Italy. E-mails: rizzi@units.it, chiapell@units.it