

CONTRIBUTION TO THE SYSTEMATICS OF *GENISTA* L. SECT. *SPARTOCARPUS* SPACH (*GENISTEAE*, *FABACEAE*) WITH EMPHASIS ON PALYNOLOGICAL DATA

Loredana RIZZI LONGO and Laura FEOLI CHIAPPELLA

Department of Biology, Via L. Giorgieri 10, I-34127 TRIESTE

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Abstract: A pollen analysis of *Genista* sect. *Spartocarpus* has been carried out on 124 samples from 15 species. The taxa were compared in terms of quantitative and qualitative pollen characters, analysed by LM and SEM. Multivariate analysis subdivides taxa into four clusters. *Genista radiata*, *G. holopetala* and *G. hassertiana*, E-Alpine-Balkan species with capitate inflorescence, form an isolate cluster that is palynologically, morphologically and karyologically homogeneous. The other species, with inflorescences of racemous type, can be grouped in three clusters: the first comprising *G. sessilifolia*, *G. nissana* and *G. aucheri*, Balkan-Anatolian taxa, the second including *G. spartioides*, *G. haenseleri* and *G. numidica*, Spanish and N-African species, the third comprising the W-Mediterranean *G. ephedroides*, *G. thyrrena*, *G. gasparrinii*, *G. cilentina*, *G. aetnensis* and *G. dorycnifolia*. Pollen characters and morphological, karyological and biogeographical data appear to be related. The arrangement proposed by Gibbs (1966), who has grouped all the examined species in sect. *Spartocarpus*, is supported by the pollen analysis. On the basis of pollen characters all taxa of *Genista* sect. *Spartocarpus* may be considered as well distinguished. The specific treatment of these taxa in Greuter *et al.* (1989) is, in general terms, confirmed by palynological data. However, the grouping of *G. radiata*, *G. holopetala* and *G. hassertiana* in the *G. radiata*-group and of *G. ephedroides*, *G. gasparrinii*, *G. thyrrena* and *G. cilentina* in the *G. ephedroides*-group is proposed.

Introduction

The tribe *Genisteeae* (*Fabaceae*) includes about twenty genera mainly distributed in the Mediterranean region. The delimitation of *Genisteeae* has long been a matter of debate: in particular the systematics of *Genista* L. is still controversial. The genus delimitation is likewise uncertain. Not all authorities agree on segregating *Cytisanthus* O. F. Lang, *Chamaespartium* Adanson (= *Genistella* Ortega), *Teline* Medicus and *Echinospartum* (Spach) Rothm. from *Genista*.

Several studies on the morphology (Gibbs 1966; Polhill 1976; Bisby 1981), anatomy (Pellegrin 1908), morphometry (Bisby & Nicholls 1977), cytotaxonomy (Sañudo 1979; Cusma Velari & Feoli Chiapella 1987a, b, 1991), serology (Cristofolini & Feoli Chiapella 1977, 1984), chemotaxonomy (Harborne 1969; Faugeras & Paris 1971) and pollination biology of the tribe (Polhill 1976; Bisby 1981) have been carried out.

Many studies concern pollen morphology. The pollen grains of *Genisteeae* show a relatively uniform morphology: single medium-sized

radiosymmetric, isopolar, tricolpate or tricolporoidate grains, with perforate tectum and pitted suprareticulate exine (Polhill 1976; Ferguson & Skvarla 1981; Misset *et al.* 1982; Rizzi Longo & Feoli Chiapella 1981a, 1993; Feoli Chiapella 1983; Cubas & Pardo 1984). In *Fabaceae*, where the commonest situation is the presence of colporate apertures, the trend towards colpoly is considered by Guinet (1981) as a trend to specialisation. According to Walker & Doyle (1975) and Guinet (1981) the tricolpate aperture, in *Genisteeae* as well as in other tribes, might be the result of a secondary reduction of the *ora* from tricolporate ancestors: this is interpreted as an apparent reversal of the evolutionary trend from tricolpate to tricolporate apertures, due, according to Guinet (1981), to the structure of the exine layers: the marked reduction of endexine would cause the disappearance of the endoaperture (*os*).

Being *Genisteeae* a stenopollinic tribe, the identification of its pollen on the basis of qualitative characters is possible only in a few

cases; for this reason biometric analyses were often undertaken in order to try to distinguish the taxa also on the basis of quantitative characters. A detailed study of pollen characters, by light and scanning electron microscope, was started on the genus *Genista*, the most heterogeneous and complex of the tribe. Pollens of some taxa of the genus *Genista*, belonging to the sect. *Spartioides* Spach (Feoli Chiapella 1982a; Rizzi Longo & Feoli Chiapella 1986, 1993; Rizzi Longo *et al.* 1986), *Voglera* (Gaertn., Mey. & Schreb.) Spach (Rizzi Longo & Feoli Chiapella 1981b; Feoli Chiapella 1983), *Acanthospartum* Spach (Rizzi Longo *et al.* 1987, 1988), and *Cephalospartum* Spach emend. P. Gibbs (Rizzi Longo *et al.* 1985; Rizzi Longo & Feoli Chiapella 1990) have been analysed. The ultrastructure of the exine of 15 species of *Genista*, chosen so as to represent all the sections of the genus, has also been examined by transmission electron microscope (Ghirardelli *et al.* 1994).

In the present study a pollen analysis of *Genista* sect. *Spartocarpus* has been carried out; preliminary results were discussed by Feoli Chiapella (1982b) and Feoli Chiapella & Rizzi Longo (1984). The analysis has been undertaken in order to contribute to the systematics of the section and to study the correlations among the different taxa.

Genista subgen. *Spartocarpus* Spach comprises about twenty species, which have been arranged by Gibbs (1966) in the following four sections: sect. *Spartocarpus*, sect. *Acanthospartum* Spach, sect. *Fasselospartum* P. Gibbs and sect. *Cephalospartum* Spach emend. P. Gibbs. The species of the subgenus *Spartocarpus* are distinguished from those of the other two subgenera of *Genista* (subgen. *Genista* and subgen. *Phyllobotrys* Spach) mainly by several characters of the corolla: other differential, but less constant, characters concern the leaves, the branching and the legume (Gibbs 1966).

The sect. *Spartocarpus* (incl. *Asterospartum* Spach, *Ephedrospartum* Spach, *Retamospartum* Spach apud Cosson) is the type section of the subgenus. It includes non-spiny shrubs with alternate, subopposite or completely opposite branching, sessile trifoliolate or, more rarely, unifoliolate leaves, with 3 vascular traces (Pellegrin 1908), broadly ovate standard, usually shorter than the keel, flowers in racemes or clusters, ovoid - acuminate 1-2 seeded legume (Gibbs 1966). Tab. 1 shows the differential characters of the species of the sect. *Spartocarpus*.

Spach (1844) placed the species known at his time and now referred to the sect. *Spartocarpus* partly in sect. *Asterospartum* and partly in sect. *Ephedrospartum*. Spach's distinction between these two sections (1844) is based on characters such as branching (opposite and alternate or fasciculate respectively), leaves (opposite, non caducous, trifoliolate and alternate, caducous trifoliolate or unifoliolate respectively) and inflorescence (terminal, subcapitate or with flowers borne opposite or subopposite in interrupted racemes and terminal racemes with alternate flowers respectively).

The inclusion of most of the species of sect. *Spartocarpus* in the genus *Cytisanthus* has been proposed (Gams 1923; Fukarek 1964; Mayer 1970) on account of the morphological characters discriminant from the other infrageneric taxa of *Genista* (opposite, decussate branches, opposite trifoliolate leaves, linear or very narrowly oblanceolate leaflets, grown together stipules). According to Cristofolini & Feoli Chiapella (1977, 1984) the examined species of sect. *Spartocarpus* clearly differ from the other species of *Genista* also serologically, showing, however, a closer affinity with *Retama* Rafin. (= *Lygos* Adanson) and various intermediate genera of Genisteeae, such as *Spartium* L. and *Echinopartum*. These authors likewise propose to maintain these species in the genus *Cytisanthus*. Other authors, on the contrary (Gibbs 1966, 1968; Polhill 1976; Bisby 1981), include the species of sect. *Spartocarpus* in *Genista*.

Examined taxa

The species of sect. *Spartocarpus* prevalently occur in the Mediterranean region. Two main distribution centers can be distinguished: one in the east (Balkan Peninsula) and one in the west (southern Spain and north-western Africa), with some species mainly occurring on the Tyrrhenian islands.

Mainly eastern species are: *Genista radiata* (L.) Scop., *G. holopetala* (Koch) Bald., *G. hassertiana* (Bald.) Buchegger, *G. sessilifolia* DC., *G. nissana* Petrović, *G. aucheri* Boiss.

Genista radiata, a south-east European orophyte, occurs in the south-eastern Alps, with some disjunct stations in the western Alps (Dauphiné, Valais, Val di Sesia), on the northern and central Apennins and in the central-western Balkan Peninsula (Buchegger 1912; Bertolani Marchetti 1960; Fukarek 1964). Scattered

Tab. 1 - Main differential morphological characters among the species of the sect. *Spartocarpus*.

	<i>G. radiata</i>	<i>G. holopetala</i>	<i>G. hassertiana</i>	<i>G. sessilifolia</i>	<i>G. nissana</i>	<i>G. aucheri</i>	<i>G. spartioides</i>	<i>G. haenseleri</i>
branches	opposite	opposite	opposite	opposite and subopposite	alternate and subopposite	subopposite and alternate	alternate and fasciculate	alternate and subopposite
leaves	trifoliolate opposite subsessile caducous	trifoliolate opposite sessile persistent	trifoliolate opposite sessile persistent	trifoliolate alternate and subopposite sessile or shortly petiolate persistent	trifoliolate alternate and subopposite sessile persistent	trifoliolate subopposite and alternate shortly petiolate persistent	unifoliolate alternate and subopposite sessile fugacious	unifoliolate alternate shortly petiolate fugacious
inflorescence	flowers subopposite in terminal clusters of 3-12 pedicel c. 1 mm or lacking	flowers opposite usually 2 or 4 per branch, subtterminal pedicel c. 1 mm or lacking	flowers opposite in terminal clusters of 2-4 (8), sometimes lower pair remote pedicel c. 1 mm or lacking	flowers alternate or sometimes subopposite singly in lax, many-flowered racemes pedicel 1 mm or less	flowers alternate or sometimes subopposite singly in lax, many-flowered racemes pedicel 1.5 mm	flowers opposite or subopposite singly in interrupted racemes pedicel 1.5 mm	flowers alternate or subopposite singly or in clusters in interrupted racemes pedicel 1 mm	flowers alternate in clusters of 2-4 on short lateral branches pedicel 2-3 mm

	<i>G. doryenifolia</i>	<i>G. aetnensis</i>	<i>G. numidica</i>	<i>G. ephedroides</i>	<i>G. thyrrina</i>	<i>G. gasparrinii</i>	<i>G. cilentina</i>
branches	alternate and subopposite	alternate and subfasciculate pendent	alternate and subopposite	alternate and subopposite mucronate	alternate and subopposite pendent	subopposite and fasciculate gracile	alternate and fasciculate
leaves	trifoliolate opposite and alternate subsessile persistent	unifoliolate alternate and subopposite subsessile fugacious	trifoliolate, upper unifoliolate alternate subsessile fugacious	trifoliolate, upper unifoliolate alternate or subopposite sessile fugacious	trifoliolate, upper unifoliolate alternate or subopposite sessile fugacious	trifoliolate, upper unifoliolate alternate sessile fugacious	trifoliolate, upper unifoliolate alternate sessile fugacious
inflorescence	flowers alternate or subopposite in congested terminal racemes pedicel 1-2 mm	flowers alternate and opposite in lax, terminal, many-flowered racemes pedicel 1-3 mm	flowers alternate or subopposite in terminal racemes of 5-20 (30) pedicel 1-2 mm	flowers alternate or subopposite in lax racemes of 5-10 pedicel 2-2.5 mm	flowers alternate or subopposite in dense, pendent many-flowered racemes pedicel 1.5 mm	flowers alternate or subopposite in terminal, lax or dense racemes of 5-20 pedicel 2 mm	flowers alternate in dense, many-flowered racemes pedicel 1.5-2 mm

stations can be found in northern Greece (Pindus and Olympus Mts, Strid 1986). Three varieties have been described: var. *radiata*, var. *sericopetala* Buchegger and var. *bosniaca* Buchegger; because

of lack of material it has been impossible to analyse this last variety, in any case based on a single specimen, but of which Gibbs (1966) himself could not confirm the status.

Genista holopetala (= *G. radiata* var. *nana* Spach), a species endemic to Liburnia, with fragmentary distribution, occurs in south-western Slovenia (Mt Čaven), in south-western Hrvatska (Velebit, Kapela and Obruć Mts, Buchegger 1912; Strgar 1963; Fukarek 1964), in Italy (area of Trieste, Poldini 1964; Feoli Chiapella & Rizzi Longo 1987).

Genista hassertiana (= *G. holopetala* var. *hassertiana* Bald.) occurs only in northern Albania and in southern Srbija, northern Makedonija and northern Greece (Buchegger 1912; Fukarek 1964; Strid 1986).

Genista sessilifolia (= *G. trifoliolata* Janka) in two slightly separated areas, the first one extending in Turkey, the other one in the south of the Balkan Peninsula (Bulgaria, southern Romania and Makedonija) and in northern Greece (Gibbs 1966, 1970; Greuter *et al.* 1989). Two subspecies have been distinguished: ssp. *sessilifolia*, distributed in Makedonija, Bulgaria, Turkey and Greece, and ssp. *romanica* (Prodan) P. Gibbs, which occurs in the region of Dobruja in Romania (Gibbs 1966). On the contrary, Greuter *et al.* (1989) placed only the populations of Turkey in ssp. *sessilifolia*, and referred all the European populations to ssp. *romanica*.

Genista nissana occurs in southern Srbija and northern Makedonija (Gibbs 1966; Mayer 1970).

In his reappraisal of the genus *Cytisanthus*, Mayer (1970) subdivides the east European species of sect. *Spartocarpus* in two series: series *Capitati*, with flowers in terminal clusters, and series *Racemosi*, with flowers in long, lax, many-flowered racemes. To the first one belong *Genista radiata*, *G. holopetala* and *G. hassertiana*, to the second *G. sessilifolia* and *G. nissana*.

Genista aucheri, an Anatolian endemic (Gibbs 1966, 1970), is distinguished from the others mainly by flowers borne singly opposite or subopposite in interrupted racemes.

The western species are: *Genista spartioides* Spach (= *G. retamoides* Cosson), *G. haenseleri* Boiss., *G. aetnensis* (Biv.) DC., *G. dorycnifolia* Font Quer, and *G. ephedroides* complex.

Genista spartioides occurs in the southern and south-eastern regions of Spain and in northern Algeria and Morocco (Willkomm 1880; Quezel & Santa 1962; Maire 1987).

Genista haenseleri is endemic to a very small area in the south of Spain, near Malaga (Willkomm 1880; Gibbs 1966).

Genista spartioides and *G. haenseleri* are

distinguished from most of the other species of sect. *Spartocarpus* by their unifoliolate, alternate or subopposite leaves and by their flowers, in racemes of clusters (rarely in racemes). *G. haenseleri* was placed by Spach (1845) among the "species excludendae" from *Genista*; he proposed its inclusion in *Cytisus* or the creation of a new genus. Later the species was included by Willkomm (1880) in *Genista* sect. *Erinacoides* Spach (subgenus *Genista*), from which, however, it is distinguished by several anatomical characters (Pellegrin 1908); Gibbs (1966) on the contrary placed it in sect. *Spartocarpus*.

Genista aetnensis occurs in natural habitats only in Sardinia and on the Etna Volcano in Sicily (Fiori 1925), while its occurrence in natural habitats in Corse has been doubted (Greuter *et al.* 1989). Spach (1845) excluded also this species from *Genista*, and devised for it a different classification, creating the genus *Dendrospartum* Spach.

Genista dorycnifolia is endemic to few areas of Ibiza, Islas Baleares (Knoche 1922; Gibbs 1966). Because of its inflorescence (congested racemes) it has an intermediate position between *G. aetnensis* and *G. ephedroides* (usually lax racemes) and *G. radiata* and allied species (terminal clusters).

The *Genista ephedroides* complex is subject to divergent views. While Gibbs (1966) placed all the taxa mentioned by Spach (1844) - *G. numidica* Spach, *G. ephedroides* DC., *G. gasparrinii* (Guss.) C. Presl - in *G. ephedroides*, more recently Valsecchi (1986b), even though admitting the close affinity among the three taxa, kept them as separate. Furthermore, Valsecchi (1986a) described a new species, *G. thyrrena*, to which she referred the populations of the Tyrrhenian islands. Greuter *et al.* (1989) accepted the distinction of the four taxa, grouping, however, *G. ephedroides*, *G. gasparrinii* and *G. thyrrena* in *G. ephedroides* aggr. and keeping *G. numidica* as a separate species. Thus, considering its exclusion from Corse, *G. ephedroides* should be a Sardinian endemic (Valsecchi 1986b; Greuter *et al.* 1989), *G. gasparrinii* (= *Spartium gasparrinii* Guss.) endemic to isolated localities on the northern coast of Sicily (Valsecchi 1986b; Brullo *et al.* 1992), *G. numidica* endemic to the coastal mountains of Algeria (Quezel & Santa 1962; Maire 1987), *G. thyrrena* endemic to the Arcipelago Ponziano and to the Isole Eolie (Valsecchi 1986a; Greuter *et al.* 1989). Recently Valsecchi (1993) for the populations of mainland Italy (Salernitano), placed by Pizzolongo

(1960) in *G. ephedroides*, and for eastern populations of Sicily proposed the new species *G. cilentina* Valsecchi. Such Sicilian populations are referred by Brullo *et al.* (1993) to the new species *G. demarcoi* Brullo, Scelsi & Siracusa. In the present paper the specimen of Castelbuono (Sicily) is reported as *G. cilentina*.

Materials and methods

124 samples have been examined in order to assess the intra- and interspecific variability of the taxa of the sect. *Spartocarpus*. Samples of each taxon deriving from several populations, scattered within the respective distributional ranges (Fig. 1), were analysed, this because in previous studies (Feoli Chiapella 1982a, 1983) a certain variability in pollen characters within the same taxon was noted. Pollen from herbarium specimens was acetolysed according to Erdtman (1969), included in glycerine 50% and observed by light microscope (LM).

The following quantitative characters (Plate 1) were examined: length of the polar axis (P), equatorial diameter (E), diameter of the grain at 1/4 of the polar axis ($D_{1/4}$, introduced in order to distinguish rhomboidal grains from ovoidal ones), length of *colpus* (P-c), width of *colpus* (E-c), width of *mesocolpium* (Mes), length of the side of the polar triangle (LTP), thickness of exine measured at the equator of the grain (ExE). For the pollen terminology see Faegri & Iversen (1964), Walker & Doyle (1975), Accorsi & Forlani (1976), Accorsi *et al.* (1983), Feoli Chiapella (1983). The ratios P/E, P/P-c, exine index IE (ExE/E), polar area index IAP (LTP/E) and $E/D_{1/4}$ were considered. The measurements were made by filar ocular micrometer mounted on a Nikon Labophot within a standard period after preparation (4 hours), in order to avoid any alteration in the dimensions (Van Campo 1966; Hanks & Fairbrothers 1976; Rizzi Longo 1986). Thirty measurements for each character and for each sample were made, since the means appear to be stabilised after 20-25 measurements (Rizzi Longo 1986).

The qualitative characters analysed by LM are the shape of the perimeter in polar view (amb), the shape of the apertures and the relative length of thickenings at the end of the furrows. Same as for quantitative measurements, 30 grains have been observed for each population.

The pollen was acetolysed, dehydrated in acetone, dried according to the critical point

technique (Anderson 1951) and coated with gold-palladium for the examination by SEM (Philips Scanning Electron Microscope SEM 500). The exine sculpture at *mesocolpium*, at *apocolpium* and at the margins of the furrows was examined in order to evaluate the morphological variation of the grain surface. The number of pits in a standard area ($49 \mu\text{m}^2$) of the *mesocolpium* has been counted at x 5000.

The species were compared in terms of their pollen characters, both quantitative and qualitative. The quantitative characters were subdivided into classes of regular intervals; the qualitative characters include several states. The average frequency of every quantitative interval and qualitative state was calculated for each taxon. Informational divergence (Lagonegro & Feoli 1981) was used as distance coefficient in order to compare the various taxa. Complete linkage clustering was applied to the matrix of distances to obtain a dendrogram (Sneath & Sokal 1973) and an eigenanalysis to order the taxa (Lagonegro & Feoli 1981). In addition, a minimum spanning tree (MST, Gower & Ross 1969) was constructed, based on the distances, that links the taxa according to maximum affinity. The significance of the differences between averages of the various taxa was assessed for all quantitative characters, using the "t-test" of Student. The computer programs used for classification and ordination are described in Feoli *et al.* (1982).

Results

The results of pollen analysis by LM and SEM are reported in Tab. 2. With regard to quantitative characters, the data for each taxon are averages of the measurements taken from thirty pollen grains from each of the examined samples. As regards qualitative characters, given the variability within the taxa, the average of frequency percentage for each character state is shown.

Fig. 2 represents the dendrogram of the examined taxa based on the characters analysed by LM and SEM (see Tab. 2). It shows the clear division of the taxa into two main clusters. The first cluster is subdivided into two subclusters: A includes *Genista radiata*, *G. holopetala*, *G. hassertiana*, distributed prevalently in the east; B comprises *G. aetnensis*, *G. dorycnifolia*, *G. ephedroides*, *G. gasparrinii*, *G. cilentina* and *G. thyrrana*, Thyrrenian - Balearic taxa. The second cluster likewise is subdivided into two subclusters:

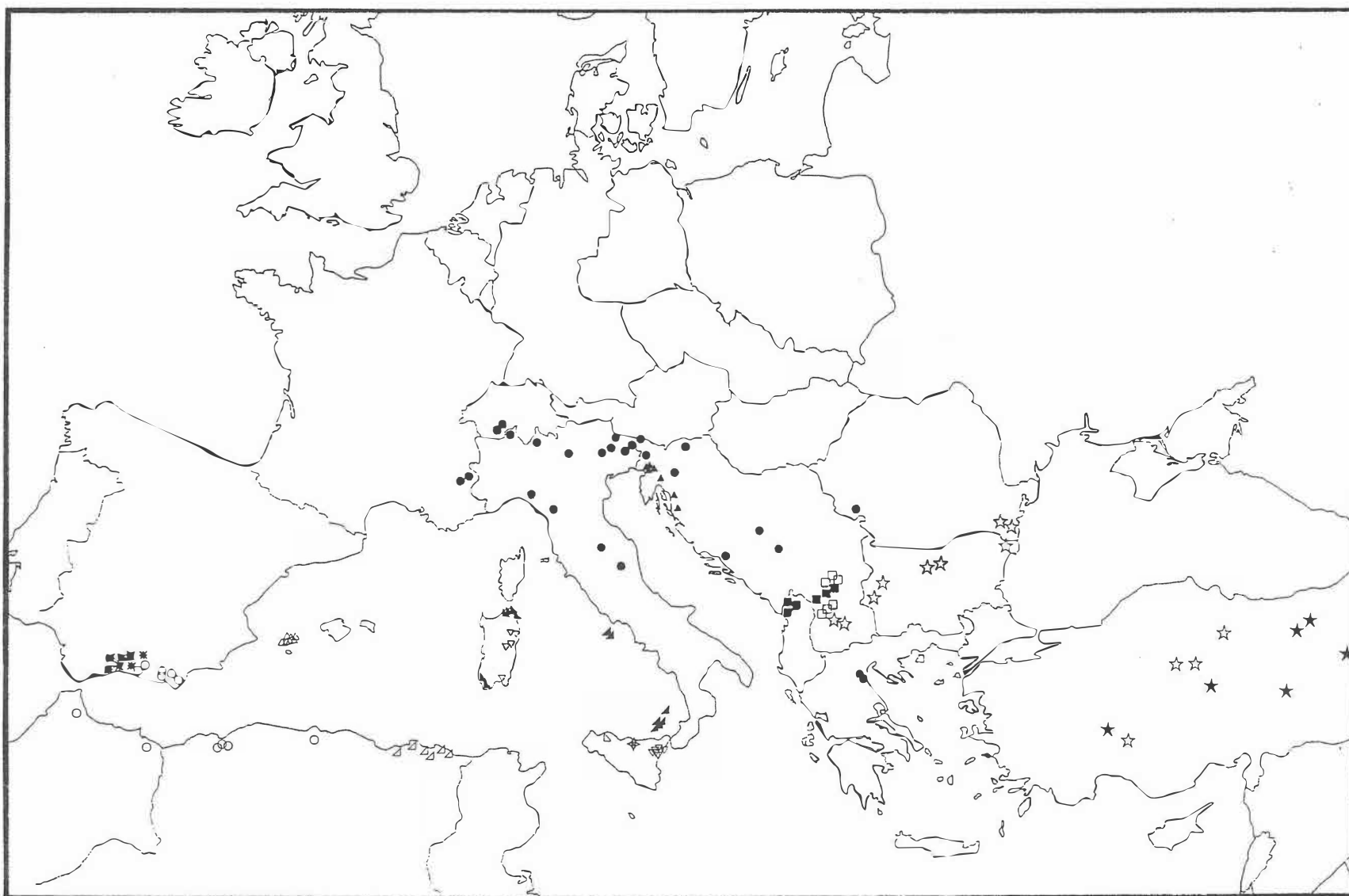


Fig. 1 - Geographical origin of the specimens studied of the taxa of *Genista* sect. *Spartocarpus*: ▽ *G. aetnensis*; ★ *G. aucheri*; ◆ *G. cilentina*; △ *G. dorycnifolia*; ▲ *G. ephedroides*; ▴ *G. gasparrinii*; ✱ *G. haenseleri*; ■ *G. hassertiana*; ▼ *G. holopetala*; □ *G. nissana*; ▷ *G. numidica*; ● *G. radiata*; ☆ *G. sessilifolia*; ○ *G. spartioides*; ▲ *G. thyrrena*.

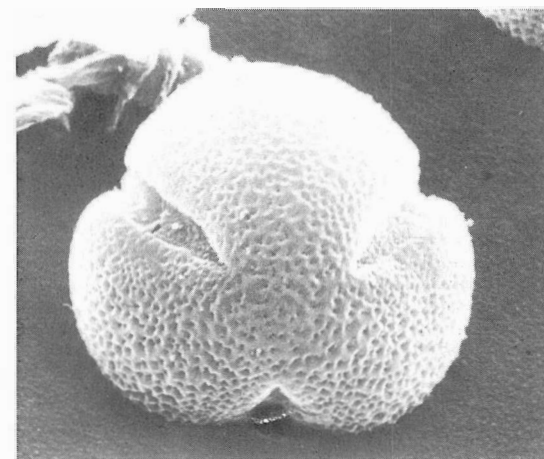
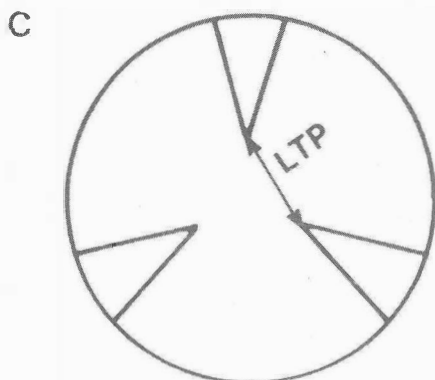
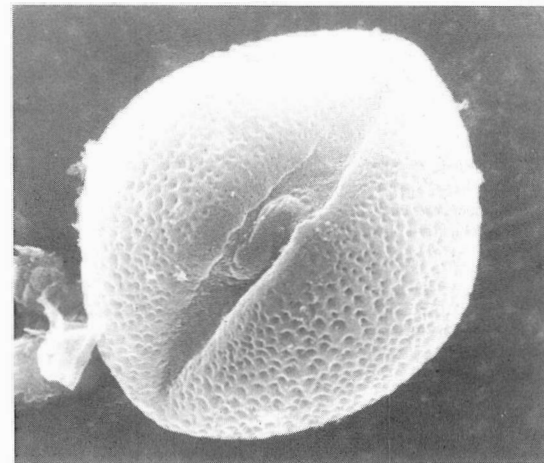
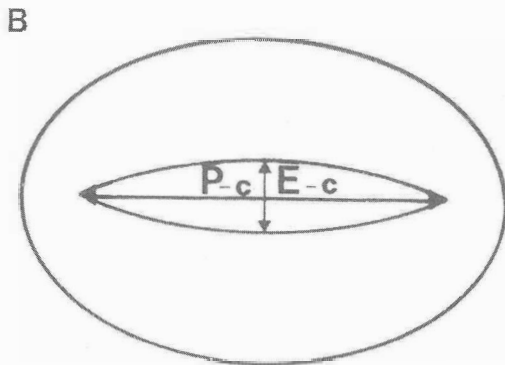
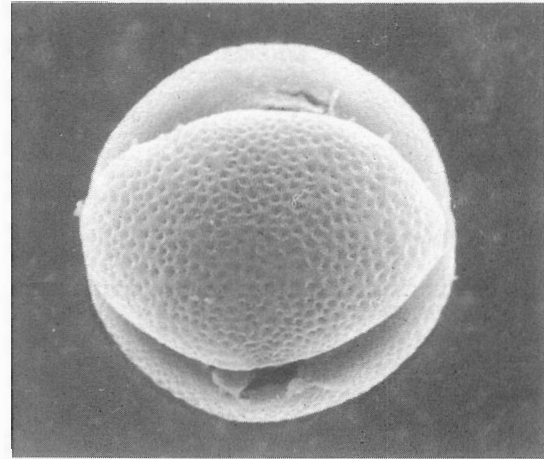
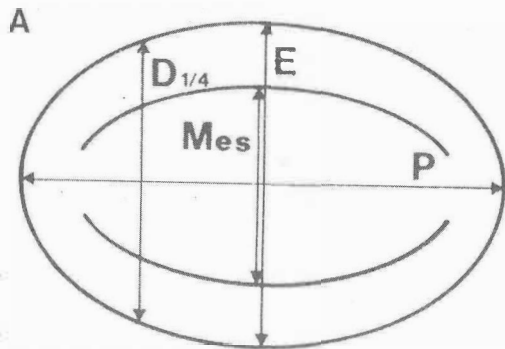


Plate 1 - Diagram of pollen grain of *Genista* in equatorial (A,B) and polar (C) view and photographs by SEM of *G. hassertiana* and *G. holoptala* in equatorial view and of *G. aetnensis* in polar view (x 2,500).

Tab. 2 - Pollen characters in *Genista* sect. *Spartocarpus*. Means and standard deviations (μm) of quantitative characters and average frequencies of qualitative character states by LM and SEM are given.

	<i>G. radiata</i>	<i>G. holopetala</i>	<i>G. hassertiana</i>	<i>G. sessilifolia</i>	<i>G. nissana</i>	<i>G. aucheri</i>	<i>G. spartioides</i>	<i>G. haenseleri</i>
QUANTITATIVE CHARACTERS (LM)								
P	25.3 ± 1.51	23.9 ± 1.10	22.1 ± 1.64	29.8 ± 3.12	27.6 ± 1.48	29.0 ± 1.50	26.7 ± 1.09	26.3 ± 1.68
E	22.0 ± 1.45	21.8 ± 1.00	20.6 ± 0.85	26.6 ± 2.55	26.5 ± 1.74	26.0 ± 1.45	24.4 ± 1.19	25.3 ± 0.84
D	15.3 ± 1.55	14.9 ± 0.86	14.2 ± 0.55	18.2 ± 1.61	17.6 ± 1.17	20.9 ± 1.64	19.2 ± 0.79	19.8 ± 0.72
P-colpus	23.2 ± 1.45	22.1 ± 1.08	19.9 ± 1.23	26.9 ± 2.86	25.1 ± 1.32	23.6 ± 1.63	22.6 ± 0.84	22.7 ± 1.92
E-colpus	1.7 ± 0.16	1.7 ± 0.05	1.8 ± 0.08	1.8 ± 0.08	1.7 ± 0.07	2.8 ± 0.10	1.6 ± 0.05	2.4 ± 0.45
Mes	14.3 ± 1.41	15.0 ± 1.50	13.8 ± 0.69	18.2 ± 2.31	18.4 ± 1.53	18.9 ± 1.92	17.6 ± 1.50	18.6 ± 1.29
LTP	5.8 ± 0.67	5.2 ± 0.28	5.4 ± 0.57	5.4 ± 0.72	5.3 ± 0.30	5.1 ± 0.72	5.0 ± 0.76	4.7 ± 0.65
ExE	1.8 ± 0.10	1.7 ± 0.06	1.8 ± 0.08	1.8 ± 0.04	1.7 ± 0.05	2.1 ± 0.14	1.9 ± 0.01	1.9 ± 0.15
P/E	1.1 ± 0.07	1.1 ± 0.06	1.1 ± 1.04	1.1 ± 0.12	1.0 ± 0.02	1.1 ± 0.07	1.1 ± 0.04	1.0 ± 0.07
E/D	1.4 ± 0.09	1.4 ± 0.14	1.5 ± 1.32	1.5 ± 0.05	1.5 ± 0.03	1.2 ± 0.04	1.3 ± 0.05	1.3 ± 0.04
P/P-colpus	1.1 ± 0.02	1.1 ± 0.02	1.1 ± 1.25	1.1 ± 0.02	1.1 ± 0.01	1.2 ± 0.03	1.2 ± 0.04	1.2 ± 0.03
LTP/E	0.2 ± 0.05	0.2 ± 0.02	0.3 ± 0.22	0.2 ± 0.03	0.2 ± 0.01	0.2 ± 0.02	0.2 ± 0.03	0.2 ± 0.02
ExE/E	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.010	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01
QUALITATIVE CHARACTERS (LM)								
Amb								
peritreme	31.8	26.0	11.2	38.1	36.5	52.8	23.8	31.9
goniotreme	4.2	2.4	0.0	4.8	0.0	3.2	13.3	8.1
ptychotreme	26.9	32.6	39.5	12.5	15.0	2.2	4.5	0.9
perigoniotreme	11.4	16.0	10.0	17.2	18.5	34.0	45.1	48.1
periptychotreme	25.7	23.0	39.3	27.4	30.0	7.8	13.3	11.0
Furrows in face view								
rectangular	59.9	58.9	55.7	55.8	70.6	36.7	19.0	21.8
fusiform	0.9	1.8	1.0	4.7	1.7	5.0	7.2	10.7
with an equatorial constriction	39.2	39.3	43.3	39.5	27.7	58.3	73.8	67.5
with straight margins	78.9	74.6	66.5	62.2	43.2	27.5	21.2	26.7
with wavy margins	21.1	25.4	33.5	37.8	56.8	72.5	78.8	73.3
Furrows in lateral view								
arcuate	76.9	57.1	57.3	52.8	45.0	48.7	38.8	38.3
angular	23.1	42.9	42.7	47.2	55.0	51.3	61.2	61.7
internal edge distinctly delimited	12.8	1.3	3.3	28.4	8.8	76.5	76.9	87.3
internal edge indistinctly delimited	87.2	98.7	96.7	71.6	91.2	23.5	23.1	12.7
Relative length of thickenings at the end of the furrows								
< 1/4	14.3	11.5	17.8	44.3	25.5	14.0	15.2	6.6
= 1/4	34.9	37.1	44.5	23.3	25.5	14.5	24.2	22.3
> 1/4	50.8	51.4	37.7	32.4	49.0	71.5	60.6	71.1
QUALITATIVE CHARACTERS (SEM)								
Exine at mesocolpium								
suprareticulate pitted	74.1	92.0	85.0	76.0	87.5	70.0	81.5	96.0
with insulae	11.9	6.0	8.0	7.9	7.5	3.0	3.5	4.0
ridged	1.9	1.0	1.0	11.2	1.7	3.0	6.0	0.0
rugulate	9.9	1.0	5.0	1.0	3.3	9.0	0.0	0.0
grooved	1.4	0.0	1.0	0.8	0.0	5.0	0.0	0.0
smooth	0.8	0.0	0.0	3.1	0.0	10.0	9.0	0.0
tapered muri	67.4	75.9	71.9	57.9	84.2	65.0	71.9	71.0
rounded off muri	32.6	24.1	28.1	42.1	15.8	35.0	28.1	29.0
lumina with regular pits	65.6	36.0	40.0	76.8	58.4	52.0	44.5	27.0
lumina with irregular pits	7.3	28.0	15.0	5.0	10.0	16.0	21.0	31.0
lumina with more than one pits	4.5	21.0	18.0	4.7	10.8	5.0	2.5	2.0
lumina with joined pits	17.6	10.0	8.0	11.7	13.3	22.0	6.0	9.0
lumina with granular processes	5.0	5.0	19.0	1.8	7.5	5.0	26.0	31.0
Exine at apocolpium								
similar to exine at mesocolpium	80.3	75.0	81.0	69.0	72.5	89.0	82.0	83.0
with less raised reticulum	12.3	9.0	9.0	17.4	11.7	1.0	8.0	6.0
with reduced number of pits	7.2	16.0	10.0	13.6	15.8	10.0	10.0	7.0
with increased number of pits	0.2	0.0	0.0	0.0	0.0	0.0	0.0	4.0
Exine at furrow margin								
similar to exine at mesocolpium	14.0	20.0	0.0	0.0	18.0	12.0	15.0	14.0
more finely reticulate	67.0	40.0	80.0	15.0	35.0	57.0	55.0	43.0
with margo	19.0	40.0	20.0	85.0	47.0	31.0	30.0	43.0
with reduced number of pits	33.0	40.0	40.0	93.0	75.0	46.0	47.0	57.0
with increased number of pits	67.0	60.0	60.0	7.0	25.0	54.0	53.0	43.0
Furrow membrane								
smooth	8.0	0.0	14.1	12.6	0.0	19.8	20.6	0.0
microgranular	28.6	39.2	18.2	62.8	99.0	60.1	48.7	40.1
granular	48.6	59.8	59.6	10.8	1.0	0.0	20.6	59.9
warty	14.8	1.0	8.1	13.8	0.0	20.1	10.1	0.0
Number of pits at mesocolpium . μm^{-2}								
0.8 - 1.6	17.4	40.0	-	22.2	-	-	-	-
1.7 - 2.4	26.0	60.0	20.0	55.6	33.3	1.0	66.0	100.0
2.5 - 3.2	26.0	-	20.0	22.2	50.0	99.0	3.0	-
3.3 - 4.1	26.0	-	60.0	-	16.7	-	1.0	-
4.2 - 4.9	4.6	-	-	-	-	-	30.0	-

- Systematics of *Genista* sect. *Spartocarpus* -

	<i>G. numidica</i>	<i>G. dorycnifolia</i>	<i>G. aetnensis</i>	<i>G. ephedroides</i>	<i>G. thyrrena</i>	<i>G. gasparrinii</i>	<i>G. cilentina</i>
QUANTITATIVE CHARACTERS (LM)							
P	27.2 ± 1.93	23.2 ± 1.67	24.1 ± 2.45	24.8 ± 2.13	24.7 ± 0.98	24.0 ± 2.12	22.9 ± 2.12
E	24.1 ± 1.47	23.4 ± 0.83	23.7 ± 1.26	23.4 ± 0.52	23.7 ± 1.14	22.8 ± 0.84	23.7 ± 0.84
D	19.5 ± 1.56	18.2 ± 0.90	17.8 ± 1.57	17.6 ± 0.23	18.1 ± 1.00	16.8 ± 0.92	17.7 ± 0.92
P-colpus	24.0 ± 0.99	19.4 ± 1.91	19.3 ± 2.06	19.5 ± 1.23	19.9 ± 0.78	19.5 ± 2.11	17.9 ± 2.11
E-colpus	2.9 ± 0.45	2.8 ± 0.15	2.0 ± 0.45	1.7 ± 0.05	1.7 ± 0.25	1.8 ± 0.25	1.8 ± 0.07
Mes	18.5 ± 2.22	17.4 ± 0.93	15.9 ± 1.47	15.2 ± 1.32	15.3 ± 1.32	17.1 ± 0.34	15.6 ± 0.34
LTP	5.4 ± 0.84	4.5 ± 0.44	5.7 ± 1.18	5.3 ± 0.42	5.4 ± 0.62	5.3 ± 0.80	5.7 ± 0.80
ExE	2.0 ± 0.15	1.9 ± 0.45	1.9 ± 0.01	1.8 ± 0.15	1.8 ± 0.05	1.9 ± 0.14	1.7 ± 0.05
P/E	1.1 ± 0.14	1.0 ± 0.06	1.0 ± 0.07	1.0 ± 0.08	1.0 ± 0.03	1.06 ± 0.03	0.96 ± 0.03
E/D	1.2 ± 0.08	1.3 ± 0.05	1.3 ± 0.10	1.3 ± 0.03	1.3 ± 0.02	1.34 ± 0.01	1.33 ± 0.01
P/P-colpus	1.1 ± 0.01	1.2 ± 0.03	1.2 ± 0.04	1.2 ± 0.03	1.2 ± 0.03	1.22 ± 0.01	1.27 ± 0.01
LTP/E	0.2 ± 0.04	0.2 ± 0.02	0.2 ± 0.04	0.2 ± 0.02	0.2 ± 0.03	0.22 ± 0.01	0.23 ± 0.01
ExE/E	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.08 ± 0.01	0.1 ± 0.01	0.08 ± 0.02	0.07 ± 0.02
QUALITATIVE CHARACTERS (LM)							
Amb							
peritreme	38.3	38.0	14.0	9.8	15.9	0.0	17.0
goniotreme	12.5	11.6	6.1	22.2	18.9	53.0	20.0
ptychotreme	5.5	1.9	7.9	0.5	1.7	0.0	0.0
perigoniotreme	32.7	42.0	48.7	57.2	49.2	47.0	53.0
periptychotreme	11.0	6.5	23.3	10.3	14.3	0.0	10.0
Furrows in face view							
rectangular	26.5	31.1	29.0	10.0	19.1	10.0	27.0
fusiform	10.7	7.3	5.7	4.3	3.7	0.0	0.0
with an equatorial constriction	62.8	61.6	65.3	85.7	77.2	90.0	53.0
with straight margins	23.3	38.7	19.8	1.3	2.3	0.0	0.0
with wavy margins	76.7	61.3	80.2	98.7	97.7	99.0	99.0
Furrows in lateral view							
arcuate	43.7	26.7	58.8	26.2	39.3	49.0	73.0
angular	56.3	73.3	41.2	73.8	60.7	52.5	25.5
internal edge distinctly delimit	94.8	82.0	47.9	58.3	45.8	43.0	30.0
internal edge indistinctly delimit	5.2	18.0	52.1	41.7	54.1	57.0	70.0
Relative length of thickenings at the end of the furrows							
< 1/4	33.3	16.6	32.4	12.8	4.6	0.0	23.0
= 1/4	31.7	18.4	24.4	20.5	26.4	23.0	50.0
> 1/4	35.0	65.0	43.2	66.7	69.0	77.0	27.0
QUALITATIVE CHARACTERS (SEM)							
Exine at mesocolpium							
suprareticulate pitted	95.0	94.0	94.3	83.3	91.3	95.0	95.0
with insulae	5.0	5.0	5.7	10.0	8.7	5.0	5.0
ridged	0.0	0.0	0.0	0.0	0.0	0.0	0.0
rugulate	0.0	1.0	0.0	6.7	0.0	0.0	0.0
grooved	0.0	0.0	0.0	0.0	0.0	0.0	0.0
smooth	0.0	0.0	0.0	0.0	0.0	0.0	0.0
tapered muri	82.5	69.0	65.0	81.7	72.5	70.0	95.0
rounded off muri	17.5	31.0	35.0	18.3	27.5	30.0	5.0
lumina with regular pits	85.0	64.0	68.0	88.4	72.7	75.0	95.0
lumina with irregular pits	10.0	10.0	12.5	3.3	8.7	15.0	5.0
lumina with more than one pit	2.5	8.0	10.0	0.0	1.2	5.0	0.0
lumina with joined pits	0.0	12.0	6.3	8.3	8.7	0.0	0.0
lumina with granular processa	2.5	6.0	3.2	0.0	8.7	5.0	0.0
Exine at apocolpium							
similar to exine at mesocolpiu	77.5	73.0	87.4	55.0	80.1	60.0	93.0
with less raised reticulum	12.5	5.0	6.9	20.0	7.5	20.0	5.0
with reduced number of pits	10.0	22.0	5.7	25.0	11.2	20.0	2.0
with increased number of pits	0.0	0.0	0.0	0.0	1.2	0.0	0.0
Exine at furrow margin							
similar to exine at mesocolpiu	0.0	5.0	10.0	0.0	0.0	0.0	0.0
more finely reticulate	45.0	5.0	62.0	65.0	25.0	36.0	70.0
with margo	55.0	90.0	28.0	35.0	75.0	64.0	30.0
with reduced number of pits	60.0	90.0	66.0	35.0	75.0	74.0	20.0
with increased number of pits	40.0	10.0	44.0	65.0	25.0	26.0	80.0
Furrow membrane							
smooth	0.0	19.8	0.0	0.0	0.0	0.0	0.0
microgranular	0.0	40.1	50.0	67.0	0.0	0.0	1.0
granular	94.9	40.1	50.0	33.0	95.0	90.0	99.0
warty	5.1	0.0	0.0	0.0	5.0	10.0	0.0
Number of pits at mesocolpium .µm⁻²							
0.8 - 1.6	43.0	-	-	-	-	-	-
1.7 - 2.4	57.0	67.0	13.0	67.0	33.0	60.0	33.3
2.5 - 3.2	-	17.0	49.0	33.0	67.0	40.0	66.7
3.3 - 4.1	-	16.0	13.0	-	-	-	-
4.2 - 4.9	-	-	25.0	-	-	-	-

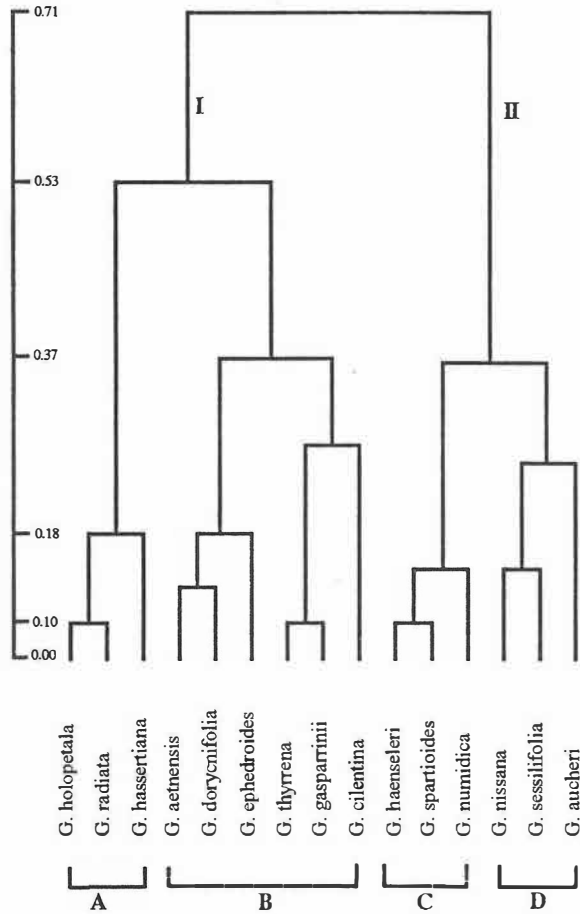


Fig. 2 - Dendrogram of the taxa of the sect. *Spartocarpus* based on the quantitative and qualitative pollen characters of Tab. 2.

C includes *G. haenseleri* and *G. spartioides*, which are very similar, and, a little separated, *G. numidica*; these are the western- and southernmost (north-western Africa) species of the section; D includes *G. nissana*, *G. sessilifolia* and, a little separated, *G. aucheri*, all taxa with an eastern distribution.

As regards quantitative pollen characters (see Tab. 2), the taxa in cluster II are characterised by larger dimensions of the polar axis (26.3-29.8 µm), of the equatorial diameter (24.1-26.6 µm) and of the width of *mesocolpium* (17.6-18.9 µm) in comparison with those of the taxa of cluster I (P: 22.1-25.3 µm; E: 20.6-23.7 µm; Mes: 13.8-17.4 µm). In cluster II *Genista haenseleri*, *G. spartioides* and *G. numidica* (subcluster C) are clearly distinguished from *G. nissana*, *G. sessilifolia* and *G. aucheri* (subcluster D) by the dimensions of the axes P ed E. The two subclusters of cluster I display even greater diversity: the width (E, D, Mes) and the ratios P/E, E/D, P/P-colpus

clearly distinguish *G. radiata*, *G. holopetala*, *G. hassertiana* (subcluster A) from *G. aetnensis*, *G. dorycnifolia*, *G. ephedroides*, *G. thyrrana*, *G. gasparrinii* and *G. cilentina* (subcluster B). Fig. 3a shows the ordination of the species based on the quantitative characters measured by LM. There is a clear separation, along the second principal axis, between the species of cluster I (subclusters A, B) and those of cluster II (subclusters C, D). Subclusters A and B are clearly separated along the third principal axis, while subclusters C and D are not so well characterized.

Tab. 3 shows the results of the comparison of the taxa according to the "t-test" of Student, carried out in order to assess the significance of the difference between averages of quantitative characters. The number of differential characters between the taxa (probability level 0.5) is reported. Among the four subclusters described on the basis of the dendrogram of Fig. 2, subcluster A seems to be the most heterogeneous: in particular three characters distinguish *Genista hassertiana* from *G. holopetala* and *G. radiata*. On the contrary, in subcluster D, no differential character distinguishes *G. nissana* and *G. sessilifolia*, while *G. aucheri* is distinguished from the others by one and two characters, respectively. Among the western species, *G. haenseleri*, *G. spartioides* and *G. numidica* (subcluster C) are remarkably

	A		D			C			B				
	<i>G. radiata</i>	<i>G. holopetala</i>	<i>G. hassertiana</i>	<i>G. sessilifolia</i>	<i>G. nissana</i>	<i>G. aucheri</i>	<i>G. spartioides</i>	<i>G. haenseleri</i>	<i>G. numidica</i>	<i>G. dorycnifolia</i>	<i>G. aetnensis</i>	<i>G. ephedroides</i>	<i>G. thyrrana</i>
<i>G. radiata</i>	X	2	3	5	5	5	5	4	4	6	3	3	3
<i>G. holopetala</i>		X	3	5	5	4	3	4	5	4	3	3	3
<i>G. hassertiana</i>			X	5	5	5	5	5	5	4	3	3	3
<i>G. sessilifolia</i>				X	0	2	3	3	2	4	3	3	3
<i>G. nissana</i>					X	1	3	2	2	4	3	3	4
<i>G. aucheri</i>						X	3	1	1	4	4	4	4
<i>G. spartioides</i>							X	0	1	3	3	3	3
<i>G. haenseleri</i>								X	0	4	3	3	3
<i>G. numidica</i>									X	3	3	2	2
<i>G. dorycnifolia</i>										X	1	1	1
<i>G. aetnensis</i>											X	0	0
<i>G. ephedroides</i>												X	0
<i>G. thyrrana</i>													X

Tab. 3 - Number of quantitative pollen characters discriminant at significant level between the taxa of the sect. *Spartocarpus* according to the "t-test" of Student (probability level: 0.5), with the exception of *G. gasparrinii* and *G. cilentina*. The subclusters A-D of the classification of fig. 2 are reported.

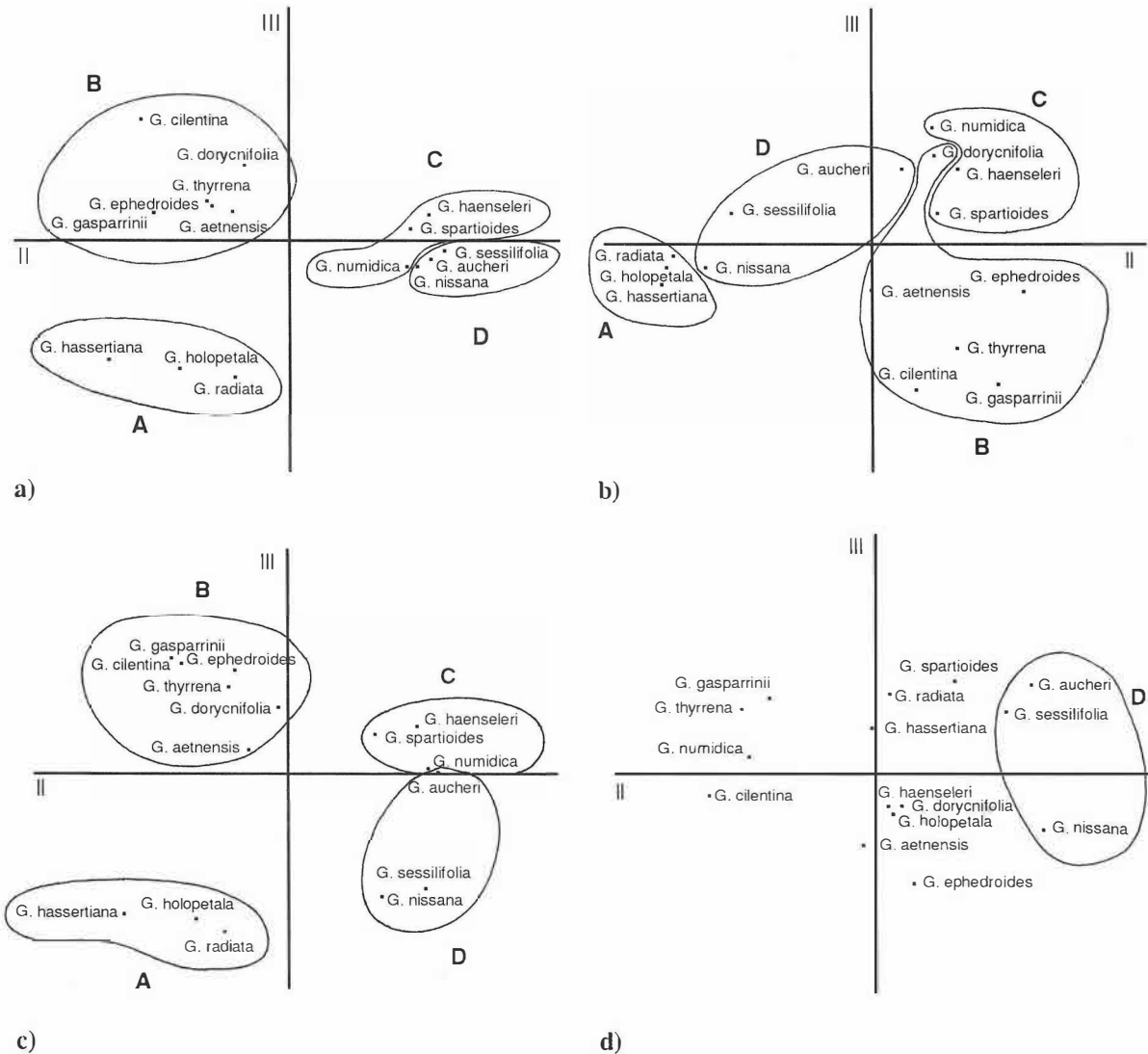


Fig. 3 - Ordinations of the taxa of the sect. *Spartocarpus* on the basis of: a) quantitative pollen characters analysed by LM; b) qualitative pollen characters analysed by LM; c) quantitative and qualitative pollen characters analysed by LM; d) qualitative pollen characters analysed by SEM.

homogeneous; only *G. numidica* has a single differential character towards *G. spartioides*. The other western species (subcluster B) are likewise considerably homogeneous: the Balearic endemic *G. dorycnifolia* is distinguished from the Tyrrhenian species *G. aetnensis*, *G. ephedroides* and *G. thyrrena* by a single character; none of these three species has any differential character with the others. The species of subcluster A display the greater diversity, particularly with respect to the eastern species of subcluster D, and to the western species of subcluster C.

The two main clusters in Fig. 2 are not

completely recognizable on the basis of qualitative characters examined by LM (see Tab. 2); there is no differential character separating them. On the contrary, a distinction is possible among some subclusters: the furrows distinguish subcluster C from D; subcluster A is distinguished from B, not only by the furrows, but by the amb too. *Genista radiata*, *G. holopetala* and *G. hassertiana* (subcluster A) in comparison with the other species of sect. *Spartocarpus*, show a higher percentage of ptychotreme grains and furrows with straight margins. The above mentioned distinctions are recognizable in the ordination of the taxa of sect.

Spartocarpus based on qualitative characters examined by LM (Fig. 3b).

Fig. 3c shows the ordination of the species based on all characters, both quantitative and qualitative, examined by LM. The characterization of the four subclusters is here more precise than in the ordinations of Figs. 3a, b; subclusters C and D, still not so well recognizable through the analysis of quantitative characters alone, are here better characterized.

The exine sculpture observed by SEM shows a certain variation both within species and within clusters: a cluster is rarely distinguishable on the basis of the exine characters examined by SEM at *mesocolpium* (Plate 2), at *apocolpium* and at the margins of the furrows (Plate 3). Anyway, single species may show a higher frequency of certain characters without being clearly characterized by this. Fig. 3d shows the ordination of the species based on the characters of the exine as examined by SEM. Only subcluster D is characterized clearly enough, even though its species are not very close.

Fig. 4 shows the ordination, based on all characters, both qualitative and quantitative, examined by LM and SEM, and the overimposed MST of the taxa. The four subclusters, already recognizable in the dendrogram of Fig. 2 and in the ordinations of Fig. 3 are even better characterized in the ordination of Fig. 4. The second axis separates the species of subclusters A and B, on the right, from those of subclusters C and D, on the left. The third axis separates the eastern species with capitate inflorescence (subcluster A) from the Tyrrhenian and the Balearic ones (subcluster B), and the eastern taxa with long racemes (subcluster D) from the Spanish and north-African ones (subcluster C). Subcluster A is the most isolated, having the lowest similarity coefficients towards the others. *G. dorycnifolia*, a Balearic endemic, links subclusters B and C. It is interesting to observe that *G. numidica* is closer to *G. haenseleri* and *G. spartioides* (subcluster C) than to *G. ephedroides*, *G. thyrena*, *G. gasparrinii* and *G. cilentina* (subcluster B). *G. aucheri* is a link between subclusters C and D.

Different groups of populations of *Genista radiata*, *G. sessilifolia*, *G. spartioides* and *G. aetnensis* were studied separately (Tab. 4). These species have such a range disjunction and/or such a high morphological variability as to induce some authors to propose the creation of infraspecific taxa.

Fig. 5 shows the ordination, with MST overimposed, of the taxa, on the basis of all

qualitative and quantitative characters, taking into account the various groups of populations (see Tabs. 2, 4).

As regards *Genista radiata*, the populations of the more eastern var. *radiata* and those of the more western var. *sericopetala* have been examined. The two varieties, although separated on pollen characters, show a close affinity.

As for *Genista sessilifolia*, three different groups of populations have been examined: the populations of the region of Dobruja in Romania (ssp. *romanica* sensu Gibbs), the populations of Bulgaria and of Makedonija, and those of Turkey. The three groups of populations are distinct, more or less equidistant and with a medium pollen affinity.

As regards *Genista spartioides*, populations of southern Spain and north-western Africa have been examined separately. Although they show a close affinity, they turned out to be distinct on the basis of pollen characters.

Sardinian and Sicilian populations of *Genista aetnensis* have been examined separately. The two groups of populations turned out to be very different on the basis of pollen characters. The Sardinian populations show their closest affinity with the taxa of *G. ephedroides* complex through *G. thyrena*; the Sicilian populations are more isolated, though still linked to *G. ephedroides*; the two groups of populations have a low coefficient of similarity.

Discussion

Genista radiata, *G. holopetala* and *G. hassertiana* (subcluster A), a group with centre of distribution in the east-Alpine Balkan area, are rather similar on the basis of the pollen characters (see Figs. 2-5). They display both a remarkable morphological similarity - opposite branches, trifoliolate opposite leaves, capitate inflorescence (Spach 1844; Buchegger 1912; Fukarek 1964; Pignatti 1982) - and a karyological homogeneity: $2n = 48$ in *G. radiata* var. *radiata* (Cusma Velari & Feoli Chiapella 1987a) and in *G. holopetala* (Cusma Velari & Feoli Chiapella 1987b), $2n = 96$ in *G. radiata* var. *sericopetala* (Zickler 1968; Cusma Velari & Feoli Chiapella 1987a; Verlaque *et al.* 1987). These species are the only ones in the section displaying a capitate inflorescence and therefore are grouped by Mayer (1970) in the series "Capitati" of *Cytisanthus*. Their cluster based on pollen characters is the most isolated.

All the other species of the section have

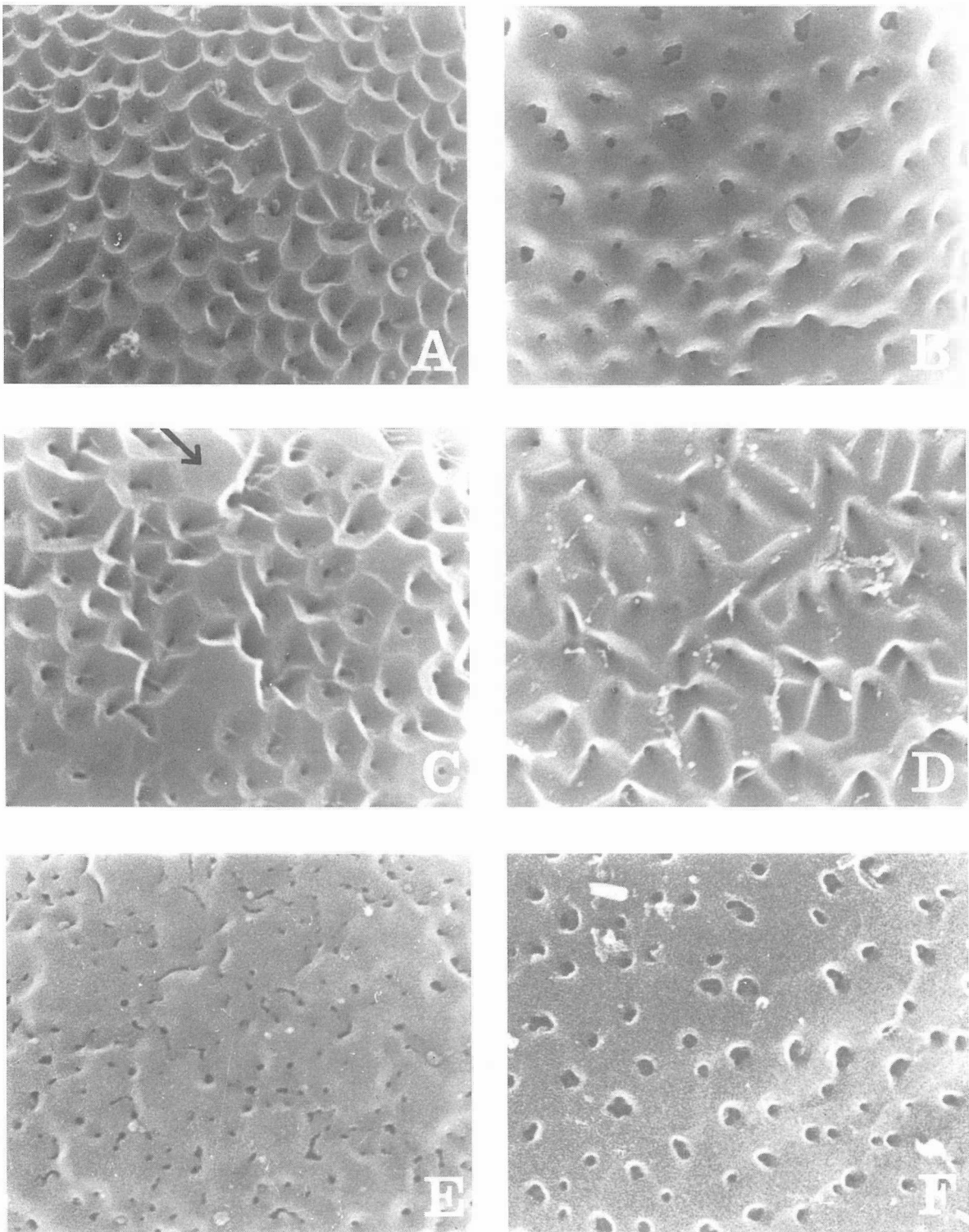


Plate 2 - Exine sculpture of the pollen of the taxa of *Genista* sect. *Spartocarpus* analysed by SEM ($\times 10,000$) at *mesocolpium*. A - suprareticulate pitted exine, tapered *muri*, *lumina* with regular pits (*G. numidica*); B - suprareticulate pitted exine, rounded off *muri*, *lumina* with irregular pits (*G. aetnensis*); C - exine with *insulae*, arrowed (*G. thyrrana*); D - ridged exine (*G. sessilifolia*); E - rugulate exine (*G. ephedroides*); F - smooth exine (*G. spartioides*).

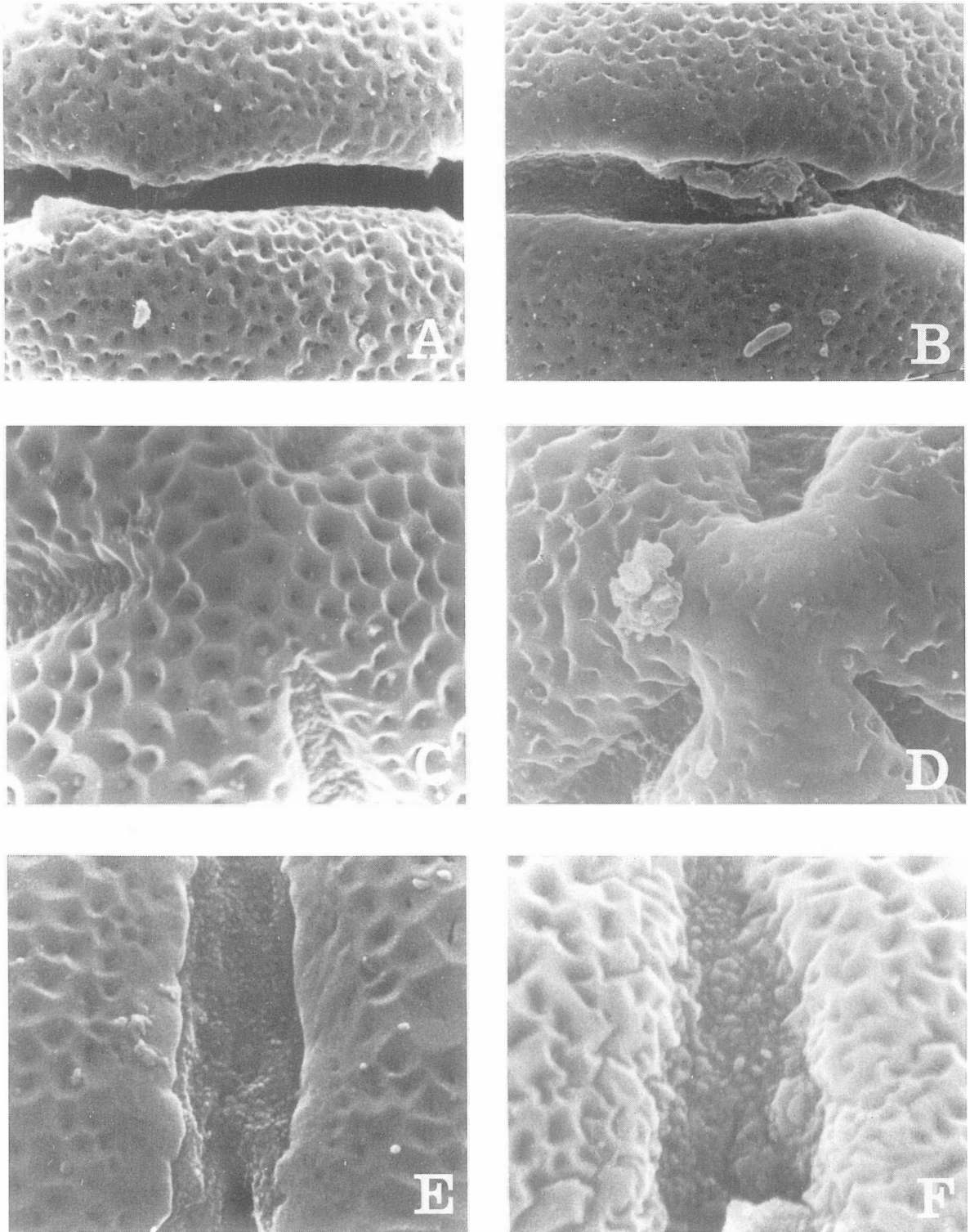


Plate 3 - Exine sculpture of the pollen of the taxa of *Genista* sect. *Spartocarpus* analysed by SEM at furrow margin (A, B) and at apocolpium (C, D); furrow membrane (E, F). A - exine similar to exine at mesocolpium (*G. holopetala* - x 5,000); B - with margo (*G. dorycnifolia* - x 5,000); C - exine similar to exine at mesocolpium (*G. haenseleri* - x 10,000); D - with less raised reticulum (*G. radiata* - x 10,000); E - microgranular furrow membrane (*G. nissana* - x 10,000); F - warty furrow membrane (*G. aucheri* - x 10,000).

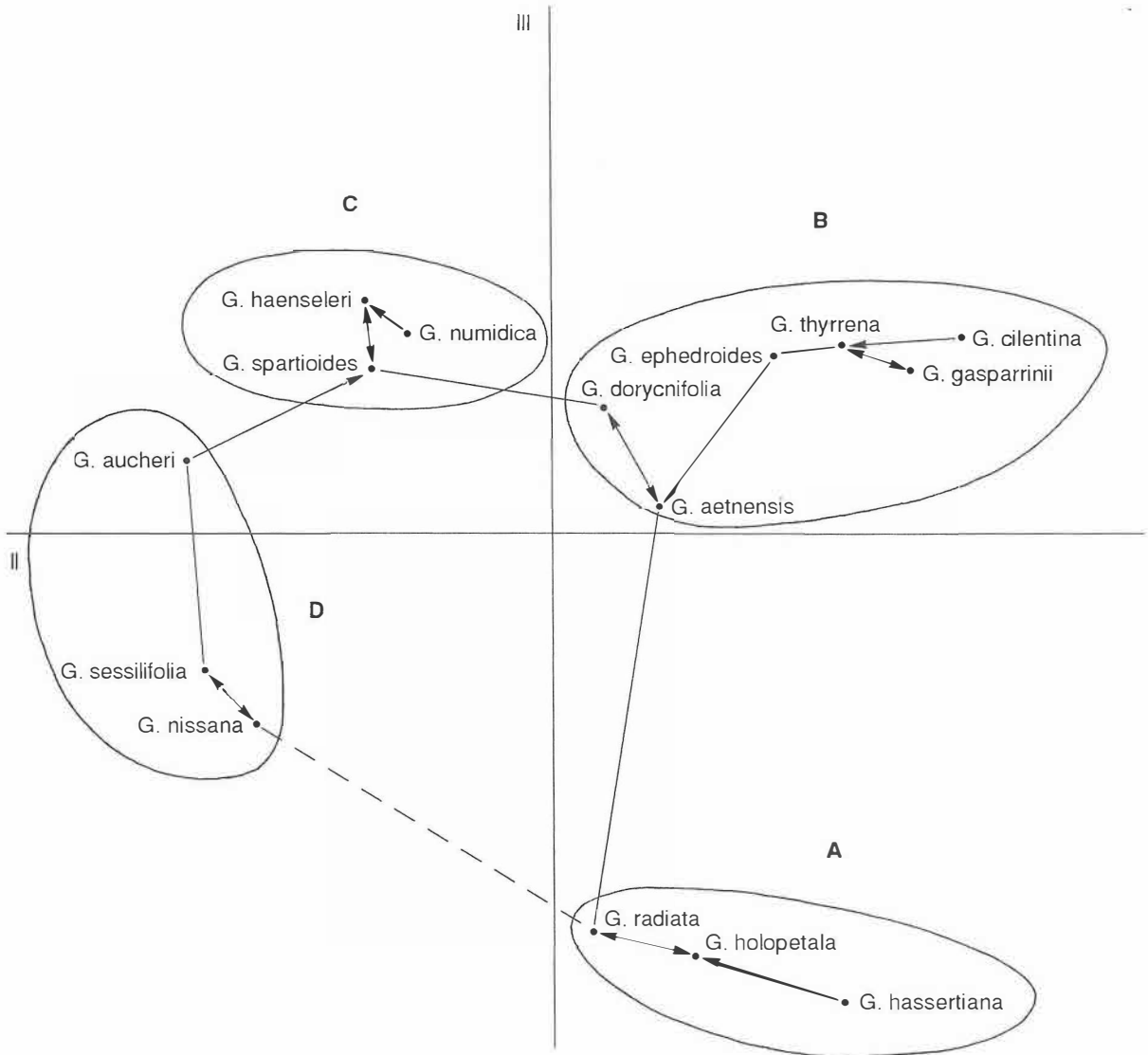


Fig. 4 - Ordination and minimum spanning tree of the taxa of the sect. *Spartocarpus* on the basis of the quantitative and qualitative pollen characters of Tab. 2.

diversified racemous inflorescences. These species can be grouped in three subclusters (B, C, D) on the basis of pollen characters (see Figs. 2-5). They also differ in distribution and in morphological characters.

Subcluster D comprises *Genista sessilifolia*, *G. nissana* and, even if more separated, *G. aucheri*, distributed in the central and southern Balkans and in Anatolia. They are homogeneous, both morphologically (subopposite or alternate branches, trifoliolate, alternate and subopposite leaves, long racemes) and palynologically. The first two species were included by Mayer (1970) in series "Racemosi" of *Cytisanthus*. As for *G. sessilifolia*,

the pollen analysis seems to confirm the existence of ssp. *romanica* sensu Gibbs, limited to the Rumanian populations. Inside ssp. *sessilifolia* sensu Gibbs, it might be more correct to separate the Turkish populations [corresponding to ssp. *sessilifolia* sensu Greuter *et al.* (1989)] from the European ones. These would correspond to *G. trifoliolata* p.p. [= *G. sessilifolia* subsp. *romanica* sensu Greuter *et al.* (1989) p.p.], *i.e.* limited to the European populations, those from Romania excluded. *G. aucheri*, an Anatolian endemic, with interrupted racemes and opposite flowers, is intermediate between *G. sessilifolia* (subcluster D), that also has similar morphological characters and

Tab. 4 - Pollen characters in different groups of populations of *Genista radiata*, *G. sessilifolia*, *G. spartioides* and *G. aetnensis*. Means and standard deviations (μm) of quantitative characters and average frequencies of qualitative character states by LM and SEM are given.

	<i>G. radiata</i> var. <i>radiata</i>	<i>G. radiata</i> var. <i>sericopetala</i>	<i>G. sessilifolia</i> ssp. <i>romanica</i>	<i>G. sessilifolia</i> ssp. <i>sessilifolia</i> (Europe)	<i>G. sessilifolia</i> ssp. <i>sessilifolia</i> (Turkey)	<i>G. spartioides</i> (Spain)	<i>G. spartioides</i> (Africa)	<i>G. aetnensis</i> (Sicily)	<i>G. aetnensis</i> (Sardinia)
QUANTITATIVE CHARACTERS (LM)									
P	25.0 ± 1.37	26.3 ± 1.68	32.5 ± 1.20	28.1 ± 2.25	31.5 ± 3.52	27.0 ± 1.54	26.4 ± 0.47	25.5 ± 2.02	22.0 ± 1.76
E	21.8 ± 1.29	22.9 ± 1.82	31.0 ± 0.78	26.3 ± 2.20	24.9 ± 1.10	24.4 ± 1.66	24.4 ± 0.82	24.3 ± 1.19	22.9 ± 1.04
D	15.1 ± 1.36	15.9 ± 2.10	20.5 ± 0.71	17.7 ± 1.46	17.8 ± 1.35	19.6 ± 0.70	18.9 ± 0.87	18.4 ± 1.60	16.9 ± 1.37
P-colpus	23.0 ± 1.39	24.0 ± 1.57	29.4 ± 1.13	25.4 ± 2.16	28.3 ± 3.71	22.7 ± 1.11	22.6 ± 0.88	20.3 ± 1.88	17.8 ± 1.67
E-colpus	1.7 ± 0.15	1.8 ± 0.16	1.8 ± 0.07	1.8 ± 0.08	1.9 ± 0.05	1.7 ± 0.01	1.6 ± 0.01	1.7 ± 0.01	2.3 ± 0.64
Mes	14.0 ± 1.38	15.4 ± 1.21	22.0 ± 1.84	18.1 ± 1.63	16.5 ± 1.58	17.3 ± 1.34	17.9 ± 1.84	15.6 ± 1.38	16.4 ± 1.79
LTP	5.8 ± 0.59	5.8 ± 0.95	5.5 ± 0.49	5.6 ± 0.88	4.8 ± 0.20	5.0 ± 0.95	4.9 ± 0.71	6.5 ± 0.37	4.6 ± 1.11
ExE	1.8 ± 0.11	1.7 ± 0.07	1.8 ± 0.01	1.8 ± 0.06	1.8 ± 0.01	1.9 ± 0.01	1.9 ± 0.01	1.9 ± 0.01	1.9 ± 0.01
P/E	1.1 ± 0.08	1.1 ± 0.04	1.0 ± 0.06	1.1 ± 0.05	1.3 ± 0.13	1.1 ± 0.04	1.1 ± 0.04	1.04 ± 0.07	1.0 ± 0.07
E/D	1.5 ± 0.09	1.5 ± 0.08	1.5 ± 0.02	1.5 ± 0.03	1.4 ± 0.06	1.2 ± 0.07	1.3 ± 0.04	1.32 ± 0.10	1.4 ± 0.12
P/P-colpus	1.1 ± 0.05	1.1 ± 0.02	1.1 ± 0.01	1.1 ± 0.02	1.1 ± 0.01	1.2 ± 0.04	1.2 ± 0.03	1.25 ± 0.04	1.2 ± 0.05
LTP/E	0.3 ± 0.04	0.2 ± 0.04	0.2 ± 0.01	0.2 ± 0.04	0.2 ± 0.01	0.2 ± 0.04	0.2 ± 0.03	0.26 ± 0.02	0.2 ± 0.05
ExE/E	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.07 ± 0.01	0.1 ± 0.01
QUALITATIVE CHARACTERS (LM)									
Amb									
peritreme	24.6	62.0	30.0	47.7	25.0	30.5	0.7	0.2	28.8
goniostreme	5.0	0.0	5.0	0.1	0.3	0.3	0.8	0.2	0.4
ptychostreme	28.3	0.9	5.0	10.0	0.8	0.3	0.0	0.5	0.0
perigonostreme	0.5	0.3	0.5	0.8	0.7	42.5	47.8	45.2	53.8
periptychostreme	29.5	0.4	48.5	0.8	28.4	11.0	0.6	33.3	0.3
Furrows in face view									
rectangular	58.6	65.2	72.0	47.8	61.5	0.6	1.0	37.1	0.6
fusiform	0.0	0.0	0.0	0.2	5.0	0.2	0.4	0.4	2.0
with an equatorial constriction	40.6	33.4	26.5	46.7	33.5	80.8	66.8	53.7	82.4
with straight margins	78.9	78.6	78.5	60.3	57.5	0.8	0.9	0.7	26.6
with wavy margins	0.9	0.9	0.9	39.7	42.5	80.3	77.3	83.7	73.4
Furrows in lateral view									
arcuate	76.8	77.2	73.0	45.9	54.8	34.3	43.2	68.6	44.2
angular	1.0	0.9	27.0	54.1	45.2	65.7	56.8	31.4	55.8
internal edge distinctly delimited	0.6	0.3	35.0	0.2	67.3	78.8	75.2	36.1	68.6
internal edge indistinctly delimited	85.9	92.8	65.0	95.7	32.7	0.9	24.8	63.9	31.4
Relative length of thickenings at the end of the furrows									
< 1/4	0.7	0.1	75.0	27.0	59.2	0.7	0.5	56.3	2.0
= 1/4	31.4	49.4	1.0	27.6	0.6	0.8	38.8	29.0	0.5
> 1/4	51.4	48.4	0.0	45.4	25.0	62.8	58.5	0.6	85.8
QUALITATIVE CHARACTERS (SEM)									
Exine at mesocolpium									
suprareticulate pitted	78.1	57.4	79.0	78.0	71.0	78.0	84.8	94.7	93.7
with insulae	0.3	30.2	0.3	8.0	0.3	2.0	0.2	0.2	0.3
ridged	0.0	2.0	0.5	12.0	0.4	2.0	10.0	0.0	0.0
rugulate	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
grooved	0.4	0.3	0.0	2.0	0.0	0.0	0.0	0.0	0.0
smooth	0.0	4.0	0.0	0.0	9.0	18.0	0.0	0.0	0.0
tapered muri	65.8	74.0	60.0	51.9	67.5	85.9	58.1	70.0	60.0
rounded off muri	34.2	26.0	40.0	48.1	32.5	0.6	41.9	30.0	40.0
lumina with regular pits	65.8	66.2	70.0	79.0	76.2	74.0	15.0	56.2	80.0
lumina with irregular pits	0.3	11.0	0.1	5.0	0.3	7.0	35.0	20.0	5.0
lumina with more than one pit	0.2	5.0	10.0	3.0	5.0	2.0	3.0	10.0	10.0
lumina with joined pits	0.7	0.6	0.5	11.0	0.5	6.0	6.0	0.3	5.0
lumina with granular processes	0.2	0.1	5.0	2.0	0.0	11.0	41.0	0.3	0.0
Exine at apocolpium									
similar to exine at mesocolpium	82.7	71.5	75.0	66.0	71.2	85.0	79.0	94.9	70.0
with less raised reticulum	0.4	21.0	15.0	18.0	0.7	7.0	9.0	0.1	10.0
with reduced number of pits	0.3	0.3	10.0	16.0	0.5	8.0	12.0	0.0	10.0
with increased number of pits	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Exine at furrow margin									
similar to exine at mesocolpium	0.5	16.0	0.0	0.0	0.0	17.0	13.0	20.0	0.0
more finely reticulate	66.7	68.0	25.0	0.1	25.7	50.0	60.0	70.0	55.0
with margo	0.8	16.0	75.0	97.5	74.3	33.0	27.0	10.0	45.0
with reduced number of pits	27.6	50.0	92.0	94.3	91.9	50.0	44.0	57.0	75.0
with increased number of pits	72.4	50.0	8.0	0.2	0.3	50.0	56.0	63.0	25.0
Furrow membrane									
smooth	0.2	18.0	0.0	16.0	0.5	0.8	0.8	0.0	0.0
microgranular	35.5	0.0	50.0	60.2	75.0	60.4	39.6	99.0	1.0
granular	41.0	76.0	0.0	0.8	0.0	0.0	39.6	1.0	99.0
warty	18.0	6.0	50.0	4.0	0.5	0.8	0.0	0.0	0.0
Number of pits at mesocolpium · μm^{-2}									
0.8 - 1.6	0.8	0.5	33.3	1.0	0.6	-	-	0.0	25.0
1.7 - 2.4	27.2	0.9	33.4	66.1	53.6	69.0	63.0	0.0	0.0
2.5 - 3.2	1.0	33.0	33.3	10.0	31.9	6.0	-	0.0	50.0
3.3 - 4.1	27.2	0.9	-	-	-	2.0	-	50.0	25.0
4.2 - 4.9	0.1	0.5	-	-	-	23.0	37.0	50.0	0.0

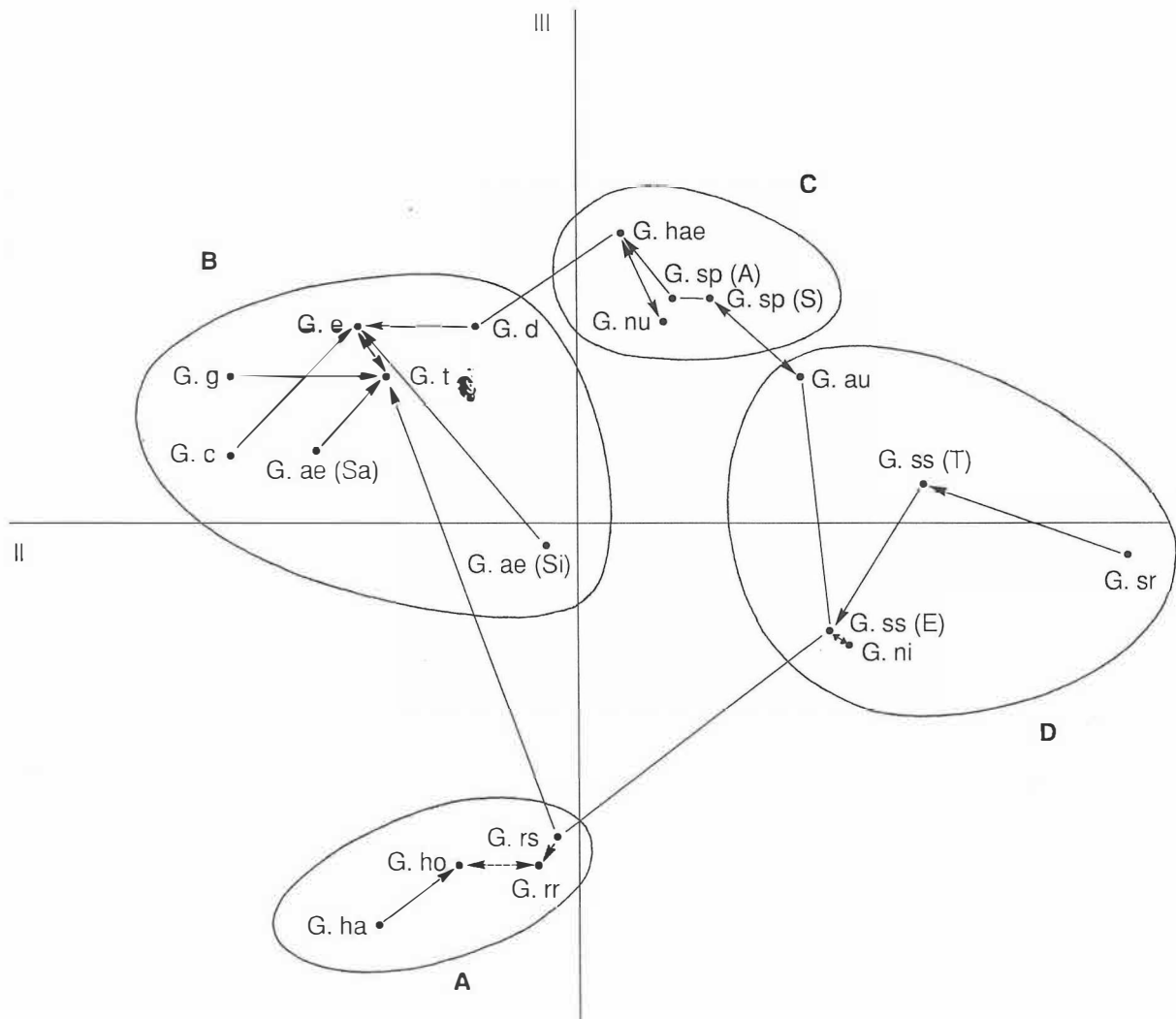


Fig. 5 - Ordination and minimum spanning tree of the taxa of the sect. *Spartocarpus* on the basis of the quantitative and qualitative pollen characters of Tabs. 2-3. Different groups of populations of *Genista radiata*, *G. sessilifolia*, *G. spartioides* and *G. aetnensis* were considered separately. G. ae (Sa) = *G. aetnensis* (Sardinia); G. ae (Si) = *G. aetnensis* (Sicily); G. au = *G. aucheri*; G. c = *G. cilentina*; G. d = *G. dorycnifolia*; G. e = *G. ephedroides*; G. g = *G. gasparrinii*; G. ha = *G. hassertiana*; G. hae = *G. haenseleri*; G. ho = *G. holopetala*; G. ni = *G. nissana*; G. nu = *G. numidica*; G. rr = *G. radiata* var. *radiata*; G. rs = *G. radiata* var. *sericopetala*; G. sr = *G. sessilifolia* ssp. *romanica*; G. ss (E) = *G. sessilifolia* ssp. *sessilifolia* (Europe); G. ss (T) = *G. sessilifolia* ssp. *sessilifolia* (Turkey); G. sp (A) = *G. spartioides* (Africa); G. sp (S) = *G. spartioides* (Spain); G. t = *G. thyrrena*.

distribution, and *G. spartioides* (subcluster C), with which has the closest pollen affinity. Therefore, this species can be considered a link between the eastern-racemous species and western ones.

Subcluster C comprises *Genista spartioides*, *G. haenseleri* and, more separated, *G. numidica*, Spanish and north-African species. *G. spartioides* and *G. haenseleri* have the westernmost distribution and display common palynological, morphological (alternate and opposite branches,

unifoliolate alternate leaves, flowers in racemes of clusters or rarely in racemes) and karyological characters: $2n = 40$ (Sañudo 1971). As regards *G. spartioides*, the pollen analysis seems to confirm the existence of a subspecific entity in southern Spain. This may correspond to subsp. *retamoides* (Spach) Maire, distinct from the populations of Morocco and Algeria; the systematics of this complex is still uncertain (see Maire 1987, Greuter *et al.* 1989).

Subcluster B comprises the west-Mediterranean species *Genista ephedroides*, *G. thyrrrena*, *G. gasparrinii*, *G. cilentina*, *G. aetnensis* and *G. dorycnifolia*. They all have alternate and subopposite branches, trifoliolate or unifoliolate, often fugacious leaves, more or less lax, many-flowered racemes. The Tyrrhenian species *G. ephedroides*, *G. thyrrrena*, *G. cilentina* and *G. gasparrinii* form a rather compact group also on the basis of their pollen characters. On the contrary, *G. numidica*, an Algerian endemic, included by Gibbs (1966) in *G. ephedroides*, stands well apart from these species as regards its pollen characters and is closer to *G. spartioides* and *G. haenseleri*, forming with them subcluster C. Thus, pollen characters do not support the inclusion of all the Sardinian, Sicilian, north-African and Tyrrhenian taxa in *G. ephedroides*, as proposed by Gibbs (1966); pollen analysis is, instead, more in accord with the arrangement proposed by Greuter *et al.* (1989), who referred *G. ephedroides*, *G. thyrrrena* and *G. gasparrinii* [to which has to be added *G. cilentina*, described later (Valsecchi 1993)] to *G. ephedroides* aggr. and maintained *G. numidica* as separate. Besides, there is a notable karyological homogeneity ($2n = 48$) among *G. ephedroides* (Villa 1980), *G. gasparrinii* (Colombo *et al.* 1979, sub *G. ephedroides*) and *G. cilentina* (Pizzolongo 1960, sub *G. ephedroides*), the only taxa karyologically examined so far. These five species are presumably schizoendemism originating from a common ancestor, as already suggested by De Marco *et al.* (1985). The early geographical isolation, due to the separation of the Sardo-Corsian block from the Alboran-Kabyria tectonic plate in the middle Jurassic, to the following fragmentation and dispersion of the Alboran plate in the period that goes from the Oligocene to the Miocene (Alvarez *et al.* 1974), as well as to the formation of the Liguro-Balearic basin in the upper Oligocene and of the Tyrrhenian basin in the upper Pliocene and in the Quaternary (Dazzaro *et al.* 1984), may be the reason of a morphological and palynological differentiation of the taxa, particularly evident in *G. numidica*.

The Sardo-Sicilian endemic *Genista aetnensis* is fairly close to the species of *G. ephedroides* aggr. not only on the basis of pollen characters, but they also display some significant morphological affinities, particularly as regards the inflorescence. The Sardinian and the Sicilian populations of *G. aetnensis* differ both for their pollen and morphological characters, particularly as regards

the dimensions of the legume. Presl (1844) distinguished the Sardinian and the Sicilian populations, referring them respectively to *Drymospartum sardoum* Presl and to *Drymospartum aetnense* (Biv.-Bern.) Presl. This distinction, though accepted by Spach (1845) under the names *Dendrospartum sardoum* Spach and *Dendrospartum aetnense* Spach, has been subsequently ignored. As regards the range disjunction, Arrigoni & Vannelli (1967) consider paleogeographical links between Sicily and Sardinia as very unlikely, and believe in a more recent arrival and establishment of *G. aetnensis* from Sardinia on the Etna Volcano.

Genista dorycnifolia, a Balearic endemic, displays the highest pollen affinity with *G. aetnensis* (especially with the Sardinian populations) and, through it, with the species of *G. ephedroides* aggr.; therefore it is a link between the Tyrrhenian taxa and the Spanish and north-African species. Furthermore, it is worth noting that the chromosome number of *G. dorycnifolia* is $2n = 48$ (Santos 1944-45; Cardona & Contandriopoulos 1983), the same of the species of *G. ephedroides* aggr. so far examined.

Subclusters A and D are geographically very close, but they are separated and differ in pollen and karyological characters. Subcluster A displays the highest pollen affinity, through *Genista aetnensis*, with subcluster B, including Tyrrhenian species. The two subclusters share the chromosome number $2n = 48$, *G. aetnensis* excluded [$n = 26$ (Forissier 1973), $2n = 52$ (Villa 1988)]. Among the species of subcluster D, only *G. sessilifolia* has been karyologically studied; its chromosome basic number is different from the others, being $2n = 22$ (Kuzmanov 1974; Krusheva 1975).

The two subclusters of the western species (B and C), all racemous, are the closest as regard pollen characters.

Eastern (subclusters A and D) and western species (subclusters B and C) stand well apart. It is worth noting that the distinction we found, based on the pollen analysis, corresponds to the segregation, based on morphological characters, established by Spach (1844) between sect. *Asterospartum* and sect. *Ephedrospartum*. The former section includes all the eastern species of sect. *Spartocarpus* known to him (*Genista radiata*, *G. holopetala*, *G. aucheri*); the latter includes the western species known to him (*G. numidica*, *G. ephedroides*, *G. gasparrinii* and *G. spartioides*), *G. aetnensis* and *G. haenseleri* excluded. As for *G.*

aetnensis, palynological as well as morphological and serological characters (Cristofolini & Feoli Chiapella 1977, 1984) suggest that its allocation to the genus *Dendrospartum*, as proposed by Spach (1845), is unjustified: it seems to be more correct to maintain it in *Genista*. *G. haenseleri* is homogeneous with the other species of sect. *Spartocarpus* also on the basis of its pollen characters. In our opinion its exclusion from *Genista* (Spach 1845) is not justified; it seems to be correct to refer it to sect. *Spartocarpus* as proposed by Gibbs (1966) on morphological basis.

The *Genista radiata* group displays a concentration of characters generally considered derived (opposite branches, opposite leaves, opposite flowers in terminal clusters); alternate branches, alternate leaves, terminal, lax racemes being considered as primitive characters (Polhill 1981). The description of *Cytisanthus*, a genus in which several species of sect. *Spartocarpus* have been included, is based on the characters of the *G. radiata* group. The question whether the section is homogeneous enough and the characters are sufficient to segregate a genus is still controversial. As a matter of fact, these characters are only partially common to all the species of sect. *Spartocarpus*, and not always displayed together. Doubts arise particularly for *G. spartioides* and *G. haenseleri*, whose characters differ more from those of *Cytisanthus*. In order to evaluate, the appropriateness of segregating most of the species of sect. *Spartocarpus* into the genus *Cytisanthus*, further comparisons, on the basis of the pollen characters, are necessary with species of the other sections of subgenus *Spartocarpus* and with taxa representing the other two subgenera *Genista* and *Phyllobotrys*.

Conclusions

The detailed morphometric analysis of the pollen of sect. *Spartocarpus* confirms the main pollen characters already described in other infrageneric taxa of *Genista*.

The quantitative characters observed by LM proved to be the most appropriate to distinguish the taxa of sect. *Spartocarpus*, as already noticed in the *Genista sylvestris* group. The qualitative characters examined by LM are less significant, but nevertheless important in separating some taxa not completely distinguishable on the basis of quantitative characters alone. The qualitative characters observed by SEM seem to be of minor

importance, even though the joint use of the three different groups of characters is the most complete in information.

It has been thus possible to separate all the examined taxa of sect. *Spartocarpus* on the basis of their pollen characters.

Not only are the species of the section palynologically different, but they also are morphologically heterogeneous, particularly those with racemous inflorescence (dense or lax, interrupted or uninterrupted racemes, racemes of clusters, unifoliolate or trifoliolate leaves, opposite or alternate branching), and karyologically heterogeneous (different basic chromosome numbers: $x = 10, 11, 6$ and/or $12, 13$). The chromosome heterogeneity of *Genista*, due to polyploidy, dispolyploidy and aneuploidy (Sañudo 1979; Verlaque 1988) is already well-known. Though being morphologically and karyologically heterogeneous, the species of sect. *Spartocarpus* are serologically more homogeneous, at least those examined: in fact, the eastern species with racemous inflorescence and the western species *G. spartioides* and *G. haenseleri*, morphologically more separated, were not analysed. It is worth noting, however, that the characters concerning the proteins of the seeds are more conservative than the phenological characters (both macromorphological and palynological).

The pollen characters, the macromorphological, karyological and biogeographical ones appear to be related.

In our opinion, taking into account all the available data, the arrangement proposed by Gibbs (1966), who has grouped all the species treated in this study in sect. *Spartocarpus*, seems to be correct. Even though the species referred by Spach (1844) to sect. *Asterospartum* and *Ephedrospartum* display a certain morphological, palynological and karyological diversity, this diversity is not so strong as to separate two sections, especially because the characters vary continuously. At this stage of the research, even the segregation of *Genista aetnensis* into the sect. *Aureospartum* proposed by Valsecchi (1993) cannot be confirmed on the basis of the pollen characters.

All the taxa of *Genista* sect. *Spartocarpus* may be considered well distinguished on the basis of the palynological analysis. The specific treatment of the taxa of the section in Greuter *et al.* (1989) is, in general terms, confirmed by pollen characters. However, *G. radiata*, *G. holopetala* and *G. hassertiana*, though clearly distinct species, display

such remarkable morphological, palynological and karyological affinities that grouping them together, as proposed in different ways by Buchegger (1812), Spach (1844), Fukarek (1964), Mayer (1970), Pignatti (1982), may be appropriate. As concerns the taxa having their origin in the fragmentation of *G. ephedroides*, it may be correct to set *G. ephedroides*, *G. thyrrina*, *G. gasparrinii* and *G. cilentina* in a group on the basis of their morphological, palynological and karyological affinities. The palynological diversity suggests that *G. numidica*, although presenting morphological similarity with these taxa, should not be included into the *G. ephedroides* group. The status of *G. demarcoi* deserves further studies. Investigations on different basis are to be carried out to solve the problem of the subdivision of *G. sessilifolia* and *G. spartioides* into subspecies.

Genista sect. *Spartocarpus* thus consist of 15 species:

Genista radiata group:

G. radiata (L.) Scop., Fl. Carniol. ed. 2, 2: 51. 1772.

G. holopetala (Koch) Bald. in Mem. R. Acc. Sci. Ist. Bologna ser. 5, 9: 524. 1902.

G. hassertiana (Bald.) Buchegger in Österr. Bot. Z. 62: 416. 1912.

Genista sessilifolia DC., Prodr. 2: 146. 1825.

Genista nissana Petrović, Dodat. Fl. Okol. Niša: 51. 1886.

Genista aucheri Boiss., Diagn. Pl. Orient. 2: 7. 1843.

Genista spartioides Spach in Ann. Sci. Nat. Bot. ser. 3, 2: 243. 1844.

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