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

Loredana RIZZI LONGO and Laura FEOLI CHIAPELLA

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

Keywords: Fabaceae, Genista, Genisteeae. Multivariate analysis. Pollen, Spartocarpus, Systematics.

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-Balkanic species with capitulate 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. lwenseleri and G. llimica, Spanish and N-African species, the third comprising the W-Mediterranean G. ephedroides, G. thyrrrena, G. gasparrinii, G. cileliilis, 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. thyrrrena and G. cileliilis in the G. ephedroides-group is proposed.

Introduction

The tribe Genisteae (Fabaceae) includes about twenty genera mainly distributed in the Mediterranean region. The delimitation of Genisteae 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 Genisteae 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 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 colpate is considered by Guinet (1981) as a trend to specialisation. According to Walker & Doyle (1975) and Guinet (1981) the tricolpate aperture, in Genisteae 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 tricolporate 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 endaperture (os).

Being Genisteae 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* (Feoli Chiapella 1982a; Rizzi Longo & Feoli Chiapella 1986, 1993; Rizzi Longo et al. 1986), *Vogliera* (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. *Fasselo-spartum* 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, *Ephedrospar'tum* Spach, *Retamos'partum* 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, ovate-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 Genistaeae, such as *Spartium* L. and *Echinospa'tum*. 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.


*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
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 Croatia (Velebit, Kapela and Obruć Mts, Buchegger 1912; Stgrar 1963; Fukarek 1964), in Italy (area of Trieste, Poldini 1964: Feoli Chiarella & Rizzi Longo 1987).

Genista hassertiana (= G. holopetala var. hassertiana Bald.) occurs only in northern Albania and in southern Serbia, northern Macedonia 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 Macedonia) and in northern Greece (Gibbs 1966, 1970; Greuter et al. 1989). Two subspecies have been distinguished: ssp. sessilifolia, distributed in Macedonia, 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 Serbia and northern Macedonia (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 Capitata, 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 excluendae" 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. gasparrini Guss. - 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. gasparrini 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. gasparrini (= Spartium gasparrini 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 Isule 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. demarcai* 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 ovoid 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 µm²) 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. hasserti* and *G. gass highlighting 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. hasserti* and *G. gasparrini* and 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. hasertiana* and *G. holopetala* 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.

#### QUANTITATIVE CHARACTERS (LM)

<table>
<thead>
<tr>
<th>Character</th>
<th>LM</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>24.3 ± 1.51</td>
<td>22.9 ± 1.10</td>
</tr>
<tr>
<td>D</td>
<td>19.3 ± 1.45</td>
<td>21.8 ± 1.00</td>
</tr>
<tr>
<td>F-colpus</td>
<td>15.3 ± 1.55</td>
<td>14.9 ± 0.86</td>
</tr>
<tr>
<td>E-colpus</td>
<td>23.2 ± 1.45</td>
<td>22.1 ± 1.08</td>
</tr>
<tr>
<td>LTP</td>
<td>1.1 ± 0.07</td>
<td>1.1 ± 0.06</td>
</tr>
<tr>
<td>PIE</td>
<td>1.4 ± 0.14</td>
<td>1.1 ± 0.14</td>
</tr>
<tr>
<td>PIE</td>
<td>1.1 ± 0.02</td>
<td>1.1 ± 0.02</td>
</tr>
<tr>
<td>Ex/E</td>
<td>0.1 ± 0.01</td>
<td>0.1 ± 0.01</td>
</tr>
</tbody>
</table>

#### QUALITATIVE CHARACTERS (LM)

<table>
<thead>
<tr>
<th>Character</th>
<th>LM</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Furrow in face view</td>
<td></td>
<td></td>
</tr>
<tr>
<td>rectangular</td>
<td>55.9</td>
<td>58.8</td>
</tr>
<tr>
<td>fusiform</td>
<td>0.9</td>
<td>1.8</td>
</tr>
<tr>
<td>with an equatorial constriction</td>
<td>39.2</td>
<td>39.3</td>
</tr>
<tr>
<td>with straight margins</td>
<td>78.9</td>
<td>74.8</td>
</tr>
<tr>
<td>with wavy margins</td>
<td>21.1</td>
<td>25.4</td>
</tr>
</tbody>
</table>

#### Qualitative length of thickenings at the end of the furrows

<table>
<thead>
<tr>
<th>Size</th>
<th>LM</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 1/4</td>
<td>14.3</td>
<td>11.5</td>
</tr>
<tr>
<td>= 1/4</td>
<td>34.9</td>
<td>37.1</td>
</tr>
<tr>
<td>&gt; 1/4</td>
<td>50.8</td>
<td>51.4</td>
</tr>
</tbody>
</table>

#### QUALITATIVE CHARACTERS (SEM)

<table>
<thead>
<tr>
<th>Character</th>
<th>LM</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>E-axis at mesocolpium</td>
<td>74.1</td>
<td>92.0</td>
</tr>
<tr>
<td>with sculpted pits</td>
<td>11.9</td>
<td>6.0</td>
</tr>
<tr>
<td>ridged</td>
<td>1.9</td>
<td>1.0</td>
</tr>
<tr>
<td>rugulate</td>
<td>9.9</td>
<td>1.0</td>
</tr>
<tr>
<td>grooved</td>
<td>1.4</td>
<td>0.0</td>
</tr>
<tr>
<td>smooth</td>
<td>12.8</td>
<td>3.3</td>
</tr>
<tr>
<td>rounded off</td>
<td>32.6</td>
<td>24.1</td>
</tr>
<tr>
<td>lumina with regular pits</td>
<td>65.6</td>
<td>36.0</td>
</tr>
<tr>
<td>lumina with irregular pits</td>
<td>7.3</td>
<td>28.0</td>
</tr>
<tr>
<td>lumina with more than one pits</td>
<td>17.6</td>
<td>21.0</td>
</tr>
<tr>
<td>lumina with joined pits</td>
<td>17.6</td>
<td>10.0</td>
</tr>
<tr>
<td>lumina with granular processes</td>
<td>5.0</td>
<td>5.0</td>
</tr>
<tr>
<td>E-axis at apocolpium similar to e-axis at mesocolpium</td>
<td>80.3</td>
<td>75.0</td>
</tr>
<tr>
<td>with lower reticulum</td>
<td>12.3</td>
<td>9.0</td>
</tr>
<tr>
<td>with reduced number of pits</td>
<td>7.2</td>
<td>16.0</td>
</tr>
<tr>
<td>with increased number of pits</td>
<td>0.2</td>
<td>0.0</td>
</tr>
<tr>
<td>E-axis at furrow margin similar to e-axis at mesocolpium</td>
<td>14.0</td>
<td>20.0</td>
</tr>
<tr>
<td>more finely reticulate</td>
<td>67.0</td>
<td>40.0</td>
</tr>
<tr>
<td>with margo</td>
<td>19.0</td>
<td>40.0</td>
</tr>
<tr>
<td>with reduced number of pits</td>
<td>33.0</td>
<td>40.0</td>
</tr>
<tr>
<td>with increased number of pits</td>
<td>67.0</td>
<td>80.0</td>
</tr>
<tr>
<td>Furrow membrane smooth</td>
<td>8.0</td>
<td>0.0</td>
</tr>
<tr>
<td>microgranular</td>
<td>26.8</td>
<td>39.2</td>
</tr>
<tr>
<td>granular</td>
<td>46.8</td>
<td>59.8</td>
</tr>
<tr>
<td>warty</td>
<td>14.8</td>
<td>1.0</td>
</tr>
</tbody>
</table>

### Number of pits at mesocolpium, μm

<table>
<thead>
<tr>
<th>Size</th>
<th>LM</th>
<th>SEM</th>
</tr>
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<tbody>
<tr>
<td>0.8-1.6</td>
<td>17.4</td>
<td>40.0</td>
</tr>
<tr>
<td>1.7-2.4</td>
<td>26.5</td>
<td>60.0</td>
</tr>
<tr>
<td>2.5-3.2</td>
<td>26.0</td>
<td>60.0</td>
</tr>
<tr>
<td>3.3-4.1</td>
<td>26.0</td>
<td>60.0</td>
</tr>
<tr>
<td>4.2-4.9</td>
<td>4.6</td>
<td>4.9</td>
</tr>
</tbody>
</table>

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<table>
<thead>
<tr>
<th>Character</th>
<th>Data</th>
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<tbody>
<tr>
<td>LTP/E</td>
<td></td>
</tr>
<tr>
<td>Exocolum</td>
<td></td>
</tr>
<tr>
<td>Exine at</td>
<td></td>
</tr>
<tr>
<td>G. numidica</td>
<td></td>
</tr>
<tr>
<td>P &lt; 0.01</td>
<td>0.1 ± 0.01</td>
</tr>
<tr>
<td>exinc at</td>
<td></td>
</tr>
<tr>
<td>G. dorycnifolia</td>
<td></td>
</tr>
</tbody>
</table>
C includes *G. haenseleri* and *G. spartioides*, which are very similar, and, a little separated, *G. numidica*; these are the western- and southernmost (northwestern 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. hasseltiana* (subcluster A) from *G. aetnensis*, *G. dorycnifolia*, *G. ephedroides*, *G. thyrenna*, *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 hasseltiana* 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
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 Tyrrenian 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 Tyrrenian 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. haenexpressi and G. spartioides (subcluster C) than to G. ephedroides, G. thyrrena, G. gasparrini and G. ciliatnina (subcluster B). G. aucmeri is a link between subclusters C and D.

Different groups of populations of Genista radiata, G. sessilifolia, G. spartioides and G. aethnensis 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 aethnensis 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. thyrrena; 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 (x10,000) 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 testae, arrowed (G. thyrrena); D - ridged exine (G. sessilifolia); E - rugulate exine (G. ephedroides); F - smooth exine (G. spathoides).
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).
Systematics of *Genista* sect. *Spartocarpus*

**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. sartorides* and *G. aetnensis*. Means and standard deviations (µm) of quantitative characters and average frequencies of qualitative character states by LM and SEM are given.

### QUANTITATIVE CHARACTERS (LM)

<table>
<thead>
<tr>
<th>Character</th>
<th>LM Means ± SD</th>
<th>SEM Means ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>D (µm)</td>
<td>25.0 ± 1.37</td>
<td>23.2 ± 1.68</td>
</tr>
<tr>
<td>E (µm)</td>
<td>5.1 ± 1.5</td>
<td>4.6 ± 1.29</td>
</tr>
<tr>
<td>E/LP</td>
<td>1.5 ± 0.09</td>
<td>1.4 ± 0.10</td>
</tr>
<tr>
<td>ExE (µm)</td>
<td>1.1 ± 0.08</td>
<td>1.0 ± 0.07</td>
</tr>
<tr>
<td>PIE (µm)</td>
<td>0.8 ± 0.02</td>
<td>0.7 ± 0.03</td>
</tr>
</tbody>
</table>

### QUALITATIVE CHARACTERS (SEM)

<table>
<thead>
<tr>
<th>Character</th>
<th>SEM Means ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Furrows in face view</td>
<td></td>
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<tr>
<td>Furrows in lateral view</td>
<td></td>
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<tr>
<td>Relative length of thickenings at the end of the furrows</td>
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### QUALITATIVE CHARACTERS (SEM)

<table>
<thead>
<tr>
<th>Character</th>
<th>SEM Means ± SD</th>
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<tbody>
<tr>
<td>Exine at microsculptum</td>
<td></td>
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<tr>
<td>with undulate</td>
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<tr>
<td>with sculpted</td>
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<tr>
<td>with smooth</td>
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<tr>
<td>with pointed</td>
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<tr>
<td>with regular petals</td>
<td></td>
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<tr>
<td>with irregular petals</td>
<td></td>
</tr>
<tr>
<td>with more than one pit</td>
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<tr>
<td>with granular processes</td>
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</tr>
<tr>
<td>Exine at macromorphology</td>
<td></td>
</tr>
<tr>
<td>similar to extre at microsculptum</td>
<td></td>
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<tr>
<td>with reduced number of pits</td>
<td></td>
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<tr>
<td>with increased number of pits</td>
<td></td>
</tr>
<tr>
<td>Exine at furrow margin</td>
<td></td>
</tr>
<tr>
<td>with smooth</td>
<td></td>
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<tr>
<td>with wavy</td>
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<td>with ridged</td>
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<td>with regular</td>
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<td>with granular processes</td>
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<td>with wavy</td>
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<tr>
<td>with granular process</td>
<td></td>
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<tr>
<td>Number of pits at microsculptum</td>
<td></td>
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</tbody>
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**Legend:**
- **LP:** Long pollinarium
- **E/D:** Exine/Pollinarium
- **ExE:** Exine
- **PIE:** Pollinarium
- **LTP:** Longitudinal furrows

**Note:** The table continues with similar entries for different species and varieties.
distribution, and *G. spartioides* (subcluster C), with which has the closest pollen affinity. Therefore, this species can be considered a link between the easternracemous 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: $2n = 40$ (Sanudo 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. thyrrena*, *G. gasparrinii*, *G. cilentina*, *G. aetnensis* and *G. dorycnifolia*. They all have alternate or subopposite branches, trifoliolate or unifoliolate, often fugacious leaves, more or less lax, many-flowered racemes. The Tyrrenian species *G. ephedroides*, *G. thyrrena*, *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 Tyrrenian 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. thyrrena* and *G. gasparrinii* (to which has to be added *G. cilentina*, described later (Valsecchi 1993)) to *G. ephedroides* agg. 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 schizoendemics 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-Kabylia 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 Tyrrenian 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* agg. 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* agg.; therefore it is a link between the Tyrrenian 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* agg. 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 Tyrrenian 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 racemose, 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. aecheri*); 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. numidica*, the...
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 racemose 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, dispoloidy 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 racemose 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. thyrrena, G. gasparrinii and G.
cilenta 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 consists of 15
species:

Genista radiata group:

- G. holopetala (Koch) Bald. in Mem. R. Acc.
- G. hassertiana (Bald.) Buchegger in Österr.

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

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

1843.

ser. 3, 2: 243. 1844.

1838.

Genista dorycynifolia Font Quer in Bull. Inst.

Genista actensis (Biv.) DC., Prodr. 2: 150. 1825.

Genista ephedroides group:

- G. ephedroides (DC.) Prodr. 2: 147. 1825.
- G. gasparrinii (Guss.) C. Presl, Fl. Sicula: xix.
  1826.
  Nat. 25: 145. 1886.
- G. demarcoi Brullo, Scelsi & Siracusa in Flora
  2: 244. 1844.

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L. RIZZI LONGO, L. FEOLI CHIAPELLA


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