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Studies on pollen morphology in *Santolina* L. (*Compositae*). The Italian species

Abstract

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The pollen morphology of the Italian species of the genus *Santolina* was examined: *S. corsica* Jordan & Fourr., *S. etrusca* (Lacaita) Marchi & D'Amato, *S. insularis* (Genn. ex Fiori) Arrigoni, *S. leucantha* Bertol., *S. ligustica* Arrigoni and *S. neapolitana* Jordan & Fourr. *S. marchii* Arrigoni, a plant of unknown origin which has become widespread, and grows spontaneously throughout Italy was also examined. Despite a general similarity among the different species, the pollen grains are individually distinguishable by the number and distribution of their spines. SEM observations can identify the differential morphological characteristics of the spines and of the appearance of the exine surface. Numerical analysis of the most significant characters showed that the *S. etrusca* pollen differs from the other species and that certain similarities exist between the *S. leucantha* pollen and *S. neapolitana* pollen. The morphology of *S. marchii* pollen is more similar to that of *S. corsica* than to that of the other species.

Introduction

Santolina L. *(Santolineae, Anthemideae, Compositae)* is a genus distributed throughout the regions of the western Mediterranean. According to Mabberley (1987), it encompasses 18 species, 5 of which grow in Europe, while Bremer (1994) states that there are only 8. The European species have been the subject of karyological, phytochemical and cytosystematic studies that have mainly dealt with the Iberian (Fernandes & Queiros 1971a, b, Fernandez Casas 1977, Valdes-Bermejo & Antunez 1981, Marco & al. 1993, Utrilla & al. 1995, Silvan & al. 1996) and Italian (Marchi & D'Amato 1973, 1979, Arrigoni 1977, 1982a, Arrigoni & Mori 1980, Flamini & al. 1994, Pagni 1995) taxa. Karyological studies revealed elements that were helpful for the understanding of the phylogenetic relationships among the taxonomic units. They demonstrated the existence of both genomic and karyotypical variability. The inadequacy of Guinea & Tutin's treatment of this genus (1976) has shown up in the light of these results. Until now, the taxonomy and geographical distribution have been re-examined only as regards the Italian species (Angiolini & Boscagli 1997, Angiolini & al. 1996, Arrigoni 1977, 1979, 1982a, b, Garbari & Bechi 1992, Bechi & al. 1996, Torricelli & al. 1999).

There are little palynological data on *Santolina*, and those which exist are primarily limited to the Iberian populations of *S. canescens* Lag. (Valdes & al. 1987), *S. rosmarinifolia* L. (Tormo & Ubera 1987, 1990), *S. viscosa* Lag. and *S. elegans* Boiss. (Blanca & al. 1991). Iconographic data of *S. chamaecyparissus* L. and *S. rosmarinifolia* L. were presented by Reille (1992, 1995).

In the present study, the morphological and morphometric variability of the pollen of the Italian taxa were studied in order to identify any similarities and/or differences, and to compare them with previous karyological and macromorphological studies (Marchi & D'Amato 1973, 1979, Arrigoni 1977, 1982a, Arrigoni & Mori 1980). Six species, which have an allopatric distribution, were studied. Four of these are diploid ($2n = 18$) species of the Italian Peninsula:

S. ligustica Arrigoni (eastern Liguria);

S. leucantha Bertol. (Apuan Alps, north-western Tuscany);

S. etrusca (Lacaita) Marchi & D'Amato (southern Tuscany, Umbria and northern Lazio);

S. neapolitana Jordan & Fourr. (Sorrento Peninsula, Campania).

Two are polyploid insular species:

S. insularis (Genn. ex Fiori) Arrigoni (central-southern Sardinia), hexaploid ($2n = 54$);

S. corsica Jordan & Fourr. (Chain of Monte Albo, Sardinia), tetraploid ($2n = 36$).

S. corsica is also present in Corsica near Bastia and Corte. Given that this species presents local morphological variations, most probably connected to some karyotypical variability (Arrigoni 1982a), there must be some genetic instability and the evolutionary processes must be relatively recent (Marchi & D'Amato 1979).

In Italy, other species of *Santolina*, such as *S. virens* Miller (= *S. viridis* Willd.) and *S. marchii* Arrigoni, are also present. The former - native to the Iberian Peninsula and France - has been found growing spontaneously only in Abruzzo, in the vicinity of L'Aquila (Tammaro & Pirone 1980). Since the latter, a pentaploid ($2n = 45$) of unknown origin, has started growing wild and spreading all over the territory (Marchi & D'Amato 1973), it was included among the species here examined.

Material and methods

The pollen grains examined in this study were obtained from fresh samples that had been collected in their natural habitat. Vouchers are kept in FI. Species names and vouchers are given under "Specimens investigated" at the end of this chapter. In preparation for light microscopy (LM), pollen grains had been dehydrated, acetolyzed (Erdtman 1969) and placed in 50% water/glycerol solution.

For scanning electron microscopy (SEM), acetolyzed pollen grains were washed in acetone, dried, and then gold-coated. Fragmented pollen grains were present in the acetolyzed materials, as it usually happens (Nilsson & Praglowski 1992). All counts and measurements were based on at least 30 grains per site of sampling. General terminology follows Nilsson & Praglowski (1992).

Exine structure was described following the outline proposed by Vezey & al. (1994). According to these authors, the exine is made up of a proximal layer, a layer of basal columellae, and a double-tectum (Fig. 18). The proximal layer consists of the foot layer and the endexine. The double-tectum corresponds to the ensemble of the internal tectum, the infratectal columellae and the external tectum, according to the terminology created by Skvarla & Larson (1965) and Skvarla & Turner (1966). Pollen sculpture terminology follows Vezey & al. (1992).

In order to carry out numerical analysis, each taxon was scored for 11 characters. The characters chosen and their states can be found in Appendix 1, 2. Observations were based on grains examined at both LM and SEM. Characters were elaborated according to Vezey & al. (1988). After linear standardization, according to the range of each variable in the original data set, agglomerative cluster analysis was performed on the Average Taxonomic Distance dissimilarity matrix. The unweighted pair-group mean algorithm (UPGMA), which had been performed using the Mantel T Test (Rohlf 1993), yielded the highest coefficient of cophenetic correlation. Eigenvectors and eigenvalues were extracted from the correlation matrix. All analyses were carried out using the procedures in the Ntsys vs. 1.8 package (Rohlf 1993).

Specimens investigated

The following is a list of the samples collected, locations, dates and the names of the collectors.

Santolina corsica Jordan & Fourr.: Sardegna, lungo la strada dalla cantoniera S. Anna a Lula (NU), 690 m, 27 Jul 1996, *N. & R. Bechi.*

S. etrusca (Lacaita) Marchi & D'Amato: Toscana, Monte Amiata, lungo la strada fra Bagni S. Filippo e Campiglia d'Orcia (SI), 800 m, 7 Jul 1996, *M. Mori;* Toscana, lungo la strada statale Cassia, al bivio per Chianciano (SI), 200 m, 19 Jul 1996, *M. Mori.*

S. insularis (Genn. ex Fiori) Arrigoni: Sardegna, passo di Genna Silana (NU), 1000 m, 30 Jul 1996, *N. & R. Bechi*; Sardegna, Iglesias (CA), presso il Monte S. Giovanni, 200 m, 4 Jul 1996, *R. Evangelisti & F. Del Carratore.*

S. leucantha Bertol.: Toscana, Alpi Apuane, strada da Campareccia a Pian della Fioba (MS), 635-720 m, 5 Jul 1996, *N. Bechi*; Toscana, Alpi Apuane, Cava dei Fantiscritti (MS), 340 m, 5 Jul 1996, *N. Bechi*; Toscana, Alpi Apuane, Foce di Pianza (MS), 1300 m, 10.7.1996, *O. Cecchi.*

S. ligustica Arrigoni: Liguria, Bonassola, scogli per la Madonetta (SP), 40 m, 23 Jun 1996, *O. Cecchi.*

S. marchii Arrigoni: Orto Botanico dell'Università di Firenze, 29 Aug 1996, *N. Bechi, M. Mariotti Lippi & M. Mori.*

S. neapolitana Jordan & Fourr.: Campania, Monte Faito, Acqua di Conca (NA), 600-800 m, 19 Jun 1996, *M. Borgongino, G. Lippi, M. Mariotti Lippi & G. Stefani*; Campania, Monte Faito, Vallone Teglia (NA), 700 m, 19 Jun 1996, *M. Borgongino, G. Lippi, M. Mariotti Lippi & G. Stefani.*

Results

The pollen grains of *Santolina* (Figs. 1-14) are generally spheroidal, rarely suboblate or subprolate. Measurements of the following dimensions, i.e. diameter (D) or polar axis (P) and equatorial axis (E), range from 30 to 40 µm. Their dimensions are smaller in *S. ligustica* and *S. neapolitana* and larger in *S. marchii* (Table 1, Fig. 15).

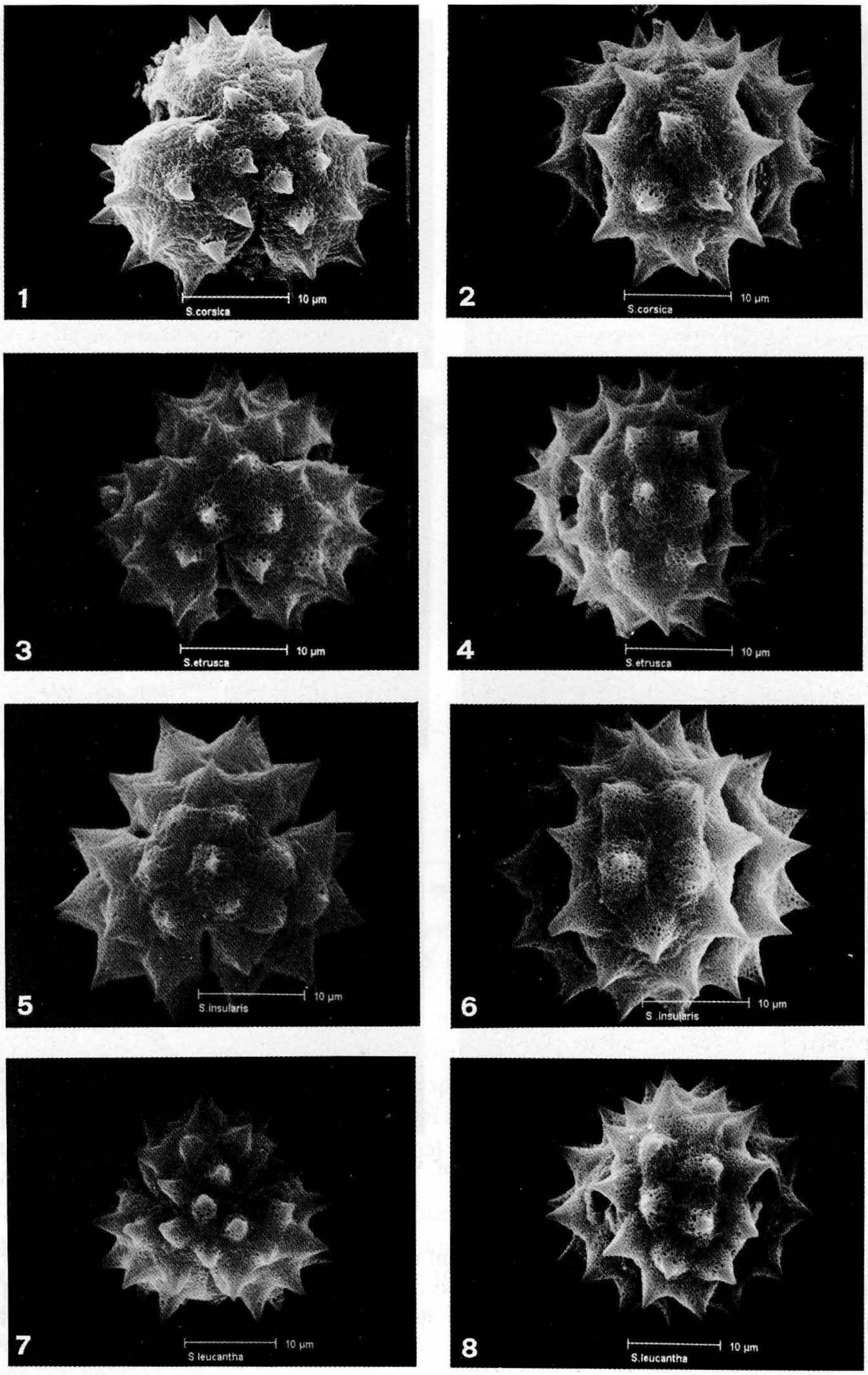
Table 1. Pollen measurements of the different species. P = polar axis; E = equatorial axis; m-M = interval range (m = minimum; M = maximum); X = mean.

	P µm		E µm		P/E	
	m-M	X	m-M	X	m-M	X
S. corsica	31.5-38.2	34.1	33.7-40.5	37.8	0.8-1	0.9
S. etrusca	29.2-33.7	32.3	33.7-36	34.3	0.8-1	0.9
S. insularis	29.2-38.2	34	31.5-38.2	35.9	0.9-1.2	0.9
S. leucantha	27-33.7	31.2	29.2-38.2	34	0.9-1	0.9
S. ligustica	24.7-33.7	29.3	27-36	32.6	0.8-1.1	0.9
S. neapolitana	24.7-33.7	30.4	27-33.7	32.3	0.8-1.1	0.9
S. marchii	33.7-38.2	34.6	36-42.7	38.5	0.8-0.9	0.9

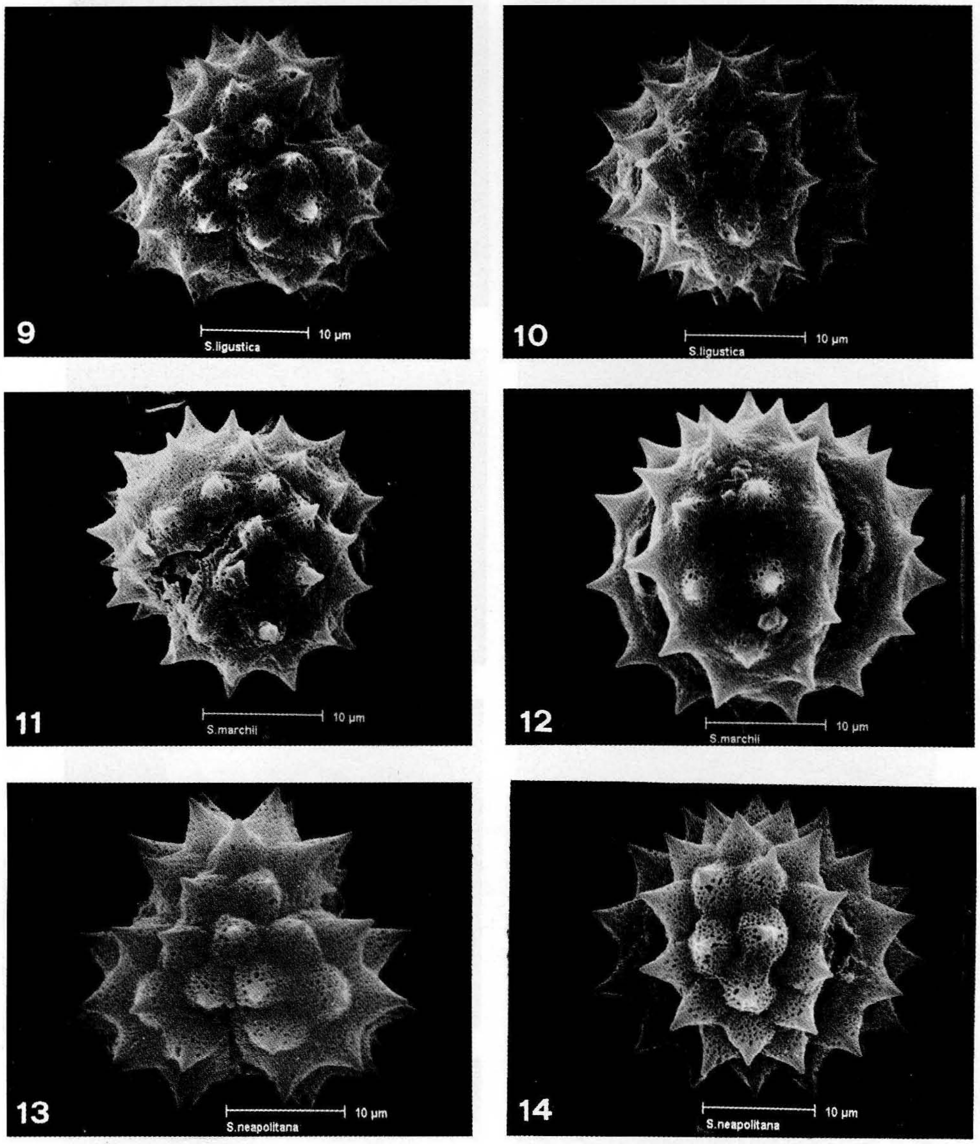
Table 2. Pollen measurements of the different species. mi = exine thickness without spines; ht = total exine thickness; Bac. = height of columellae.

	mi µm		ht µm		Bac µm	
	m-M	X	m-M	X	m-M	X
S. corsica	4.5-6.7	5.4	9-11.2	9.8	3.6-4	3.8
S. etrusca	4.5-6.7	5.1	6.7-9.2	8.5	2.7-3.6	2.9
S. insularis	3.4-6.7	5.7	6.7-10.1	9.1	3.1-4	3.6
S. leucantha	4.5-6.7	5.2	7.9-11.2	9.4	2.2-4	3
S. ligustica	3.4-6.7	4.9	6.7-10.1	8.7	2.7-4	3.4
S. neapolitana	4.3-6.7	4.6	6.7-11.2	9.3	2.2-3.6	2.8
S. marchii	4.5-6.7	6.6	9-11.2	10.7	3.6-4.9	4.2

The pollen grains are evidently echinated (Figs. 1-14): the most frequent number of spines found was 50. We found this number in all the species except *S. etrusca*, which usually has 57. Usually, *S. corsica* has 50 spines but in about 25 percent of the specimens studied 38 spines were found. The arrangement of the spines on the surface of the grains follows a precise pattern (Fig. 16). With the exception of *S. etrusca*, a polar spine is always recognizable (Fig. 16). Occasionally, several spines were missing or had merged. The latter phenomenon was observed more often in *S. corsica* and *S. leucantha* grains, which, sometimes, bore only 35 spines.



Figs. 1-8. Polar and equatorial views of grains of: **1-2,** *Santolina corsica;* **3-4,** *S. etrusca*; **5-6,** *S. insularis*; **7-8,** *S. leucantha*. SEM.



Figs. 9-14. Polar and equatorial views of grains of: **9-10,** *Santolina ligustica*; **11-12,** *S. marchii*; **13-14,** *S. neapolitana*. SEM.

In addition to the number and arrangement of the spines, the overall appearance of the grain was determined by the angles that the distal and proximal portions of each spine form with the tangent of the surface of the tectum (Fig. 17). In equatorial view, differences among the measurements of these angles were found: approximately 10° in *S. corsica* and *S. leucantha*, 20° in *S. insularis*, *S. ligusticà* and *S. neapolitana*, 30° in *S. marchii*, and 40° in *S. etrusca*.

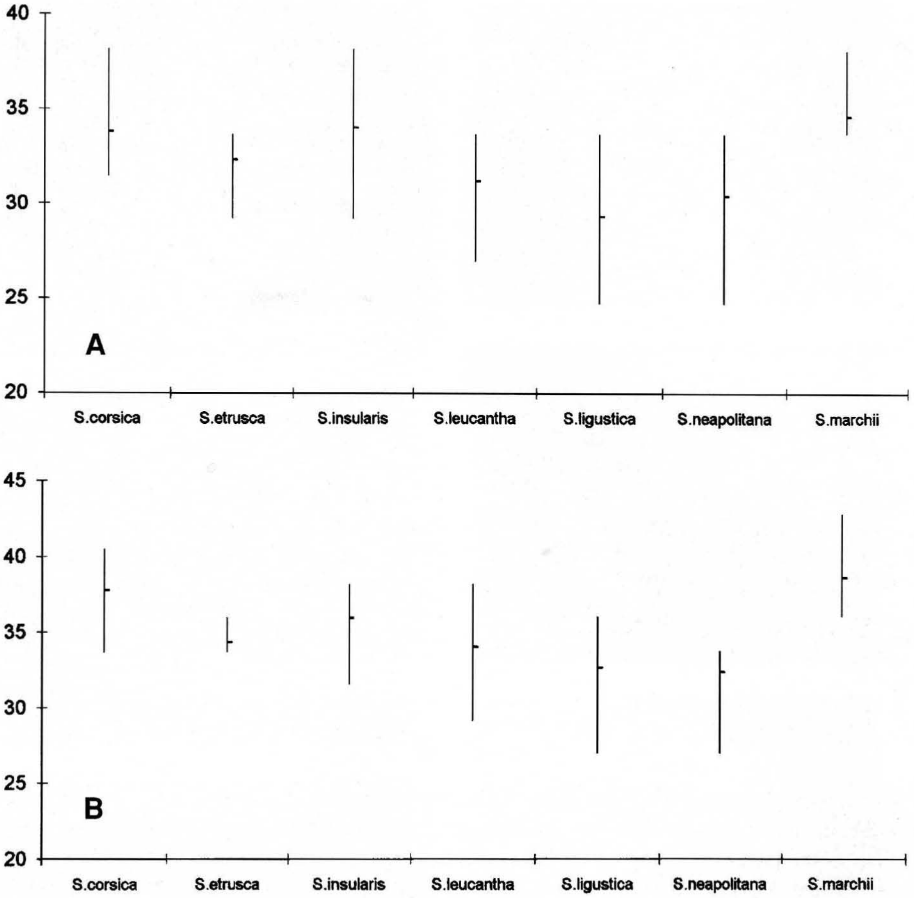


Fig. 15. Comparative diagram of the values (µm) of: **A**, polar axis and **B**, equatorial axis in the different species. The dimensions are smaller in *S. ligustica* and *S. neapolitana*; larger in *S. marchii*.

The stratified exine has an overall thickness which ranges from 4.6 µm in *S. neapolitana* to 6.6 µm in *S. marchii*, when the spines are excluded. The total exine thickness, closest to the equator, where the spines were the most developed, ranges from 8.5 µm in *S. etrusca* to 10.7 µm in *S. marchii* (Table 2).

In all the examined species, the proximal exine layer is homogeneous and measures approximately 1 µm.

The basal columellae, which were the longest vertical elements, are widened at the base and digitate at the distal end. In all the species examined, with the exception of *S. etrusca*, the columellae branch off at different heights into branches with different dimensions. Generally, the columellae further divide up, assuming an overall tree-like aspect (Fig. 19). In *S. etrusca*, the columellae divide more or less at the same height, each giving rise to several branches that are, in turn, very similar in form and dimensions and resemble the elongated portion of the infratectal columellae (Fig. 20). This different sort of ramification accounts for the different appearance of the optical sections in the thickness of the exines in the various species.

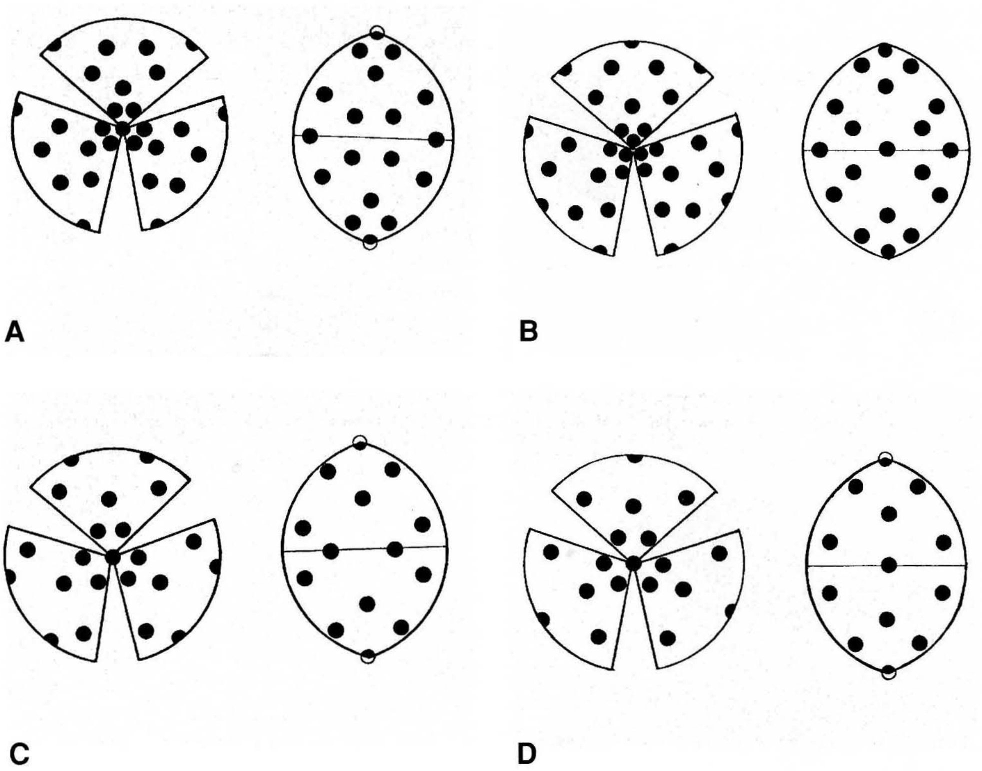


Fig. 16. Pattern of distribution of the spines in *Santolina* species: **A,** 50 spines; **B,** 57 spines; **C,** 38 spines; **D,** 35 spines. Pattern A is the most frequent. A polar spine is always recognizable, with the exception of the pattern B observed in *S. etrusca*. *S.corsica* presents grains with 50 (pattern A), 38 (pattern C) and 35 (pattern D) spines. *S. leucantha* presents grains with 50 (pattern A) and 35 (pattern D) spines.

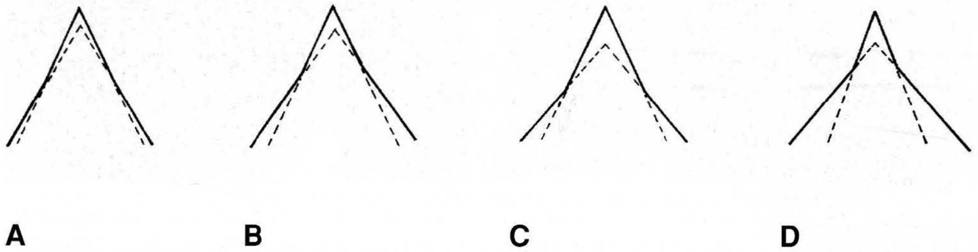
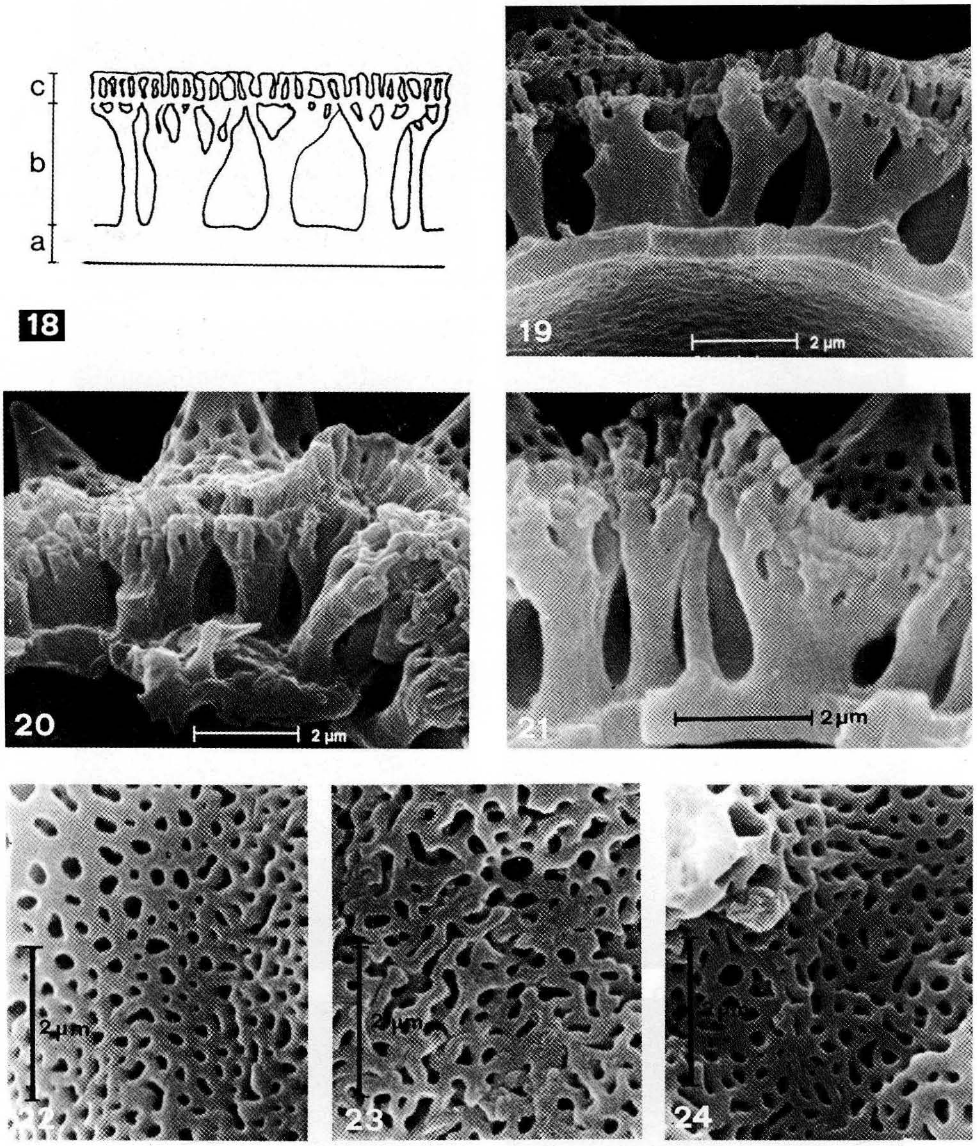


Fig. 17. Outline of the spines: **A,** *S. corsica, S. leucantha;* **B,** *S. insularis, S. ligustica, S. neapolitana;* **C,** *S. marchii;* **D,** *S. etrusca.*

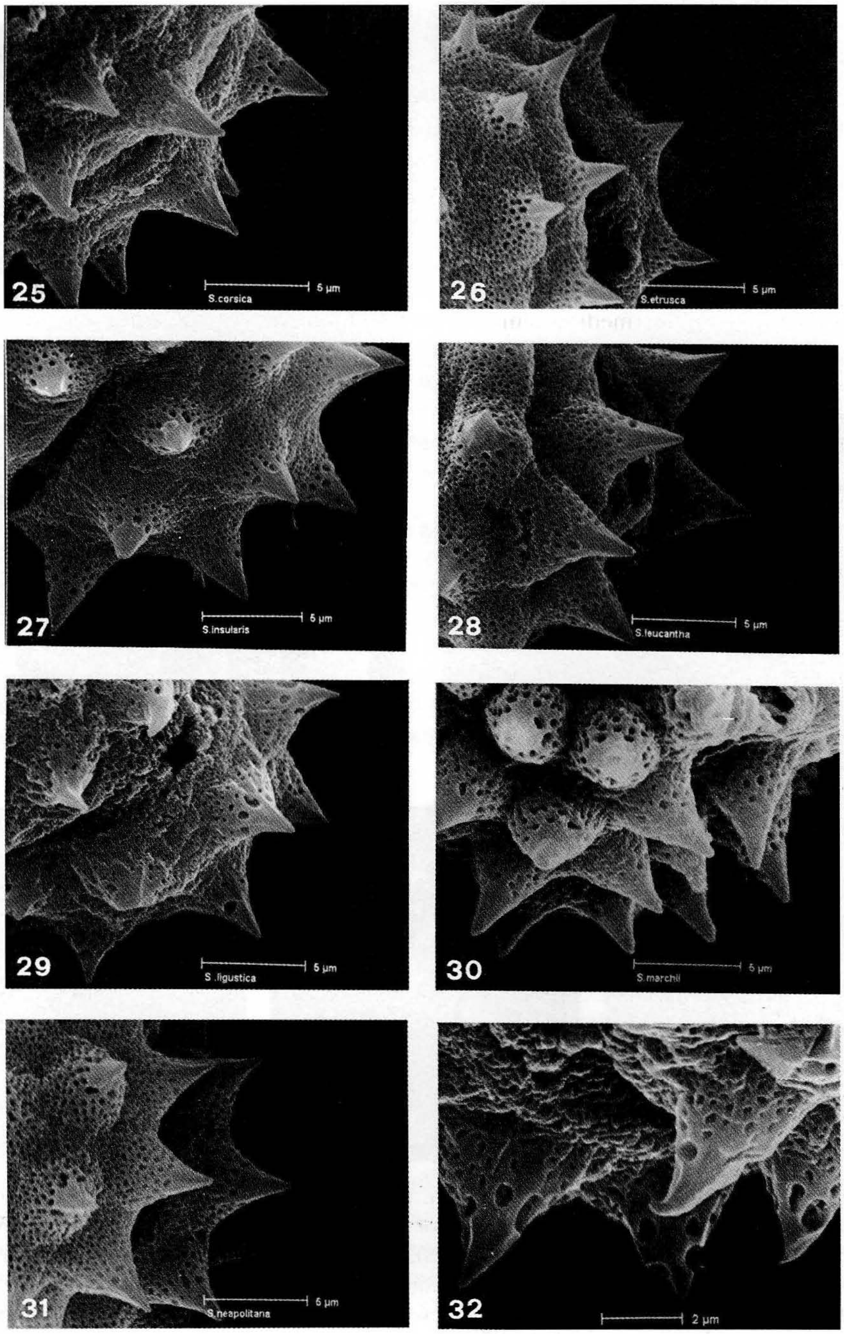
At times, the distal extremities of the latter ramifications of the basal columellae seem slightly widened: in those cases, they appear to contribute to the formation of the internal tectal layer (Fig. 21).

The double-tectum consists of non-ramified vertical columellae of much smaller dimensions than those of the basal columellae.



Figs. 18-24. **18,** exine stratification in *Santolina*: **a,** proximal layer (endexine and foot layer); **b,** basal columellae; **c,** double tectum. **19,** section of the pollen grain wall of *S. insularis*. SEM. **20,** section of the pollen grain wall of *S. etrusca*. SEM. **21,** section of the pollen grains wall of *S. leucantha*: the basal columellae appear to contribute to the formation of the internal tectal layer. SEM. **22-24,** detail of the exine surface in the mesocolpial area: **22,** *S. insularis;* **23,** *S. corsica;* **24,** *S. etrusca*. SEM.

These columellae have widened extremities and they are about 8 µm high (Fig. 19-21). The partial fusion of their proximal extremities gives rise to an internal tectal layer which has an irregular appearance and an ill-definable thickness.



Figs. 25-32. Exine surface with spines in *Santolina* species. SEM: **25,** *S. corsica;* **26,** *S. etrusca;* **27,** *S. insularis;* **28,** *S. leucantha;* **29,** *S. ligustica;* **30,** *S. marchii;* **31,** *S. neapolitana;* **32,** spines of *S. ligustica* pollen grain. The distal portion of the spine may be affected by relatively large holes. SEM.

The basal columellae also seem, at times, to contribute to the formation of the layer (Fig. 21), as mentioned above. The external tectal layer (Figs. 18-21), instead, originates as a result of the partial fusion of the distal extremities of the infratectal columellae. It should be noted that the columellae, located near the spines, slightly differ in height from the others. The external tectal layer is interrupted by numerous perforations, each of which measures much less than 1 µm (Figs. 22-24), designable as scrobiculate. These perforations have a more or less circular shape in *S. neapolitana* and *S. insularis* (Fig. 22); they are elongated, sinuous and, at times, confluent in *S. ligustica* and *S. corsica* (Fig. 23). In the other species, intermediate situations were observed (Fig. 24). In *S. corsica* and *S. ligustica* the external surface of the exine is irregularly rugulate; in the other species it was smooth or almost smooth.

The spines consist of a proximal part that forms an angle of between 40° and 50° with the tangent on the surface of the tectum and a distal part that forms one of between 60° and 80°, with the same tangent (Fig. 17). The proximal part has perforations, while the distal part is smooth, imperforate, and at times has slight ribbing or splining (Figs. 25-31). In *S. ligustica* relatively large holes may affect even the distal portion of the spines (Fig. 32). The distal holes of the spines have larger dimensions than those of the others on the rest of the tectum: they were usually arranged in a more or less regular fashion. In *S. corsica*, the distal holes of the spines tend to form a regular ring that determines a preferential fracture-line of the spine (Figs. 1, 25).

Santolina grains are 3-zonocolporate (Figs. 1-14). However, some grains of *S. marchii* had more apertures than the other species; the axes of these apertures were not perfectly parallel to each other.

Each aperture consists of a longitudinal colpum with pointed extremities and a circular or slightly lalongated os in the median region. The length of the colpum is between 15 and 19 µm; the highest values were observed in *S. corsica* and *S. insularis*.

Discussion

The grains of the Italian species of *Santolina* can be ascribed to the *"Anthemis"* type of Stix (1960). The grains of *S. rosmarinifolia* L. (Tormo & Ubera 1987), *S. elegans* Boiss. in DC., *S. viscosa* Lag. (Blanca & al. 1991) and *S. canescens* Lag. - more precisely included in the *"Anthemis arvensis"* type (Valdes & al. 1987) - which are all Iberian species, had already been attributed to this pollen type. The same grains can also be classified as "Anthemoid", according to Skvarla & al. (1977).

The general characteristics found in the Italian species are the same as those reported for the Iberian species (Tormo & Ubera 1987, Valdes & al. 1987, Blanca & al. 1991). The dimensions (D or P and E) of the grains of *S. rosmarinifolia* fit within the variability range of the Italian diploid species, while those of *S. canescens*, *S. elegans* and *S. viscosa* are smaller. Given that the thickness of the exine in the Iberian species was quite similar to the highest values found in the Italian species, and that the grains of the former species had smaller dimensions, we have hypothesized that the grains of the Iberian species will be more massive than those of the latter. This point will be investigated at some future time. Spines with very large perforations at the base, similar to those of the Italian species (Figs. 25-31), have been observed in *S. viscosa* and *S. elegans* (Blanca & al. 1991). A dimensional comparison between the spines in our study and those of the Iberian species is difficult. In fact, the measurements of the Iberian species, when reported, refer to a schematic model (Tormo & Ubera 1987) which does not correspond to the Italian species. Indeed, in the latter, no more than 3 spines were found to be aligned at the equator. The polar spine is not always present (Fig. 16).

In the Italian species, numerical analysis of the differential palynological characters, which became evident during the course of our investigations (Appendix 1, 2), led to the realization of a dendrogram. This dendrogram shows the similarities which exist among the taxa being studied (Fig. 33).

The characteristic which resulted constant were used. The distribution of the holes on the spines, which can vary in other Compositae (Salgado-Labouriau 1982), but which is rather constant in the studied grains, was also used.

Anomalous *S. marchii* grains, already noted by Marchi & D'Amato (1973) have not been considered.

The first dichotomy of the dendrogram separates *S. etrusca* from the others. *S. etrusca* has a different shape from the others and its number of spines is unlike that of the other species. Furthermore, its spines are arranged according to a model in which the polar spine is not recognizable (Fig. 16). *S. etrusca* also differs because of the structure of its exine. This difference is due to the pattern of ramification of the basal columellae (Fig. 20).

From a macromorphological point of view (Arrigoni 1979, 1982b), this species is unlike all the others: its indumentum gives an olive-green colour to the flowering shoots instead of a greyish or green one and the colour of its flowers is typically greenish-yellow instead of yellow or white.

The second dichotomy based on the overall dimensions of the grains (D or P and E), separates the polyploid species *(S. corsica, S. insularis, S. marchii)* from the diploid ones *(S. leucantha, S. neapolitana, S. ligustica).*

Within these two groups, further dichotomies were determined and correlated with the characters of the exine surface and other dimensional features, e.g. the width of the mesocolpium and the height of the basal columellae (Table 2). The height of the basal columellae was chosen as the primary characteristic for the numerical analysis instead of the total measurement of the exine as a whole, since it was the only component responsible for the differences in thickness among the species.

If we do not consider the P and E values, the resulting dendrogram (Fig. 34) shows that the similarities among the species are independent of their dimensions and, therefore, independent of their ploidy level. Using this criterion, similarities between the grains of *S. corsica* and *S. marchii* emerge. However, from a macromorphological point of view (Arrigoni 1979, 1982a), these two species are not very similar. On the other hand, the karyotypical affinity between *S. insularis* and *S. corsica*, which are both polyploids (Marchi & D'Amato 1979), was not confirmed on the palynological level, except for the large dimensions of their grains (Fig. 33 and Fig. 34).

In the two dendrograms, the greatest degree of resemblance was found between the grains of *S. leucantha* and *S. neapolitana*. The similarities based on palynological features have not been confirmed by macromorphological systematic-value characters (Arrigoni 1979). Indeed, *S. leucantha* and *S. neapolitana* differ in their indumentum, length of foliar lacinias, and the dimensions of their capitulum, their number per scape and the colour of the flowers.

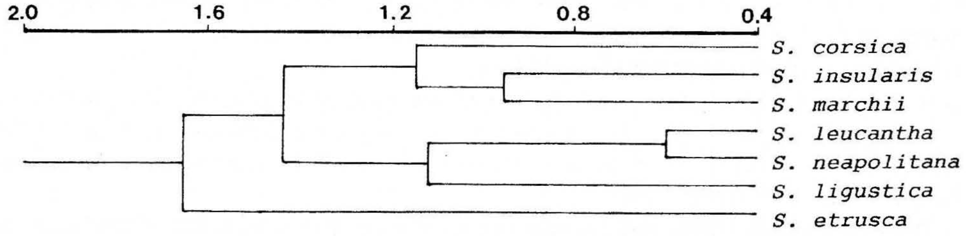


Fig. 33. Dendrogram showing dissimilarity distances of the examined taxa. P and E values are included. Matrix correlation: r = 0.83637.

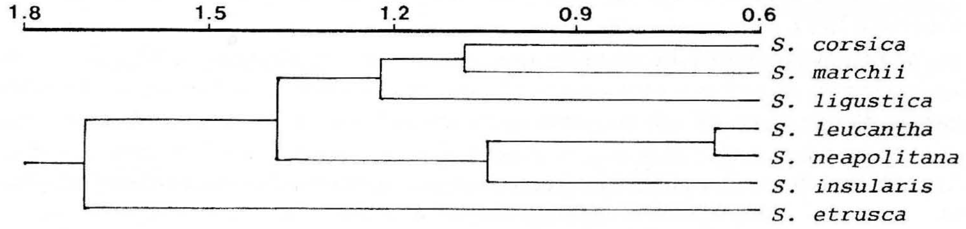


Fig. 34. Dendrogram showing dissimilarity distances of the examined taxa. P and E values are not considered. Matrix correlation: r = 0.85883.

Based on the above, we can conclude that the different size of the pollen of the insular populations *(S. corsica* and *S. insularis)* can be explained by the different ploidy level of the species involved. In the case of peninsular units *(S. etrusca, S. leucantha, S. ligustica* and *S. neapolitana)* which are all diploids with very similar pollen morphology, the speciation processes must be ascribed to different mechanisms which, at present, have not been identified.

Among these units, the highest degree of diversification appears to have affected *S. etrusca,* as it results from a palynological point of view too.

Appendix 1. List of pollen characters - measures or states - scored for the examined taxa.

E = mean value of the equatorial diameter;
P = mean value of the polar axis;
Ex = exine thickness without spines;
Bac = height of columellae;
Mesoc = width of mesocolpium;
Sp = most frequently recorded spine numbers;
An = difference of the measures of the angles of the spines (Fig. 4);
ES = exine surface: 0 = smooth with circular perforations, 1 = quite smooth with elongated perforations, 2 = rugulate with elongated-sinuate perforations;
Fo = regular ring of foramina on the spine: 0 = absent, 1 = present (Fig. 12);
FD = foramina on the distal portion of the spine: 0 =absent, 1 = present (Fig. 11);
Br = type of columella branching: 0 = all the branching at the same level, 1 = branching at different levels.

Appendix 2. Data matrix of eleven pollen characters of the examined taxa.

	E	P	Ex	Bac	Mesoc	Sp	An	ES	Fo	FD	Br
S. corsica	37.8	34.1	4.4	3.8	17.6	50-38	10	0	1	0	1
S. etrusca	34.3	323	3.4	2.9	15.6	57-57	40	1	0	0	0
S. insularis	35.9	34	3.4	3.6	17.1	50-50	20	2	0	0	1
S. leucantha	34	31.2	4.2	3	15	50-50	10	1	0	0	1
S. ligustica	32.6	29.3	4.6	3.4	16.1	50-50	20	0	0	1	1
S. marchii	38.5	34.6	4	4.2	17.8	50-50	30	0	0	0	1
S. neapolitana	32.3	304	4.6	2.8	14.1	50-50	20	2	0	0	1

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