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Taxonomy and distribution of the genus *Santolina* (Asteraceae) in Italy

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SUMMARY

The *Santolina chamaecyparissus* complex includes 13 species of dwarf aromatic evergreen shrubs from the western Mediterranean Basin. Five native species occurring in Italy are currently accepted. Four of them are endemic to relatively restricted areas in the peninsula, whereas *S. corsica* Jord. & Fourr. is endemic to Corsica and Sardinia. The taxonomic treatments of Italian S*antolina* have been changing significantly in the past, probably due to the misinterpretation of naturalised populations of *S. chamaecyparissus*, a widely cultivated pentaploid species, which occasionally escapes from cultivation through agamospermy or vegetative propagation. In this study, we carried out the first quantitative morphometric and comparative niche analyses concerning the four species endemic to continental Italy (*S. etrusca*, *S. ligustica*, *S. neapolitana*, and *S. pinnata*). Morphometric analyses (PCoA, Random Forest, and univariate analyses) show that these species can be easily distinguished by combinations of character states, whereas niche analyses (Schoener's D and similarity test) suggest that they occur in distinct climatic conditions. Based on our results, we fully confirm the taxonomic distinctiveness of these species. An updated identification key, including all *Santolina* species occurring in Italy, is presented.

INTRODUCTION

The *Santolina chamaecyparissus* L. complex includes 13 species of dwarf, aromatic, evergreen shrubs that are endemic to the western Mediterranean Basin (Giacò et al. 2021). *Santolina* species typically occur in Mediterranean environments, usually on limestone, although species growing on ophiolites and siliceous substrates are known (Arrigoni 1982, Tison et al. 2014, Carbajal et al 2019). Five native Italian species are currently accepted. Four diploid species are recorded for the peninsula, where they are endemic to relatively restricted areas, whereas the polyploid *Santolina corsica* Jord. & Fourr., a species showing both tetraploid and hexaploid cytotypes, is endemic to Sardinia and Corsica (Giacò et al. 2022, De Giorgi et al. 2022). In addition, *S. virens* Mill. and *S. chamaecyparissus* s.str. are recorded as aliens (Galasso et al. 2018a). The former is a diploid species endemic to Spain (Carbajal et al. 2019), which is recorded as naturalized only in Abruzzo (central Italy) (Tammaro & Pirone 1980), and sometimes cultivated. The latter is a widely cultivated pentaploid, possibly of anthropogenic origin, frequently used in gardens and hedges (Giacò et al. 2021). *Santolina chamaecyparissus* can reproduce vegetatively or through agamospermy, and it can occasionally escape from cultivation forming naturalized populations (Arrigoni 1977). The occurrence of this species throughout the peninsula has tricked previous botanists who studied the taxonomy and distribution of *Santolina* in Italy. Indeed, the taxonomic circumscription of Italian taxa varied greatly depending on the author, also due to the different interpretation of *S. chamaecyparissus* s.str. For instance, Bertoloni (1853) listed three taxa for Italy, whereas Fiori (1903) reported six. The taxonomic framework provided by the latter author was quite confusing, and the same author (Fiori 1927) later proposed a clearer taxonomic treatment listing five taxa, all considered as varieties of *S. chamaecyparissus*. More recently, Guinea (1970) reported the same number of taxa as Fiori (1927), but he considered them as subspecies of *S. pinnata* Viv. However, only six years later, the same author (Guinea 1976) reduced the number of Italian taxa to just three. A long-lasting taxonomic stability was achieved after the studies carried out by Palmer Marchi (Marchi & D'Amato 1973, Marchi et al. 1979) and Pier Virgilio Arrigoni (1977, 1979, 1982). Arrigoni (1982) reported six native species, all fully allopatric, in addition to the alien *S. chamaecyparissus* (= *S. marchii* Arrigoni). Recently, the only relevant change was due to De Giorgi et al. (2022), who reduced *S. insularis* (Gennari ex Fiori) Arrigoni, a putative Sardinian endemic, to a heterotypic synonym of *S. corsica*, integrating several lines of quantitative evidence. However, no quantitative observation has been carried out on native species from continental Italy. Therefore, the aim of this study is to assess with statistical support the morphological and ecological distinction of these continental species in order to provide an updated synopsis of the genus in Italy.

MATERIALS AND METHODS

Morphometric analyses

For each species, the topotypical population was sampled. Given the relatively larger distribution range of *S. etrusca*, an additional population located at the southernmost portion of its range was sampled. The list of the sampled populations is reported in Table 1. For each population, 20 flowering individuals were sampled. Thirty-seven morphological characters (29 quantitative and 8 qualitative) were measured (Table 2).

Table 1. Sampled populations and vouchers of *Santolina* species from continental Italy.

Species	**Population**	**Vouchers**
S. etrusca (Lacaita) Marchi & D'Amato	Italy, Tuscany, Radicofani [WGS84: 42.954283 N, 11.778340 E]	*G. Astuti* and *P. De Giorgi*, 14 July 2020, PI 040480–040501
S. etrusca (Lacaita) Marchi & D'Amato	Italy, Lazio, Bassano in Teverina [WGS84: 42.487438 N, 12.327856 E]	*G. Astuti* and *P. De Giorgi*, 14 July 2020, PI 040468–040479
S. ligustica Arrigoni	Italy, La Spezia, Levanto [WGS84: 44.230000 N, 9.589120 E]	*G. Astuti* and *S. Chiletti*, 22 July 2019, PI 030947–030971
S. neapolitana Jord. & Fourr.	Italy, Campania, Castellammare di Stabia [WGS84: 40.658447 N, 14.498790 E]	*P. Caputo* and *D. De Luca*, 7 August 2020, PI 040502–040521
S. pinnata Viv.	Italy, Tuscany, Apuan Alps, Forno [WGS84: 44.084178 N, 10.183817 E]	*G. Astuti* and *P. De Giorgi*, 9 July 2020, PI 040442–040461

Characters were measured with a digital caliper or using the software ImageJ, v.1.52b (http://rsb.info.nih.gov/ij, accessed on 30 July 2022). In the latter case, a 1200 dpi scan of the portion to measure was obtained with an Epson Perfection 2480 Photo scanner. To measure the percentage of leaf and stem tomentosity (fs_hair, ss_hair, fsl_hair, and ssl_hair in Table 2), a portion of a leaf and stem was photographed with a digital camera mounted on a WILD Heerbrugg M420 stereomicroscope. Then, using ImageJ, the tomentosity was calculated dividing the portion of the selected area covered by tomentum by the total selected area. The tomentosity of the non-flowering stems (ss_hair) was transformed into an ordered factor using the following classes: 0–5% (hairless or almost hairless), 6–30% (slightly pubescent), 31–60% (pubescent), 61–90% (tomentose), 91–100% (densely tomentose). Instead, the tomentosity of the inter-floral bracts (sq_if_hair in Table 2) was categorized depending on the number of hairs: 0–3 (glabrous), 4–10 (slightly pubescent), 11–25 (pubescent), 26–50 (tomentose), 51 or more (densely tomentose). After measurements, the specimens were reposited at the Herbarium Horti Botanici Pisani (PI, herbarium acronym follow Thiers 2022). Digital images of each specimen measured in this study can be found at JACQ Virtual Herbaria: https://www.jacq.org/.

Table 2. Morphometric characters and their description of *Santolina* species native to continental Italy. QC = quantitative continuous, QD = quantitative discrete, CO = ordered factor, and Y/N = bimodal.

Code	Description of the Character	Type	Tool
Vegetative parts			
fs_length	Length of the flowering stem (cm)	QC	Ruler
br_ratio	Ratio between the highest ramification of the flowering stem and fs_len	QC	Ruler
dist_cap_lf	Distance between the highest leaf on the stem and the floral head (mm)	QC	Caliper
fs_n_br	Number of branches of the flowering stem	QD	
fs_n_nodes	Number of nodes of the flowering stem	QD	
ss_length	Length of the non-flowering stem (cm)	QC	Ruler
ss_n_nodes	Number of nodes of the non-flowering stem	QD	
ss_hair	Tomentosity of the non-flowering stem	CO	ImageJ
fs_hair	Degree of tomentosity of the flowering stem (%)	QC	ImageJ
fsl_n_seg	Number of segments on the flowering stem leaf (the longest)	QD	
ssl_n_seg	Number of segments on the non-flowering stem leaf (the longest)	QD	
ssl_length	Length of the non-flowering stem leaf (mm)	QC	ImageJ
ssl_petiole_length	Length of the petiole of the non-flowering stem leaf (mm)	QC	ImageJ
ssl_seg_length	Length of the segment of the non-flowering stem leaf (mm)	QC	ImageJ
ssl_seg_dist	Distance between the segments of the non-flowering stem leaf (mm)	QC	ImageJ
ssl_seg_type	Segments of the non-flowering stem leaf pointed at apex	Y/N	
fsl_length	Length of the flowering stem leaf (mm)	QC	ImageJ
fsl_petiole_length	Length of the petiole of the flowering stem leaf (mm)	QC	ImageJ
fsl_seg_length	Length of the segment of the flowering stem leaf (mm)	QC	ImageJ
fsl_seg_dist	Distance between the segments of the flowering stem leaf (mm)	QC	ImageJ
fsl_seg_type	Segments of the non-flowering stem leaf pointed at apex	Y/N	
ssl_hair	Degree of tomentosity of the non-flowering stem leaf segment (%)	QC	ImageJ
fsl_hair	Degree of tomentosity of the flowering stem leaf segment (%)	QC	ImageJ
Floral head			
cap_diam	Diameter of the floral head involucre (mm)	QC	Caliper
flowers_col	Color of the flowers (white, pale yellow, yellow)	CO	

flowers_type	Involucre covered by the flowers	Y/N	
flower_length	Length of the floral tube (mm)	QC	ImageJ
flower_tooth_length	Length of the floral tooth (mm)	QC	ImageJ
sq_ext_length	Length of the external involucral bract (mm)	QC	ImageJ
sq_ext_width	Width of the external involucral bract (mm)	QC	ImageJ
sq_int_length	Length of the internal involucral bract (mm)	QC	ImageJ
sq_int_width	Width of the internal involucral bract (mm)	QC	ImageJ
sq_if_length	Length of the inter-floral bract (mm)	QC	ImageJ
sq_if_width	Width of the inter-floral bract (mm)	QC	ImageJ
sq_if_n_hair	Tomentosity of the inter-floral bract (hairless/slightly pubescent/pubescent/hairy/densely hairy)	QD	ImageJ
sq_ext_hair	Tomentosity of the external involucral bract (hairless/only on the margin/everywhere)	CO	ImageJ
sq_int_hair	Tomentosity of the internal involucral bract (hairless/only on the margin/everywhere)	CO	ImageJ

A Principal Coordinate Analysis (PCoA) based on Gower distance was used to visualize the morphological relationships among species in a multivariate space. Then, a Random Forest method was used to test the correct classification of species, considered as *a priori* groups. This latter analysis was conducted using the package "randomForest" version 4.6-14 (Liaw & Wiener 2002) in R environment. The Random Forest method was applied 100 times, each time randomly splitting the dataset in two equal-sized subsets, i.e. the training and test sets. Finally, based on the 100 reiterations, a confusion matrix reporting the mean percentage values of classification was built.

As univariate analyses, pairwise comparisons comparing each quantitative variable for each species were conducted. For variables with equal variance (Bartlett test $p > 0.05$), ANOVA followed by the Tukey-Kramer post hoc test was conducted. For variables with unequal variance (Bartlett test $p < 0.05$), the Welch t test with the Hochberg correction was conducted. When a significant difference was detected (Tukey-Kramer or Welch t test with $p < 0.05$), the index of effect size Cohen's d was calculated (Cohen 1988, Aoki 2020). The Cohen's d is a standardized measure of the distance between two means. For instance, if Cohen's d = 1, then the two means are distant as one standard deviation. In order to avoid considering characters with a high overlap, significant differences were considered relevant only when Cohen's d > 1.2, i.e., differences detected are "very large" according to the classification proposed by Savilowsky (2009).

The results of univariate analyses of the present study and the results published by De Giorgi et al. (2022) and Carbajal et al. (2019) were used to develop an updated identification key for all the *Santolina* species occurring in Italy.

Niche analysis

We calculated ecological niche using occurrences data obtained from herbarium and literature data (see "Distribution of *Santolina* in Italy") and supplemented with field observations, as in the case of *S. ligustica*. Occurrence points referred to populations that are now considered extinct were discarded from the analysis. Niche overlap among species was measured via Schoener's D (1970), directly from present climatic conditions that prevail at the level of current occurrence records with the 'ecospat' package (Di Cola et al., 2021). The values of D overlap range from 0 (no overlap) to 1 (full overlap). We used similarity test introduced by Warren et al. (2008) to determine whether two environmental niches are more or less similar than would be expected by chance, comparing the environmental conditions occupied by a taxon. The observed climatic niche overlap between two taxa was compared with the overlap measured between the niche of one taxon and randomized niche of the other taxon. Significant values ($p < 0.05$) indicate that the ecological niche of species are either or less similar than predicted by chance. We repeated the randomization procedure 100 times using a 5 km background area calculated around the points occurrence.

Distribution of *Santolina* in Italy

The distribution of *Santolina* in Italy was studied by surveying the herbaria AUR, BOLO, FI, LY, MPU, P, and PI (acronyms follow Thiers 2022). Additional floristic information was obtained from the literature (Lacaita 1925, Marchi et al. 1979, Arrigoni et al. 1982, Angiolini 2001, Angiolini & Bacchetta 2003) and by consulting the online database Wikiplantbase #Italia (Peruzzi et al. 2019-). All the records were georeferenced and used to build a distribution map.

RESULTS

Morphometric analyses

The first three axes of PCoA (Fig. 1) explain 68.63% of the overall morphological variability. The four species are well distinct in the multivariate space, showing no overlap.

Random Forest (Table 3) returned a high mean percentage value of correct classification (99.15 %). Indeed, only *S. neapolitana* was slightly misclassified with *S. etrusca*.

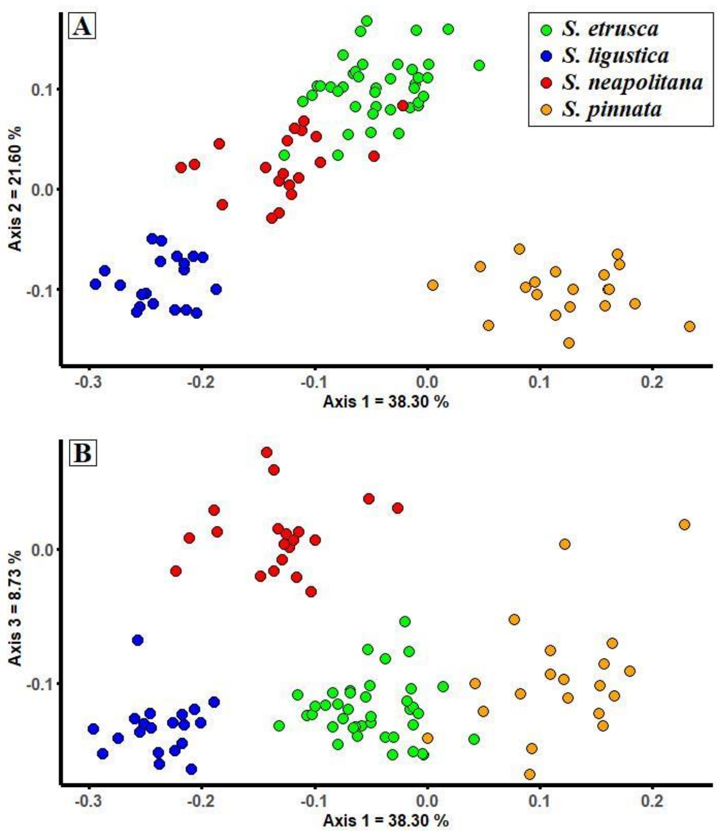

Figure 1. PCoA based on Gower distance illustrating the morphometric variability of the *Santolina* species native to continental Italy. Scatter plot of the first two axes (A); scatter plot of the first and third axes (B).

Table 3. Results of the Random Forest classification by assuming the four *Santolina* species native to continental Italy as a priori groups. Values are percentages.

	S. etrusca	*S. ligustica*	*S. neapolitana*	*S. pinnata*
S. etrusca	100	0	0	0
S. ligustica	0	100	0	0
S. neapolitana	3.4	0	96.6	0
S. pinnata	0	0	0	100

In Table 4, the mean values ± standard deviation of all the quantitative characters are reported for each species. Overall, the number of scarcely overlapping significant characters detected among the studied species is high (Table 5). The lowest number of such characters (8) was detected in the comparison between *S. neapolitana* and *S. ligustica*; conversely, the highest number (16) was detected comparing *S. pinnata* and *S. ligustica*.

Table 4. Mean values ± standard deviation of all the quantitative characters in the four *Santolina* species native to continental Italy. Character codes follow Table 2.

Character	***S. etrusca***	***S. ligustica***	***S. neapolitana***	***S. pinnata***
fs_length (cm)	26.9 ± 6.0	17.9 ± 4.6	20.1 ± 3.4	23.3 ± 4.6
br_ratio	0.8 ± 0.1	0.7 ± 0.2	0.5 ± 0.3	0.4 ± 0.2
dist_cap_lf (mm)	22.1 ± 11.5	16 ± 8.9	27.1 ± 12.5	65.4 ± 26
ss_length (cm)	16.8 ± 5.5	10.6 ± 4.1	8.7 ± 3.4	6.4 ± 3.9
cap_diam (mm)	5.9 ± 0.8	4.0 ± 0.6	6.2 ± 1.0	6.1 ± 1.3
sq_ext_length (mm)	2.9 ± 0.3	2.7 ± 0.5	2.7 ± 0.4	3.1 ± 0.4
sq_ext_width (mm)	1.1 ± 0.2	0.9 ± 0.1	1.1 ± 0.3	1.2 ± 0.1
sq_int_length (mm)	3.2 ± 0.3	2.6 ± 0.3	2.8 ± 0.3	3.4 ± 0.5
sq_int_width (mm)	1.2 ± 0.2	0.9 ± 0.1	1.1 ± 0.2	1.2 ± 0.2
sq_if_length (mm)	3.3 ± 0.3	2.6 ± 0.3	2.7 ± 0.2	3.1 ± 0.3
sq_if_width (mm)	0.9 ± 0.2	0.8 ± 0.1	1.0 ± 0.2	1 ± 0.2
flower_length (mm)	3.7 ± 0.5	2.6 ± 0.3	3.0 ± 0.4	3.5 ± 0.6
flower_tooth_length (mm)	1.0 ± 0.1	0.8 ± 0.1	1.0 ± 0.1	1.0 ± 0.2
ssl_length (cm)	42.8 ± 9.9	34 ± 9.2	43.8 ± 6.3	41.9 ± 8.7
ssl_petiole_length (mm)	5.1 ± 2.6	7.6 ± 2.2	6.7 ± 2.4	6.3 ± 2.5
ssl_seg_length (mm)	2.4 ± 0.6	3.0 ± 0.9	3.7 ± 1.2	4.6 ± 1.3
ssl_seg_dist (mm)	1.1 ± 0.4	1.2 ± 0.5	1.1 ± 0.5	1.4 ± 0.7
fsl_length (mm)	28.4 ± 5.4	22.3 ± 5.8	29.1 ± 5.7	30.5 ± 5.4
fsl_petiole_length (mm)	2.8 ± 1.7	5.6 ± 2.5	4.4 ± 2.4	5.1 ± 2.1
fsl_seg_length (mm)	1.9 ± 0.4	2.3 ± 0.7	2.6 ± 0.7	3.7 ± 0.6
fsl_seg_dist (mm)	0.9 ± 0.4	1.2 ± 0.3	0.9 ± 0.4	1.3 ± 0.4
fs_n_br	3.1 ± 1.7	4.2 ± 3.5	2.8 ± 2.1	1.8 ± 1.4
fs_n_nodes	24.4 ± 2.8	20.2 ± 3.4	16.7 ± 2.8	18.8 ± 3.6
ss_n_nodes	24.9 ± 4.8	20.0 ± 3.9	17.1 ± 4.1	20.0 ± 6.0
ssl_n_seg	95.8 ± 20.0	53.5 ± 10.8	83.2 ± 16.1	52.3 ± 13.5
fsl_n_seg	67.8 ± 12.4	33.0 ± 8.9	60.2 ± 13.5	34.5 ± 9.0
ssl_hair (%)	49.8 ± 22.3	82.8 ± 14.9	78.8 ± 13.9	0.3 ± 0.9
fsl_hair (%)	11.6 ± 15.2	74.0 ± 17.6	55.1 ± 27.0	0.2 ± 0.6
fs_hair (%)	40.6 ± 16.6	92.2 ± 6.2	68.7 ± 21.3	0.8 ± 1.3

Table 5. Univariate morphometric analyses of the *Santolina* species native to continental Italy. Pairwise comparisons between species: in the lower triangle of the table, the characters that are significantly different with Cohen's d > 1.2 are reported, whereas in the upper triangle, the number of these characters is reported. Characters letters are: a = fs_length, b = br_ratio, c = dist_cap_lf, d = ss_length, e = cap_diam, f = sq_ext_length, g = sq_ext_width, h = sq_int_length, i = sq_int_width, j = sq_if_length, k = sq_if_width, l = flower_length, m = flower_tooth_length, n = ssl_length, o = ssl_petiole_length, p = ssl_seg_length, q = ssl_seg_dist, r = fsl_length, s = fsl_petiole_length, t = fsl_seg_length, u = fsl_seg_dist, v = fs_n_br, w = fs_n_nodes, x = ss_n_nodes, y = ssl_n_seg, z = fsl_n_seg, A = ssl_hair, B = fsl_hair, C = fs_hair.

	S. etrusca	***S. ligustica***	***S. neapolitana***	***S. pinnata***
S. etrusca	0	15	12	12
S. ligustica	a,d,e,h,i,j,l,m,s,w,y,z,A,B,C	0	8	16
S. neapolitana	a,b,d,h,j,l,p,w,x,A,B,C	e,k,l,m,n,y,z,C	0	9
S. pinnata	b,c,d,p,s,t,w,y,z,A,B,C	b,c,e,g,h,i,j,k,l,m,p,r,t,A,B,C	a,h,j,t,y,z,A,B,C	0

Niche analysis

The niche overlap is low in almost all pairs of species, except between *S. ligustica* and *S. etrusca*, where the Schoener's D value is 0.228. The results of the similarity test are not significant in all cases tested (Table 6), indicating that the low niche overlap values were due to habitat availability in the background areas rather than an effect of habitat selection.

Table 6. Results of niche similarity test in environmental spaces among the different *Santolina* species native to continental Italy. Backgrounds were defined by applying 5 km buffer zones around occurrence points. ns = not significant.

	S. ligustica	***S. neapolitana***	***S. pinnata***
S. etrusca	0.000 ns\ns	0.000 ns\ns	0.082 ns\ns
S. ligustica	\	0.228 ns\ns	0.000 ns\ns
S. neapolitana	\	\	0.006 ns\ns

DISCUSSION

Our results suggest that the four *Santolina* species native to continental Italy represent good taxonomic hypotheses, since they show both distinct morphologies and climatic niche preferences. Indeed, the low values of niche overlap evidence that the four species live in different environmental conditions. However, our morphometric analyses are not totally in accordance with Arrigoni (1982, 2018). Indeed, some diagnostic characters used in his studies, such as the shape of the capitula, the morphology of the inter-floral bracts, and the shape of flowers, were preliminarily discarded from our analyses since they were extremely varying, often within the same individual. On the contrary, the flower colour, a diagnostic character also used by Arrigoni (1982, 2018), proved very useful to distinguish fresh plants. *Santolina ligustica* and *S. pinnata* are the only two species of the genus showing white flowers, *S. etrusca* shows pale-yellow flowers, whereas *S. neapolitana* shows yellow flowers as most of other *Santolina* species. If flower colour is not available, as in herbarium specimens or withered plants, species from continental Italy can still be distinguished by a combination of quantitative diagnostic character states (see identification key). In addition, these species can be easily distinguished by their fully allopatric distribution ranges (Fig. 2).

Santolina ligustica (Fig. 3A) is endemic to western Liguria (northern Italy), where it occurs in a very restricted area, mostly on ophiolites. Due to the small range and threats caused by human activities, it was considered by Torricelli et al. (2000) as Critically Endangered (CR), albeit Orsenigo et al. (2018) more recently assessed it as Near Threatened (NT). *Santolina pinnata* (Fig. 3B) is endemic to the Apuan Alps (Tuscany, central Italy), where it grows mostly on marble. This species is currently considered as Least Concern (LC) by Orsenigo et al. (2018). However, according to Varaldo et al. (2021a), both *S. pinnata* and *S. ligustica* may dramatically lose in the future a great portion of their suitable habitat due to climate change.

Santolina etrusca (Fig. 3C) is endemic to southern Tuscany, a small portion of Umbria, and northern Lazio (central Italy), where it is abundant on river terraces (Angiolini & Boscagli 1997, Angiolini & De Dominicis 1998). According to Angiolini (2001), the range of *S. etrusca* was wider in the past, since there are herbarium records from the nineteenth century which documented its presence also in northern Tuscany. After field investigations, the author concluded that those populations are now extinct. In the FI herbarium, we studied specimens from northern Tuscany, and we fully confirmed their identity. Despite *Santolina etrusca* exhibits a wider distribution range with respect to the other Italian peninsular species, it was assessed as Near Threatened (NT) by Orsenigo et al. (2018), mostly because of human-induced habitat modifications.

Finally, *S. neapolitana* (Fig. 3D) was so far considered endemic to the peninsula of Sorrento, Monti Picentini, and Monte Stella (Campania, southern Italy), where it grows on limestone (Del Guacchio et al. 2020). Due to habitat fragmentation and the high susceptibility to habitat modifications, this species was assessed as Endangered (EN) by Orsenigo et al. (2018). *Santolina neapolitana* is widely known as a noteworthy Campanian endemic species (Arrigoni 2018, Del Guacchio et al. 2020), but during our herbarium surveys we located four duplicate specimens (two at FI and two at MPU) that were collected near Lungro, Calabria (southern Italy). These specimens have capitula with a wide involucre, leaves with long segments, and flowering stems that are branched in the low-middle portion, matching the morphology of *S. neapolitana*. The collectors, who originally identified these specimens only at the genus level, were the well-known botanists Pietro Porta, Rupert Huter, and Gregorio Rigo, who much contributed to early botanical explorations of southern Italy (Galasso et al. 2018b, Bernardo et al. 2020). This collection is also listed by Porta (1879) in his report of the trip made by the three botanists in 1877. The occurrence of a *Santolina* population in Calabria was still reported in Fiori (1905, 1927) and Guinea (1970). However, these authors identified this population as *S. insularis*, now included within the variability of what is currently accepted as *S. corsica*. Conversely, P.V. Arrigoni identified the two specimens at FI as *Santolina marchii* (i.e. *S. chamaecyparissus* L.), and this accounts for the lack of any mention of *S. neapolitana* in Calabria in all his studies (Arrigoni 1979, 1982, 2018). We personally conducted a field investigation in the same localities mentioned by Porta (1879), and we conclude that the population of *S. neapolitana* from Calabria is nowadays extinct.

The peculiar allopatric geographic pattern shown by the peninsular *Santolina* species, all diploid (Giacò et al. 2022), was interpreted by previous scholars as the result of the fragmentation of a formerly wider pre-glacial distribution range (Arrigoni 1979). Under this scenario, extant species should be considered as schizoendemics (Siljak-Yakovlev & Peruzzi 2012). The current restricted ranges of peninsular Italian endemics may also be explained by a scarce competitiveness and/or scarce dispersal ability. Indeed, *Santolina* species are known to occur in very selective and arid environments, where competition with other species is usually low (Torricelli 2000; Angiolini & Bacchetta 2003, Carbajal et al. 2019). In addition, the cypselae in this genus typically lack of structures adapted for dispersal, which is mostly barochorous (Carbajal et al. 2019). A phylogenomic study using NGS approaches is currently ongoing to understand the biogeographic history of *Santolina*. Preliminary results (Varaldo et al. 2021b) suggest that *S. etrusca*, *S. ligustica*, and *S. neapolitana* form three distinct clades collectively monophyletic, whereas *S. pinnata* is sister to other diploid species occurring in southern France, Iberian Peninsula, and the Balearic Islands. This pattern of relationships is fully congruent with our morphometric results.

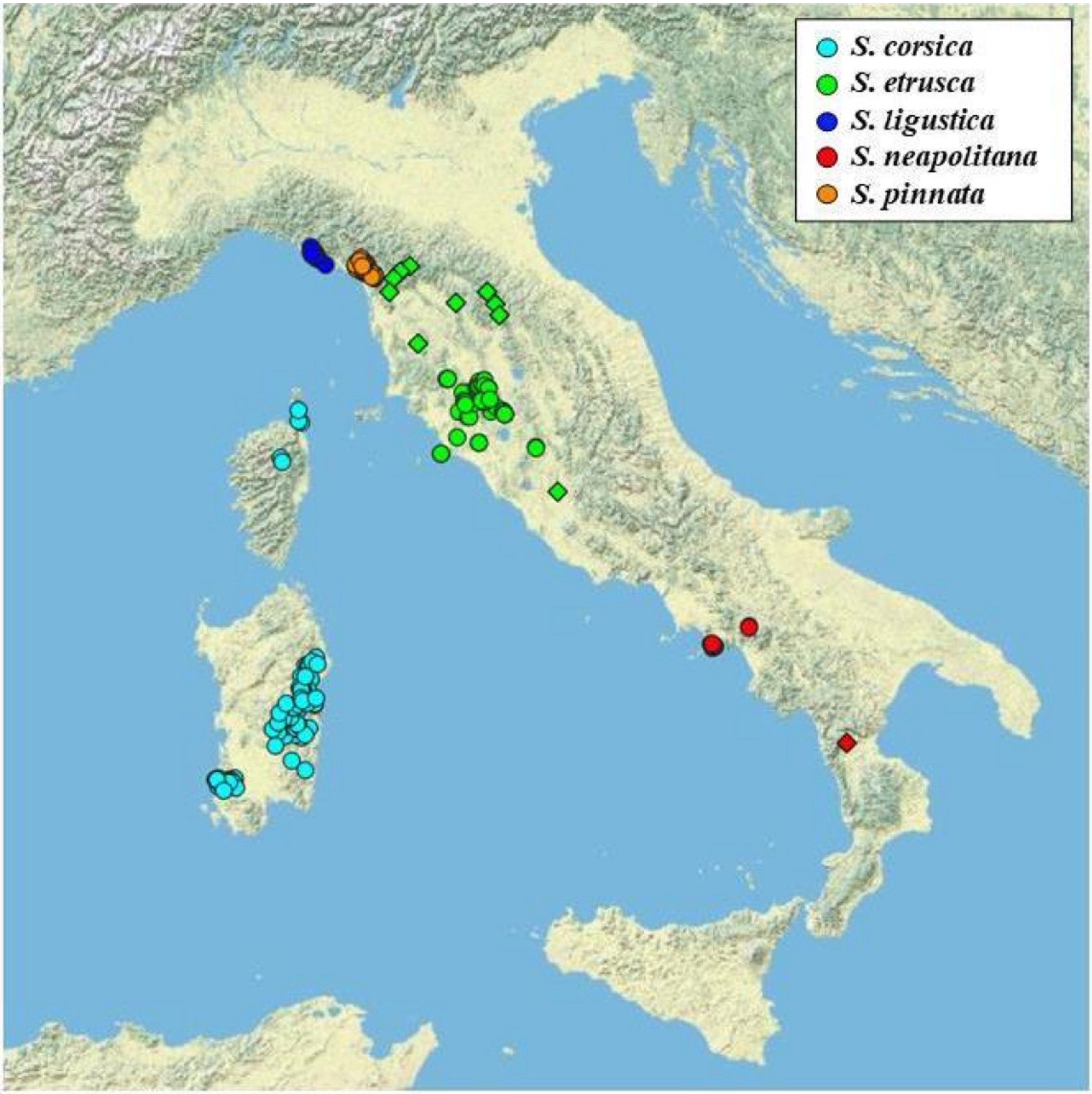

Figure 2. Distribution of the *Santolina* species native to Italy. Diamonds represent historical populations (< 1950) not confirmed in recent times.

Identification key

For identification purposes, both non-flowering and flowering stems are needed. Since the flower colour in herbarium specimens is often lost, we built a key based mostly on morphometric characters. Measures should be taken on flowering or fruiting plants. When measuring, only the longest stems, leaves and leaf segments, and the largest capitula for each individual should be considered.

1. Plant glabrous or almost glabrous ……….... 2
1. Plant tomentose at least on the non-flowering stems ……………………………..……...……...…. 3

2. Leaf segments well developed (> 2 mm). Flowers white. Spontaneous plant (Apuan Alps) ……….. *S. pinnata*
2. Leaf segments very short (< 1 mm). Flowers yellow. Cultivated/alien plant ………. *S. virens*

3. Capitula with involucre 3–5 mm wide, coupled with leaves of the non-flowering stems with segments 2–6 mm long. Flowers white ……..……………………..……...… *S. ligustica*
3. Capitula with involucre 5–8(–10) mm wide, or involucre 3–5 mm wide coupled with leaf segments < 2 mm. Flowers yellow ..…….…… 4

4. Leaves of the flowering stems with segments 1.5–4 mm long. Leaves of the non-flowering stems with segments 1.5–5(–8) mm long. Floral teeth usually > 1 mm ……...………………… 5
4. Leaves of the flowering stems with segments 0.5–1.5(–2) mm long. Leaves of the non-flowering stems with segments 0.5–2 mm long. Floral teeth < 1 mm ...………...……….……… 6

5. Flowering stems branched in the upper portion, the highest branch is often located at more than 3/4 of the stem. Non-flowering stems 10–30 cm. Leaves of the flowering stems with segments 1.5–2.5 mm long. Flowers pale yellow ……..…………………………….….... *S. etrusca*
5. Flowering stems branched or not branched, but the highest branch is never located at more than 3/4 of the stem. Non-flowering stems mostly shorter than 10 cm. Leaves of the flowering stems with segments 1.5–4 mm long. Flowers yellow ………………… *S. neapolitana*

6. Tubular portion of the flowers usually < 4 mm long. Leaves of the flowering stems with 20–150 segments, 10–45 mm long. Pollen vital. Plant native to Corsica and Sardinia ...…… *S. corsica*
6. Tubular portion of the flowers usually > 4 mm long. Leaves of the flowering stems with 10–20(–40) segments, 10–20 mm long. Pollen aborted. Cultivated/alien plant ……………..…………… *S. chamaecyparissus*

Specimens seen

Santolina corsica. **France**. Corsica, Bastia, 10 July 1868, *O. Debeaux s.n.* (LY0341551! and LY0341533!); Corsica, Cap. Corse à Luri, July 1898, *Mandon s.n.* (LY0341555!); Corsica, Bastia, maquis et rochers sur les versants du Pigno, sous Cardo, 10–25 Jul 1868, *O. Debeaux s.n.* (LY0003141!); Corsica, lieux arides près Corte, 27 June 1906, *H. Gysperger s.n.* (PI018124!); Corsica, sulla cresta del Monte Pigno nei pressi di Bastia, substrato calcareo, 850 m s.l.m. circa, 7 July 2020, *A. Giacò & L. Peruzzi s.n.* (PI036636–036647!). **Italy, Sardegna**. Monti d'Iglesias a S. Benedetto, s.d., *P. Gennari s.n.* (FI002787! [lectotype of *Santolina insularis*, Arrigoni et al. 1982]); Sardinia, Provincia del Sud Sardegna, nelle garighe nei pressi di San Benedetto, Iglesias (Carbonia-Iglesias). 550 m s.l.m. circa, 14 June 2020, *G. Bacchetta, S. Cambria, P. De Giorgi & A. Giacò s.n.* (PI036068–03608!); Sardinia, Provincia del Sud Sardegna, Buggerru (Carbonia-Iglesias), Pranu Sartu [WGS84: 39.393611 N, 8.391666 E], nei pressi del mare su substrato calcareo, 70 m s.l.m. circa, 14 June 2020, *G. Bacchetta*, *S. Cambria, P. De Giorgi & A. Giacò s.n.* (PI036613–036625!); Sardinia, Oristano, ricca popolazione nella gariga lungo la vecchia linea ferroviaria nei pressi di Laconi (Oristano), 640 m s.l.m. circa, substrato calcareo, 15 June 2020, *G. Bacchetta, S. Cambria, P. De Giorgi & A. Giacò s.n.* (PI036052–036067!); Sardinia, Massiccio del Gennargentu [WGS84: 40.058586 N, 9.293333 E], lungo il sentiero che da Bruncu Spina porta a Monte Spada, su metamorfiti paleozoiche, 1350 m s.l.m. circa, 16 June 2020, *G. Bacchetta, S. Cambria, P. De Giorgi & A. Giacò s.n.* (PI036106–036121!); Sardinia, Oliena (Nuoro), Monte Corrasi [WGS84: 40.256036 N, 9.425972 E], substrato calcareo, 1200 m s.l.m. circa, 17 June 2020, *G. Bacchetta, S. Cambria, P. De Giorgi & A. Giacò s.n.* (PI036648–036663!); Sardinia, Monte Albo di Lula (Nuoro), [WGS84: 40.559385 N, 9.634941 E], gariga a dominanza di *Santolina*, substrato calcareo, 800 m s.l.m. circa, 16 June 2020, *G. Calvia, P. De Giorgi & A. Giacò* (PI036122–036136!).

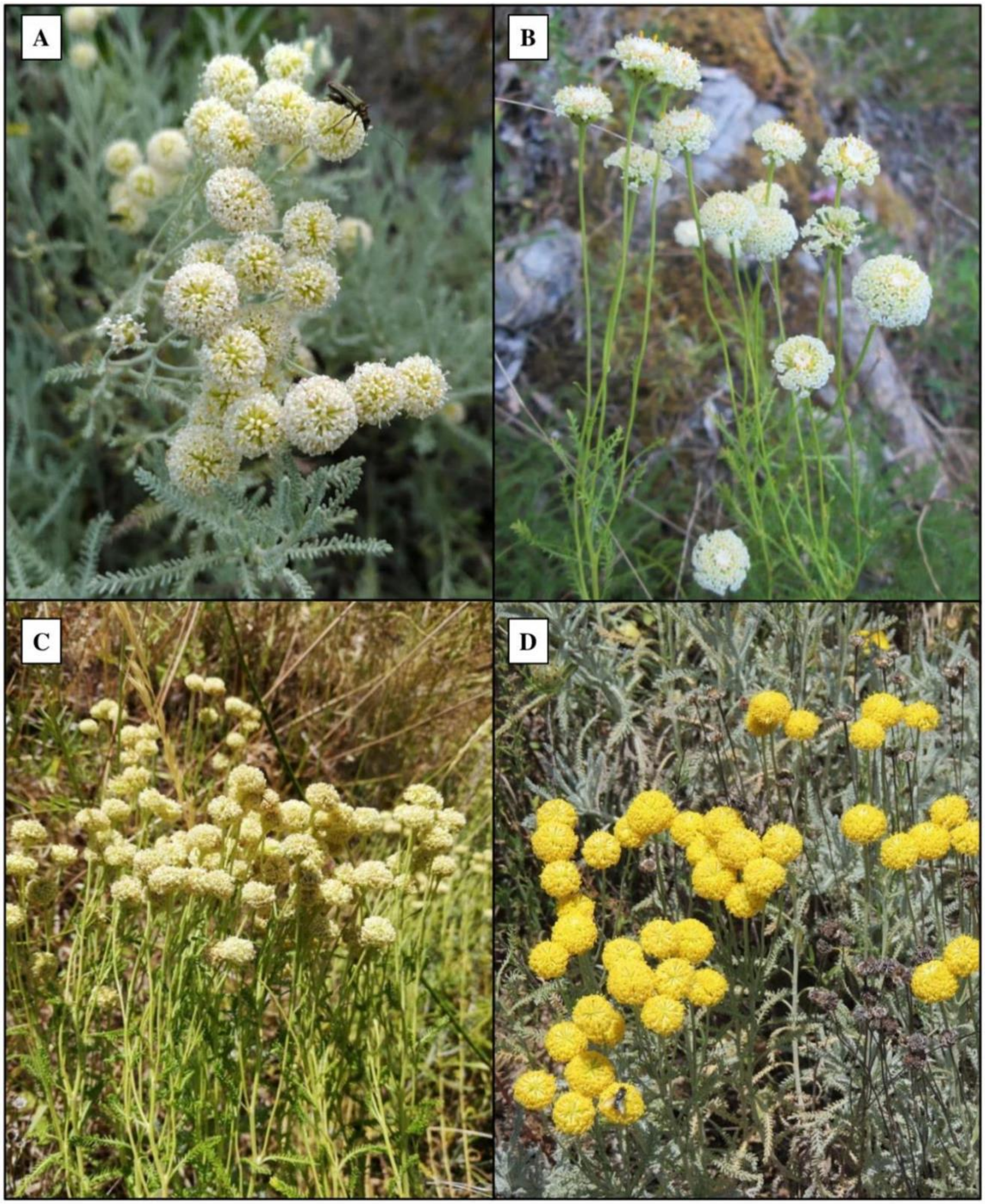

Figure 3. Pictures of continental Italian *Santolina* species in their natural habitat. *Santolina ligustica* (A), photo by G. Astuti (2019, Liguria, Deiva Marina); *S. pinnata* (B), photo by P. De Giorgi (2020, Tuscany, Apuan Alps, Forno); *S. etrusca* (C), photo by L. Peruzzi (2019, Tuscany, Arcidosso); *S. neapolitana* (D), photo by P. Caputo (2020, Campania, Castellammare di Stabia).

Santolina ligustica. **Italy, Liguria**. Levanto, ad rupes montis Rossola prope Levanto, August 1878, *H. Groves s.n.* (AUR06243!, GAP023874!, LY0715653!, LY0341673–0341675!, MPU1057247!, MPU1057248!, P04381090!, P03290270!, P03315567!); Liguria, Deiva Marina, fra Piazza e Castagnola, zone ofiolitiche, 16 July 1975, *P.V. Arrigoni s.n.* (FI001816! [holotype, Arrigoni 1977]); Liguria, Levanto, sugli affioramenti ofiolitici lungo la SS332 che da Piazza porta a Levanto (La Spezia), 22 July 2019, *G. Astuti & S. Chiletti s.n.* (PI030947–030971!).

Santolina etrusca. **Italy, Tuscany**. Pistoia, castagneti sotto Lizzano nell'Appennino Pistoiese, August 1856, *O. Beccari s.n.* (FI!); Grosseto, nell'alveo del fiume Albegna vicino al Monte Amiata, July 1859, *J. Porcelli s.n.* (SIENA); Siena, Presso le docce dei Bagni di Vignone, su calcare concrezionato, August 1860, *G. Campani s.n.* (FI!); Siena, via tra Bagno Vignone e Arcidosso, 17 June 1864, *T. Caruel s.n.* (PI!); Roccalbegna, 21 June 1864, *T. Caruel s.n.* (PI!); alle falde del Monte Amiata nella regione dell'olivo, 3 July 1873, *S. Sommier s.n.* (FI!); in aree sassose alle pendici settentrionali del Monte Amiata, 3 July 1873, *E. Levier s.n.* (FI!); Monte Amiata ai Bagni di San Filippo, 30 July 1873, *S. Sommier s.n.* (FI!); Val di Lima vicino alle fabbriche, Bagni di Lucca, August 1873, *J.F. Duthie s.n.* (FI!); in glareosis prope flumen Orcia sub oppidum Radicofani abundat, July 1875, *H. Groves s.n.* (BM000909643!); Casentino lungo il fiume Rassina, October 1833, *B. Ricasoli s.n.* (FI!); presso la stazione del Monte Amiata, 26 April 1882, *G. Arcangeli s.n.* (PI!); Casteldelpiano, 28 May 1883, *F. Parlatore s.n.* (FI!); a Cutigliano presso Lizzano (Lima), 17 July 1886, *E. Levier s.n.* (FI!); vicino a Rassina, July 1886, *E. Levier s.n.* (FI!); Casentino, August 1887, *F. Costa Righini s.n.* (FI!); Monte Amiata, August 1887, *F. Costa Righini s.n.* (FI!); da Rassina salendo a Chitignano, comune lungo la strada montuosa del Casentino, 17 September 1892, *S. Sommier s.n.* (FI!); Bagni di Lucca, alle fabbriche nel letto della Lima, August 1893, *S. Sommier s.n.* (FI!); La Marsiliana in Maremma di Macinaiole, 30 June 1919, *P. Pellegrini s.n.* (PI!); ai Bagni di San Filippo presso Castiglion d'Orcia, 20 June 1920, *P. Pellegrini s.n.* (PI!); Mt. Amiata, Casteldelpiano, suolo siliceo, m. 600, 3–4 July 1924, *A. Fiori s.n.* (FI!); Radicofani, stony valley of Orcia, 14 July 1924, *C. Lacaita 26906* (BM000909645! [lectotype, Giacò et al. 2021], BM000909644!, FI058570!); Casentino a Rassina, su suolo siliceo, m. 320, 4 July 1927, *A. Fiori s.n.* (FI!); Mt. Amiata, lungo la strada Seggiano-Madonna della Querce, nel bosco misto a leccio e roverella presso Osteria Ansitonia (400–450m), June 1971, P*.V. Arrigoni & E. Nardi* (FI!); Querceto presso Madonna della Querce, 4 June 1971, *P.V. Arrigoni s.n.* (FI!); Orbetello, lungo l'Albegna, in località Marsiliana, 23 July 1973, *P.V. Arrigoni & C. Ricceri s.n.* (FI!); depositi alluvionali dell'Albegna a ovest di Saturnia, 23 July 1973, *P.V. Arrigoni & C. Ricceri s.n.* (FI!); ai lati della strada per Arcidosso (Grosseto) al bivio per Stribugliano (Mt. Amiata), circa 600 m, 30 July 1973, *F. Garbari s.n.* (PI!); Civitella Paganico, su scarpata della strada per la stazione di Roccastrada ad un Km circa da Paganico, 13 July 1974, *P.V. Arrigoni, E. Nardi & M. Raffaelli s.n.* (FI!); ai Bagni di Vignone presso Quirico d'Orcia (Siena), July 1980, *P. Pellegrini s.n.* (PI!); nei pressi di Sant'Angelo in Colle, Stazione FS, fiume Orcia, 1 July 1989, *R.M. Baldini s.n.* (FI!); Tuscany, Siena, Contignano (Radicofani, Siena), lungo il greto del fiume Orcia presso la strada sterrata che porta che porta all'azienda agricola il Pero, 14 July 2022, *G. Astuti & P. De Giorgi s.n.* (PI040468–040479!); Tuscany, Grosseto, Pietra Sorbella, Arcidosso (Grosseto) WGS84: 42.855231 N, 11.465207 E, ambiente aperto su diaspro, 28 June 2020, *J. Franzoni & M. Franzoni s.n.* (PI051753!). **Lazio**. Viterbo, Bassano Scalo (Bassano in Teverina, Viterbo), lungo un viottolo sterrato tra il cavalcavia dell'autostrada e quello della ferrovia, 14 July 2020, *G. Astuti & P. De Giorgi s.n.* (PI040480–040501!).

Santolina neapolitana. **Italy, Campania**. Napoli, Castellammare di Stabia, Monte Sant'Angelo, 12 July 1846, *E. Cosson s.n.* (LY0826374! [lectotype, Del Guacchio et al. 2020]); Monte S. Angelo di Castellammare, 22 August 1891, *T. Caruel s.n.* (FI058911! [lectotype of *S. chamaecyparissus* var. *pectinata* f. *semivirescens* Fiori, Del Guacchio et al. 2020); Napoli, Lungo la strada da Castellammare a

Vico presso lo Scrajo sulle rocce alla parte del mare, 14 June 1897, *M. Guadagno s.n.* (PI018133!); Campania, Napoli, San Michele, sotto il santuario Vico Equense (Napoli), 8 July 2020, *P. Caputo & D. De Luca* (PI040502–040521!). **Calabria**. Calabria III, district. Castrovillari, in muris culturam cingent., pr. Lungro, sol. calcar., 4–500 m, 25 July 1877, *R. Huter, P. Porta, G. Rigo 669* (FI, two specimens!, MPU784459!, MPU958890!).

Santolina pinnata. **Italy, Tuscany**. M. Procinto (Alpi Apuane), s.d., *P. Pellegrini s.n.* (PI030083!): ad scaturigines Frigidae supra Fornole, 1807, *A. Bertoloni s.n.* (BOLO! [neotype, Garbari & Bechi 1992); Via della Volta e foce di Mosceta (Versilia), July 1897, *P. Pellegrini s.n.* (PI030080!); Alpe di Palagnana (Versilia), July 1899, *P. Pellegrini s.n.* (PI030081!); Cave del Forno/Biforco, 4 July 1934, *P. Pellegrini s.n.* (PI030084!); Sorgenti del Frigido (Massa), July 1940, *P. Pellegrini s.n.* (PI030082!); Tuscany, Massa-Carrara, sul sentiero che da Forno (Massa) porta al Pizzo della Bandiera, 9 July 2020, *G. Astuti & P. De Giorgi* (PI 040442–040461!).

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