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Taxonomic Revision of *Geranium* sect. *Dissecta* (Geraniaceae)

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ABSTRACT. *Geranium* section *Dissecta* (Geraniaceae) consists of four species centered in Eurasia, between the Mediterranean region and the Himalaya Mountains. In contrast to the current literature, we consider *G. chelikii*, and *G. davisianum* to be synonyms of *G. sintenisii*, and *G. pallens* to be a synonym of *G. asphodeloides*. We also accept *G. dissectum* and *G. crenophilum*, the latter sometimes considered as subspecies of *G. asphodeloides*. A multivariate morphometric study showed that some quantitative characters such as deeply divided leaves, shorter and narrower petals, and shorter filaments clearly distinguished the annual *G. dissectum*. The characters contributing most to separation of the three remaining perennial species were petal width and the length of glandular hairs of stem and pedicels. In *G. asphodeloides* and *G. dissectum* the rootstock and stem base has a very starch-rich parenchyma in the cortex, while in *G. sintenisii* and *G. crenophilum* the starch-rich parenchyma is mainly developed in the pith. A new key is provided, as well as new and detailed descriptions. *Geranium crenophilum* and *G. sintenisii* are here illustrated for the first time. Nine lectotypes and a neotype are designated, and distribution maps are presented. Analyses of the plastid *trnL-trnF* spacer, nuclear ITS sequences, and morphological data reveal that sect. *Dissecta* is strongly supported as monophyletic. In these analyses *G. dissectum* appeared as sister group to the rest of the species.

RESUMEN. *Geranium* sección *Dissecta* (Geraniaceae) está formada por cuatro especies cuya área principal es eurasiática, entre la región Mediterránea y las montañas del Himalaya. En este estudio consideramos *G. chelikii* y *G. davisianum* como sinónimos de *G. sintenisii* y *G. pallens* como sinónimo de *G. asphodeloides*. Además, aceptamos *G. dissectum* y *G. crenophilum*, este último considerado a veces como subespecie de *G. asphodeloides*. Un análisis morfométrico mostró que los caracteres cuantitativos más importantes para diferenciar *G. dissectum* son sus hojas profundamente divididas, sus cortos y estrechos pétalos y sus cortos filamentos estaminales. Los principales caracteres cuantitativos que separan las especies perennes son la anchura de los pétalos y la longitud de los pelos glandulíferos de tallo y pedicelos. El rizoma y la base del tallo de *G. asphodeloides* y *G. dissectum* se caracterizan por un parénquima con células ricas en almidón situado en el cortex, mientras que, en *G. sintenisii* y *G. crenophilum*, dicho parénquima se localiza principalmente en médula. Se presenta una nueva clave, así como nuevas y detalladas descripciones y mapas de distribución para cada una de las especies y se eligen nueve lectótipos y un neótipo. *Geranium crenophilum* y *G. sintenisii*, son aquí dibujados por primera vez. Tanto el análisis cladístico de los caracteres morfológicos, como el de las secuencias de ADN de un marcador cloroplástico (*trnL-trnF*) y uno nuclear (ITS) indican que la monofilia de la sect. *Dissecta* está fuertemente apoyada. En estos análisis *G. dissectum* aparece como grupo hermano de las restantes especies.

The genus *Geranium* L. comprises ca. 400 species in temperate areas and tropical mountains throughout most of the world (Aedo et al. 1998a). A brief history of the generic delimitation and infrageneric classification, as well as a description of the genus can be found in Aedo (1996). In addition, a key for subgenera and sections can be found in Aedo et al. (1998b and 1998a, respectively).

According to the currently accepted classification (Yeo 1984), *Geranium* is divided into three subgenera: subgen. *Erodioidea* (Picard) Yeo, subgen. *Robertium* (Picard) Rouy, and subgen. *Geranium*. Subgenus *Erodioidea*, which includes 22 species in four sections, was recently monographed (Aedo 1996, 2001): two sections are in the Mediterranean and western Asia, one is centered in the mountains of tropical East Africa, and one is in southern Brazil and northern Argentina. According to Yeo's (1984) sectional classification, subgen. *Robertium* comprises 30 species in eight sections, two of them not yet revised (Yeo 1973, 1992; Aedo et al. 1998b).

Geranium subgen. *Geranium*, the largest subgenus, comprises over 370 species, grouped in at least 10 sections. Section *Tuberosa* (Boiss.) Reiche (Davis 1970), sect. *Neurophyllodes* A. Gray (Carlquist and Bissing 1976), sect. *Azorelloida* Aedo, Muñoz Garm. & Pando, sect. *Neoandina* Aedo, and sect. *Paramensia* R. Knuth (Aedo et al. 2002), sect. *Trigonium* Dumort. (Aedo 2003), and sect. *Gracilia* R. Knuth (Aedo et al. 2003) have already been revised. Most species are in sect. *Geranium*, which probably will be subdivided when satisfactory knowledge of the subgenus is obtained. Knuth's (1912, 1931) subdivision (32 sections) of the genus has been questioned by numerous authors, though without advancing an alternative until Yeo's (1984) review. However, Knuth's sections should be reconsidered when a new classification of the whole subgen. *Geranium* is undertaken.

Knuth's (1912) monograph of *Geranium*, based on limited material available at that time, classified species of sect. *Dissecta* (which belong to subgen. *Geranium*) in two different groups. *Geranium dissectum* was

included in sect. *Columbina* W. D. J. Koch, which was an aggregate of annual species now considered as belonging to different groups. *Geranium asphodeloides* and *G. sintenisii* were included in sect. *Pyrenaica* R. Knuth. In *G. asphodeloides*, Knuth (1912) accepted three varieties: a) *genuinum*, b) *hispidum*, and c) *nemorosum*. He considered *G. crenophilum* as a synonym of the second variety, but included plants from NW Turkey (*G. asphodeloides* s. str.), Caucasus (*G. asphodeloides* s. str.), and Lebanon (*G. crenophilum*). Additionally, Knuth (1912) considered *G. tauricum* a synonym of *G. collinum* Stephan ex Willd., a species of sect. *Geranium*. As an unavoidable consequence of this scarcity of material (one specimen studied in *G. sintenisii*, and two in *G. crenophilum*), the taxonomic treatment was incomplete and morphological descriptions lacked some important features of rootstock, roots, petals, fruits, indumentum, etc. Thus, Knuth's key has some ambiguous couplets (e.g., *G. sintenisii* is entered by "flores valde numerosi" as opposite to "Flores vix numerosi" in *G. asphodeloides*, when they have no differences in this character). Additionally, Knuth's (1912) distributions were just preliminary (without maps) and no drawings were provided.

Major floras of the Eastern Mediterranean region and neighboring territories accept *G. dissectum*, but provide different treatments for *G. asphodeloides* and related perennial species. For instance, Bobrov (1949) accepted *G. pallens* as endemic from the Caucasus, and *G. tauricum* as endemic from Crimea, both treated here as synonyms of *G. asphodeloides*. Mouterde (1966) accepted *G. asphodeloides* and *G. crenophilum* as a part of the Lebanon flora, but included *G. pallens* as a synonym of the latter. Davis (1967) treated the Turkish taxa as subspecies of *G. asphodeloides* (subsp. *asphodeloides* and subsp. *sintenisii*). However, he included in subsp. *sintenisii* all specimens with glandular hairs, a part of which are identified here as *G. asphodeloides* s. str.

During the 1980s two new species of this section were proposed, both from Turkey. *Geranium davisianum* was described by Peşmen and Güner (Peşmen 1980), and *G. chelikii* by Kit Tan and Yildiz (1989). Unfortunately, these authors distinguished their species against *G. asphodeloides*, not against *G. sintenisii*.

The species of sect. *Dissecta* have the "seed ejection-type" of fruit discharge and the mericarp has a prong at the lower end. It is an important character, unique in *Geranium*, suggesting that sect. *Dissecta* is a natural group (Yeo 1984). *Geranium asphodeloides*, *G. sintenisii*, and *G. crenophilum* are large-flowered perennials, while *G. dissectum* is a small-flowered annual, generally considered as autogamous. They are distributed from Macaronesia to the western Himalayas, while *G. dissectum* has been introduced to many temperate areas throughout of the world.

Following our recent revisions of several *Geranium*

sections (Aedo 1996, 2001, 2003; Aedo et al. 1998b, 2002, 2003), and in pursuit of a comprehensive monograph of the genus, we present here a revision of section *Dissecta*.

MATERIALS AND METHODS

This revision is based on more than 630 herbarium specimens from the following herbaria: B, BC, BISH, BM, BRIT, CAN, COI, CONC, CORD, DAO, E, F, G, GA, ILL, K, KE, LE, LP, M, MA, MAE, MO, MPU, MUB, NA, NEU, NY, O, P, PACA, PERTH, PH, QFA, RENO, RO, S, SALA, SGO, SS, TAA, TEX, UC, W, and WVA. Furthermore, microfiches, color slides, digital photographs, and other data have been examined from JBSD and LINN. Curators from BP, CHARL, CL, GOET, L, LW, LY, PH, and PRE kindly answered our request, but they did not find any of the requested specimens in their herbaria, or could not send them.

Unfortunately, we have had difficulties in obtaining some types on loan. The most relevant cases are those of F. Schur. Schur's original material is spread through several herbaria. Some of them did not respond to our request, while the remaining have none of Schur's original material requested. The dispositions of names for which no type material could be located or obtained are based on the opinions of previous authors. Where no reliable justification was found, these names are included in an "Excluded Names" section.

Roots and rootstocks were cut with a SLEE-MAINZ-MTC microtome, stained with Fasca mixture (Tolivia and Tolivia 1987) or with Sudan red and Malachite green, and photographed under optical microscopy. For scanning electron microscopy (SEM), samples were glued to aluminium stubs, coated with 40–50 nm gold, and examined with a JEOL-TSM T330A scanning electron microscope at 15 kV.

Pollen was counted for at least six specimens in each species and Pollen/Ovule ratio (P/O) was calculated according to Cruden (1976, 1977). The number of viable ovules in *Geranium* is 5, one for each mericarp. The ovary initially has ten, but five degenerate during flower development. Thus, we have calculated the ratio P/O considering only the viable ovules, that is: number pollen grain of one anther \times 10 anthers / 5 ovules. Protandry was studied in flowers of living specimens for *G. asphodeloides* and *G. dissectum*, and in herbarium specimens in the remaining species. Only two species could be cultivated and analyzed directly for autogamy during this work; they were *G. asphodeloides* and *G. dissectum*. Their flowers were bagged and the proportion of mature fruits developed was counted.

Forty quantitative characters were recorded and measured using a Mitutoyo CD-15CD digital caliper. Each character was analyzed for its mean and median values, range, standard deviation and significance, using the STATISTICA package. To represent the variability of each descriptor within species, box-plots containing medians and percentiles were prepared. A basic matrix was produced, from which some characters were removed since they were redundant or showed little variability. The parameters used as descriptors are summarized in Table 1. Separation of the taxa was tested by means of Discriminant Analysis (DA). This method (Sneath and Sokal 1973), which requires a priori assignment of OTUs to groups, indicates whether the recognized groups are statistically definable entities or whether there is too much variation within groups to allow separation. For DA, the raw matrix was obtained, the results sorted in discrete groups, and calculations carried out using the Statistica package version 6 (www.statsoft.com).

Quantitative and qualitative characters were used in the key, being the most discriminant quantitative characters inferred from box-plots. Several interesting characters have broad ranges of variability that caused some difficulties for their use. In order to avoid these problems the ranges are included in brackets in the key (even

TABLE 1. Standardized coefficients obtained in DA for canonical variables.

	Root 1	Root 2
Stem eglandular hairs length	0.34984	0.19063
Stem glandular hairs length	-0.72231	0.45387
Second sinus length	0.52406	0.20315
Segment lobes number	-0.05005	0.07057
Stipules length	0.15922	0.25524
Petiole eglandular hairs length	-0.27157	-0.32385
Petiole glandular hairs length	-0.12605	0.03678
Peduncles length	0.71219	-1.19985
Pedicels glandular hairs length	-0.25617	0.48986
Cymule length	-1.27390	1.02035
Sepals length	-0.34250	0.05111
Sepals eglandular hairs length	0.52792	0.16771
Sepals glandular hairs length	0.43325	-0.30647
Petals length	-0.48573	0.10414
Petals width	0.54969	-0.99398
Filaments length	-0.88627	-0.30786
Gynoecium length	-0.39188	0.44475
Eigen values	22.57999	7.33949
Total cumulative proportion	0.66441	0.88038

considering that in some rare cases they differed considerably from the mean values). The most frequent and useful values are done by percentiles and are shown outside the brackets.

Fifteen sequences from eight individuals (representing four species of *Geranium* sect. *Dissecta* and one outgroup) were obtained from silica-dried leaves. Approximately 20 mg per individual of leaf tissue from fresh (collected in the field) or herbarium material was used, and DNA was extracted using a DNeasy Plant Mini Kit (QIAGEN Laboratories, Germany). Then, the nrITS and chloroplast *trnL-trnF* spacers were sequenced (Table 2) for forward and reverse strands. DNA was amplified using PCR (Polymerase Chain Reaction) and the primers ITS-4 and ITS-5 and 17SE and 26SE (White et al. 1990) for the ITS-spacer (Baldwin 1992); and E and F primers for the *trnL(UAA)-trnF(GAA)* spacer (Taberlet et al. 1991). PCR conditions for amplification are explained in Fiz et al. (2002). Amplified products were purified using spin filter columns (PCR Clean-up kit, MoBio Laboratories, California). Cleaned products were sequenced, placed in a contig file and edited using the program Seqed (Applied Biosystems). The boundaries of the ITS1, 5.8S, ITS2, and *trnL-trnF* sequences were determined by comparison with *Nicotiana tabacum* L. (Shinozaki et al. 1986) available in the Genbank. Clustal X 1.62b was used for the alignment of the sequences, followed by manual adjustment. *Geranium palmatum* Cav. was chosen as outgroup based on the ITS, *rbcl*, and *trnL-trnF* analyses of Geraniaceae. It belongs to subg. *Robertium*, which is the sister group of subg. *Geranium*, which includes sect. *Dissecta* (Price and Palmer 1993; Aldasoro et al. unpublished data).

Phylogenetic analyses of molecular and morphological matrices (Tables 3, 4) as well as total evidence analysis (TreeBase study

accession number S1266, matrix accession numbers M2209-2210) were performed using PAUP*4.0 (Swofford 1999). Heuristic searches were replicated 100 times with random taxon-addition sequences, Tree Bisection-Reconnection (TBR) branch swapping, and with the options MULPARS and STEEPEST DESCENT in effect. Exhaustive searches were also carried out. Support for monophyletic groups was assessed by both "fast" bootstrapping (10000 resamplings of data) and "full" bootstrapping (100 resamplings) using the heuristic search strategy as indicated above. Genetic distances between pairs of sequences were obtained using the Neighbor-Joining method with Kimura 2-parameter distance model (Kimura 1980; Saitou and Nei 1987).

RESULTS

Morphology. DURATION AND HABIT. All species of *Geranium* sect. *Dissecta* except *G. dissectum* are perennial herbaceous plants. *Geranium dissectum* has weak, ramified roots; *G. asphodeloides* and *G. crenophilum* share \pm horizontal and cylindric rootstocks, with a bundle of thick fleshy, fasciculate roots (they resemble that of the genus *Asphodelus* L., Asphodelaceae) and *G. sintenisii* has \pm vertical, short, turnip-shaped rootstock, lacking fasciculate roots. Several other species of *Geranium* sometimes have fleshy roots, such as *G. lainzii* Aedo, *G. brasiliense* Progel, and *G. palustre* L., but these normally grow in wet habitats. In contrast, *G. asphodeloides* and *G. crenophilum* grow in meadows and sometimes on rocky slopes.

To examine their anatomical structure, rootstocks were cut and stained. In *Geranium*, secondary xylem usually develops in rays while bundles are in an outer position forming a ring. These xylem rays can have many lignified tracheary elements and fibers. Reserve tissues are commonly spread in the cortex and the pith (Yeo 1973). However, several other distribution types can be found in certain *Geranium* species (Aedo et al. 2002). In sect. *Dissecta*, the rootstock and stem base show structural differences among species: in *G. asphodeloides* and *G. dissectum* most parenchymatous, starch-rich cells are situated in the cortex while the pith is filled with tracheary elements (Fig. 1A-C). In *G. sintenisii* and *G. crenophilum* the starch-rich parenchyma is developed in the pith, and in the outer part there is a secondary xylem forming deep rays with many tracheary elements (Fig. 1D). The greater development of secondary xylem in these species leads to

TABLE 2. Voucher information for species of *Geranium* included in the cladistic analysis, with GenBank accession numbers for *trnL-F* and ITS sequences, respectively.

<i>G. asphodeloides</i> - Turkey: Evciler, Kaz Dagı, <i>Castroviejo</i> 15220 (MA-643795) AY944424, AY944414.
<i>G. asphodeloides</i> - Turkey: Bandirma, Erdek, <i>Castroviejo</i> 15201 (MA-643792) AY944425, AY944415. <i>G. crenophilum</i> - Lebanon: Ehden, <i>Pabot s.n.</i> (G) AY944419, AY944412. <i>G. dissectum</i> - Chile: La Araucania, Yupehue, <i>Aedo</i> 7175 (MA-683001) AY944421, AY944413. <i>G. dissectum</i> - Spain: Teruel, Valderrobles, <i>Aedo & al.</i> 5077 (MA-626485) AY944420, -. <i>G. sintenisii</i> - Turkey: road Torul to Trabzon, <i>Nisa & al.</i> 712 (MA-688913) AY944423, AY944417. <i>G. sintenisii</i> - Turkey: Gümüşhane, road Yeniyl to Yagmurdere, <i>Herrero & al.</i> 1402 (MA-687191) AY944422, AY944416. <i>G. palmatum</i> - Portugal: Madeira, Porto Moniz, <i>Vargas</i> 277PV00 (MA- 654940) AY944418, AY944411.

TABLE 3. Data matrix used in the cladistic analysis of morphological characters of *Geranium* sect. *Dissecta*. Characters and character states are explained in Table 4.

	1	2	3	4	5	6	7	8	9	10	11	12
<i>G. sylvaticum</i>	0	1	0	0	0	0	0	0	0	0	0	0
<i>G. palmatum</i>	0	1	0	0	1	1	0	1	1	0	0	0
<i>G. asphodeloides</i>	0	2	0	0	1	0	0	0	1	1	1	1
<i>G. crenophilum</i>	0	2	1	1	1	0	0	1	1	1	1	1
<i>G. sintenisii</i>	0	1	1	1	1	0	0	1	1	1	1	1
<i>G. dissectum</i>	1	0	0	0	1	1	1	0	1	0	1	1

more wood production, also consistent with their growth in icy habitats.

All species have stems with a phellogen that produces layers of cork that peel off easily (Fig. 1B), but the phellogen is more developed in *G. sintenisii* and *G. crenophilum*. Additionally, in these species the stems are usually protected by stipule remains and petioles of old leaves. Both cork and leaf remains may protect the stem against cold and snow.

INDUMENTUM. Three trichome types have been found in the species studied here, all of them simple and uniseriate (Theobald et al. 1979): a) Eglanular, unicellular hairs of variable length (0.2–1.6 mm), usually with an ornamented surface. According to Payne (1978), these could be included in the “subulate” type. They have been found in all species, and are present in all organs of the plant (Fig. 2A, 2B). b) Glandular hairs, with 2–4 cells, smooth; the foot consists of cylindrical cells or of decussate cells and the head is always unicellular; two subtypes can be distinguished: b1) medium (0.2–1 mm long) and straight, found in all species (Fig. 2A–C), and b2) long (to 3.4 mm long) and a bit tortuous, restricted to *G. crenophilum* and *G. sintenisii* (Fig. 2A). c) Short glandular hairs (<40 µm long), smooth, usually composed of two cells, although they sometimes have a bicellular foot (Fig. 2A). They are present in all species studied but are not consid-

ered in the descriptions because they are only evident at high magnification.

LEAVES. The leaves of all species of sect. *Dissecta* are polygonal in outline, cordate, palmatifid, with 5–7 segments. Basal leaves frequently form a deciduous rosette, while cauline leaves are opposite. However, *G. dissectum* sometimes has alternate cauline leaves in the lower third of the stem. All species have palmatipartite leaves, but those of *G. dissectum* are more deeply divided, almost palmatisect.

INFLORESCENCES. The cymules in this section are usually 2-flowered (rarely 1-flowered), as in many other species of subg. *Geranium*. *Geranium dissectum* cymules are shorter than the adjacent leaf, while in the other three species cymules overtop the subtending leaf.

CALYX. Sepals are not accrescent, smooth, and 3-nerved in the four species of the section. The most significant sepal feature is the size of sepal indumentum, there are longer glandular hairs in *G. crenophilum* (0.3–1.5 mm), and *G. sintenisii* (0.3–1.4 mm), while they are shorter in *G. asphodeloides* (0.3–1 mm) and *G. dissectum* (0.2–0.8 mm).

COROLLA. The flowers are actinomorphic showing purplish petals in the four species of this section. The petals usually have an entire apex, except in *G. dissectum*, which is shallowly notched. All species have a

TABLE 4. Characters and character states used for cladistic analysis of *Geranium* sect. *Dissecta*.

1. Habit: 0 = perennial, 1 = annual.
2. Rootstock type: 0 = lateral roots thin, rootstock absent, 1 = vertical rootstock with lateral roots thin, not fleshy, 2 = horizontal or slanted rootstock bearing thick, fleshy, and fasciculate roots.
3. Rootstock structure parenchyma: 0 = parenchymatous tissue formed starch-rich cells situated in the cortex, pith showing a secondary xylem with many tracheary elements, 1 = most parenchymatous, starch-rich cells developed in the pith, starch-rich cells scarce or absent in the cortex.
4. Rootstock structure growth: 0 = not well developed cork in the outer part of rootstock, 1 = outer part of the rootstock developed with many layers of cork.
5. Leaf position: 0 = alternate, 1 = opposite.
6. Leaf division: 0 = shallowly palmatipartite, 1 = deeply palmatipartite.
7. Cymule/leaf ratio: 0 = overtopping the subtending leaf, 1 = not overtopping the subtending leaf.
8. Glandular hairs on inflorescence: 0 = short, 1 = long.
9. Petal claw: 0 = without claw, 1 = with claw.
10. Nectary indumentum: 0 = glabrous, 1 = hairy.
11. Mericarp prong: 0 = absent, 1 = present.
12. Seeds: 0 = ellipsoid, 1 = subspheric.

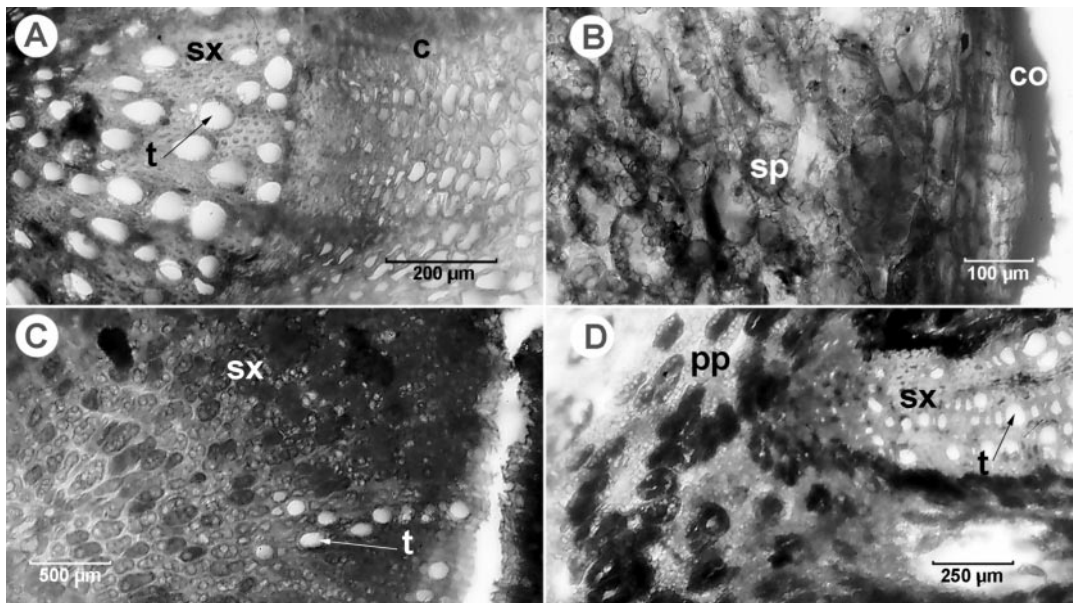


FIG. 1. Optical microscope photographs showing anatomical features of rootstock, all transverse sections. A. Upper part of the root in *Geranium dissectum*, showing secondary xylem with tracheary elements and the cortex [Aedo 2035 (MA)]; B. Cortex of *G. asphodeloides* showing secondary parenchyma with abundant starch grains and cork [Castroviejo 15220 (MA)]; C. Inner part of rootstock of *G. asphodeloides* showing secondary xylem with tracheary elements [Castroviejo 15220 (MA)]; D. Inner part of rootstock of *G. sintenisii* showing pith with storage parenchyma and abundant starch grains and the secondary xylem with tracheary elements [Herrero 1402 (MA)]. Abbreviations: c = cortex; co = cork; pp = pith with parenchymatous storage cells; sp = secondary parenchyma with storage cells; sx = secondary xylem; t = tracheids.

short claw with some cilia. The three perennial species have longer petals (8.5–16.3 mm long), while those of *G. dissectum* are shorter (2.9–5.8 mm long). Petals of *G. sintenisii* are narrow: 3.5–4.8 mm, while those of *G. asphodeloides* and *G. crenophilum* are wider: (4.8–)6.1–8.5 mm and 5–9.4 mm, respectively. Consequently, *G. asphodeloides* and *G. crenophilum* have the largest petal surface, that of *G. sintenisii* is slightly smaller, and *G. dissectum* has the smallest (Figs. 3, 6F, 6G).

Petal size is correlated with reproductive success in *Geranium* as well as in many other genera (Bell 1985; Phillip and Hansen 1999). Consequently, longer petals are expected in allogamous taxa, yet the opposite trend has sometimes been reported (Bertin and Newman 1993). In our case the petal surface is significantly correlated with number of pollen grains per anther ($r = 0.781$; $p < 0.0000$), but there is a large gap between *G. dissectum* and the perennial species (Fig. 3) and there is no correlation between the two variables in the latter group of species. Petal surface is also correlated with other parameters such as anther length ($r = 0.789$; $p < 0.0000$) and gynoecium length ($r = 0.676$; $p < 0.0000$), showing a similar pattern.

POLLINATION. Only two species were analyzed for autogamy during this work; they were *G. asphodeloides* and *G. dissectum*. In *G. asphodeloides* only 4% of fruits in bagged flowers developed, while in *G. dissectum* the proportion reached 85%. These data indicate that only

G. dissectum is efficiently self-pollinated. The other two large-flowered species should also present a weak self-pollination as can be deduced from two sources: 1- higher P/O rates than *G. dissectum* (Table 5; Cruden 1976, 1977), and 2- after comparing herbarium specimens of *G. sintenisii* and *G. crenophilum* with low and high fruit production, we observed a very low number of mature fruits in plants with fewer pollen grains on the stigmas of open flowers, suggesting reduced activity by pollinators; conversely, most specimens of *G. dissectum* had a similar number of pollen grains on the stigma (generally low) and a high fruit production.

According to Philipp (1985), most perennial species of *Geranium* produce large flowers with pronounced protandry, avoiding selfing processes. In other species, a decrease in protandry is accompanied by a reduction in flower size, and at the same time increased chances for self-pollination; this situation occurs in *G. dissectum*. Cruden (1976, 1977) emphasized that the Log pollen/ovule ratios (Log P/O) are correlated with breeding system. A substantial decrease in Log P/O suggests a change from allogamy to autogamy. The species studied here show two different groups: perennials with mean values between 2.99 and 3.02 and the only annual (*G. dissectum*) with 2.05 (Table 5).

In *G. dissectum*, the flowering period ranges from January to October (excluding South Hemisphere specimens), but most plants flower from April to June (Fig.

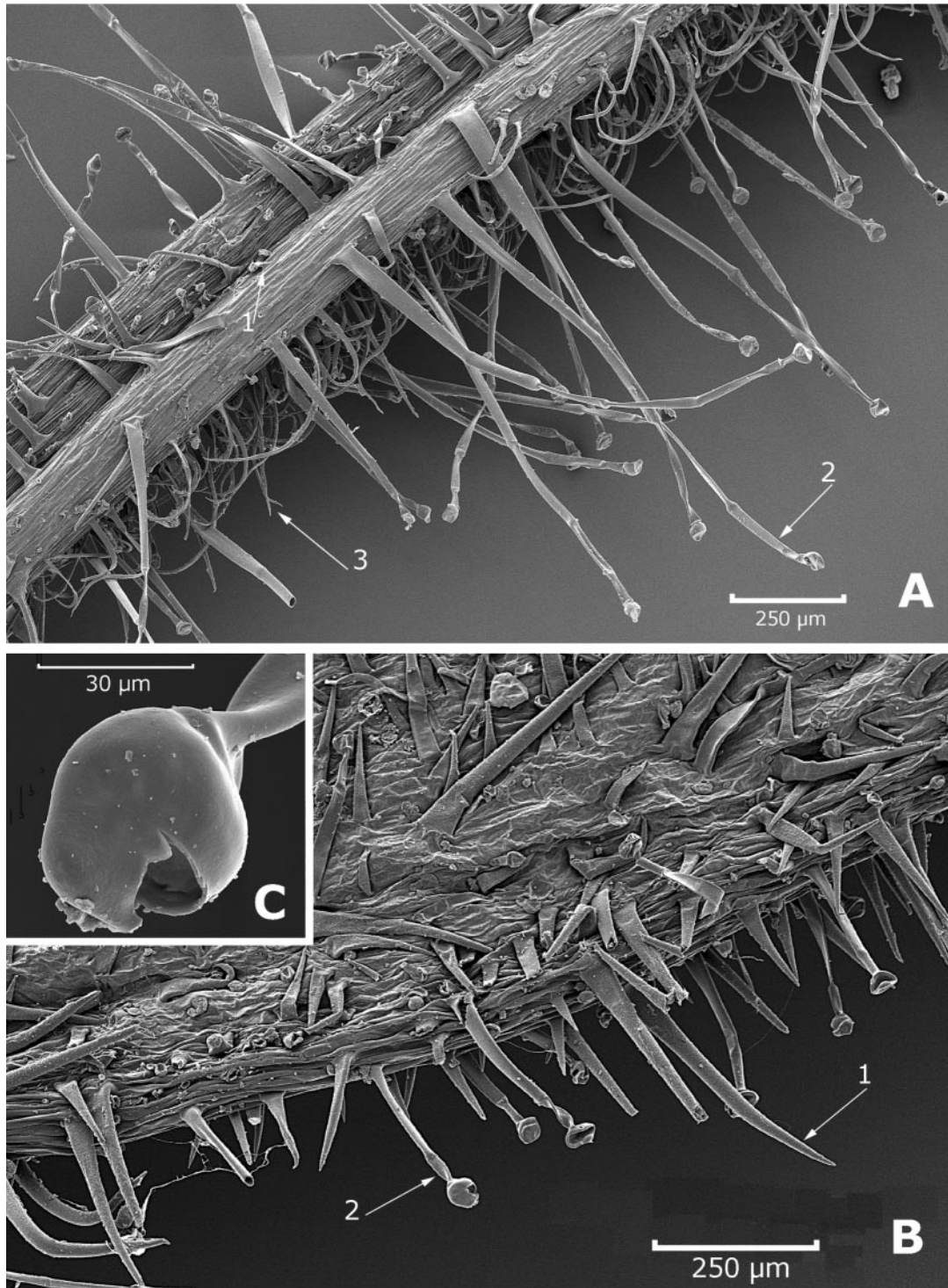


FIG. 2. SEM photographs showing trichome types found in *Geranium* sect. *Dissecta*. A. Pedicel of *G. sintenisii* showing: (1) short glandular hairs, (2) long and tortuous glandular hairs, and (3) eglandular hairs (Herrero & al. 1402, MA). B. Pedicel of *G. asphodeloides* showing: (1) eglandular hairs, and (2) medium and straight glandular hairs (Castroviejo 15308, MA). C. Apex of a long and straight glandular hair (Castroviejo 15308, MA).

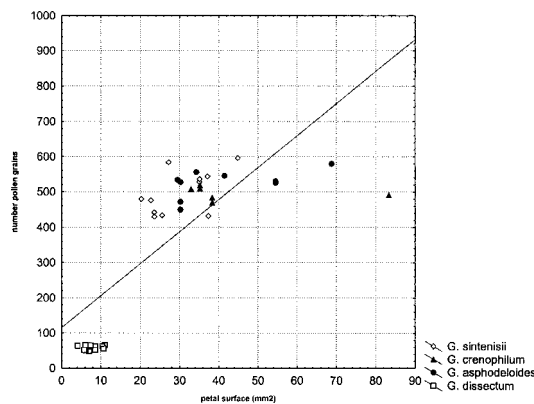


FIG. 3. Scatter plot of mean number of pollen grains per anther vs. petal surface in *Geranium* sect. *Dissecta*.

4B). As expected, in the perennial species this period is shorter: from March to July in *G. asphodeloides* and from May to August in *G. crenophilum* and *G. sintenisii*. *Geranium crenophilum* and *G. sintenisii* probably flower later than *G. asphodeloides* because they grow at higher elevations (Fig. 4A).

STAMENS, POLLEN, AND NECTARIES. In *Geranium* there are 10 stamens grouped into two whorls of different length, with the stamens of the external whorl maturing before those of the inner whorl. However, in *G. dissectum* both whorls usually ripen at the same time. The filaments of sect. *Dissecta* are lanceolate with an abruptly narrowed apex in *G. dissectum*, both whorls are included inside the flower. They are ciliate along the filament in *G. dissectum*, but only at its base in the remaining species. The filaments of both whorls are shorter in *G. dissectum* (1.8–3 mm the external and 1.2–2.1 mm the internal) and longer in the perennial species (5.7–8.4 mm the external and 5–7.8 mm the internal).

Pollen of species studied here is characterized by reticulate exine ornamentation with distinctly baculate, clavate, or gemmate supracteal elements (Fig. 5A, B) as in other *Geranium* species (Weber 1996). According to Stafford and Blackmore (1991), pollen of *G. dissectum* has a 63–79 μm polar diameter and 62–80 μm of equatorial diameter. Pollen of the perennial species is similar in size to that *G. dissectum*.

The five hemispherical nectaries are arranged alternately to the external whorl of staminal filaments.

They are glabrous in *G. dissectum* and exhibit a tuft of hairs at the top of each nectary in *G. asphodeloides*, *G. crenophilum*, and *G. sintenisii*. The nectaries are longest in *G. asphodeloides* and *G. sintenisii*, shorter in *G. crenophilum*, and smallest of all in *G. dissectum* (Fig. 4C). This is consistent with a lower production of nectar in the autogamous *G. dissectum*.

All these data indicate that *G. dissectum* is mainly autogamous while *G. asphodeloides*, *G. crenophilum*, and *G. sintenisii* are mainly allogamous. This is congruent with the fact that these three species are protandrous while *G. dissectum* shows adichogamy. As in *G. sessiliflorum* (Philipp 1985), self-pollination could happen by inward movement of the stamens, bringing them into contact with the stigma lobes. *Geranium sintenisii* shows smaller petals than the other two perennials while *G. crenophilum* shows smaller nectaries, which could indicate a trend to autogamy; however these three species have similar pollen production (Fig. 3, 4C; Table 5).

GYNOECIUM. *Geranium asphodeloides*, *G. crenophilum*, and *G. sintenisii* have a longer gynoecium (3.4–8.8 mm) than *G. dissectum* (1.1–3 mm). The stigmas are glabrous in the three perennials, whereas those of *G. dissectum* are hairy, with eglandular, antrorse hairs on the abaxial surface. These hairs could favor capture of pollen grains dispersed by flower movements.

FRUIT. *Geranium* sect. *Dissecta* is assigned to subgenus *Geranium*, which exhibits the “seed ejection-type” of fruit discharge (Yeo 1984). In this type of fruit, a single seed is actively discharged by the explosive recurvature of the awn, with the rest of the awn and the mericarp wall remaining attached to the columella. Most sections of subg. *Geranium* have a cluster of bristles at the lower end of the mericarp. These bristles are always borne on a callus and prevent the seed from falling out prematurely in the pre-explosive interval. In sect. *Dissecta*, the seed is retained in the mericarp during the pre-explosive interval by a part of the mericarp wall, which projects as a prong. This prong has the same texture as the rest of the mericarp wall and it functions in the same way as the bristles (Fig. 5C, D).

The fruit is shorter in *G. dissectum* (15.1–18.5 mm long) than in the remaining species (14.7–20.9 mm long). Mericarps are similar in size and are smooth and brownish in all species. The rostrum has a nar-

TABLE 5. Pollen-ovule ratio and fruit production in bagged flowers of *Geranium* sect. *Dissecta* (sd.: standard deviation; n.s.: not studied).

Taxa	pollen number/anther		Pollen-ovule ratio	Log pollen-ovule ratio	Mature fruits produced in bagged flowers (percentage of fruits ripen divided by total number of flowers)
	mean	sd			
<i>G. asphodeloides</i>	524.6	40.27	1049.2	3.02	4%
<i>G. crenophilum</i>	497.1	18.42	994.2	2.99	n.s.
<i>G. sintenisii</i>	498.3	62.03	996.6	2.99	n.s.
<i>G. dissectum</i>	55.91	11.48	111.82	2.05	85%

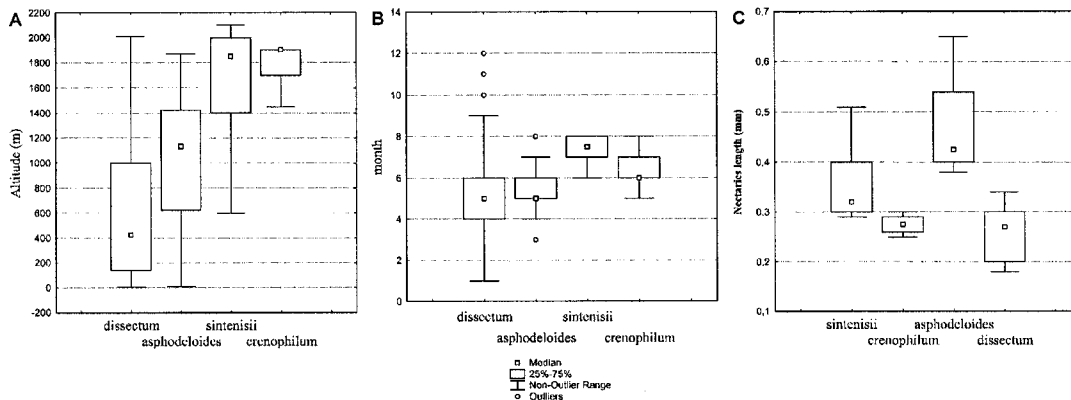


FIG. 4. Box plot showing elevation ranges (A), flowering period (B), and nectary length (C) in species of *Geranium* sect. *Dissecta*.

rowed apex, shorter in *G. dissectum* (1.6–2.7 mm long) than in the remaining species (3.7–6.9 mm long).

SEEDS. The seeds are usually brownish, more or less subspheric, reticulate, without spots, with scattered stomata. The seed coat is finely reticulate at a magnification of 30 \times , but SEM shows that the reticulate surface is due to the prominence of the outer and middle layers of the outer integument. Seeds have a similar size in the four species and have a short hilum (usually 1/8 as long as the perimeter) (Fig. 5E, F).

The cotyledons are always conduplicate, one half of each cotyledon lying in the primary fold of the opposite cotyledon. They are pale green, and have entire margins, truncate bases, and short petioles, as found in sect. *Batrachioidea* (Aedo et al. 1998b).

Chromosome Numbers. The chromosome number varies from $2n = 22$ to $2n = 30$. All chromosome counts carried out in *G. dissectum* gave $2n = 22$ (Gauger 1937; Warburg 1938; Löve and Löve 1945; Gadella and Kliphuis 1966; Májovský 1974; Löve and Kjellqvist 1974; Alves and Leitão 1976; Skalińska et al. 1976; De Leonardis et al. 1981; Strid and Franzén 1981; Kirschner et al. 1982; Van Loon 1984b; Hollingsworth et al. 1992; Díaz Lifante et al. 1992; Lövkqvist and Hultgard 1999). There are contradictory counts for *G. asphodeloides*, one of the perennial species. In *G. asphodeloides*, Warburg (1938) reported $2n = 28$ and Strid and Franzén (1981) $2n = 30$ plus some fragments, but the number most frequently found in this species was $2n = 24$ (Van Loon and Oudemans 1982; Van Loon 1984a; Baltisberger 1991). Guittonneau (1975) reported $2n = 26$ for *G. asphodeloides* subsp. *sintenisii*. However, he kindly sent us the voucher for this count (kept in his private herbarium), and this specimen is really *G. asphodeloides*. Guittonneau also informed us that " $2n = 26$ " was an error and the true number for this specimen was $2n = 28$.

Habitat and Distribution. The area with highest diversity is the eastern Mediterranean, with three en-

dem species. Among these species, *G. crenophilum* and *G. sintenisii* are restricted to rather small areas, NE Lebanon and NE Turkey, respectively. In contrast, *G. asphodeloides* grows from Sicily to the Caucasus, in a longitudinal range comprising ca. 2500 km. Finally, *G. dissectum* is a weed distributed worldwide; it is probably indigenous to the Eurasian portion of its range, but it has probably been introduced into many temperate areas of North America, South America, Australia, Hawaii, Japan, and South Africa. In the tropics it is only found in the mountains of Haiti.

Geranium dissectum grows in disturbed habitats, while the rest of species grow in less altered environments, such as meadows, streams or channel banks. *Geranium crenophilum* and *G. sintenisii* prefer mountains, while *G. asphodeloides* and *G. dissectum* grow from sea level to ca. 2000 m (Fig. 4A).

Numerical Analyses. To represent the variability of each quantitative character within species, box-plots containing medians and percentiles were prepared. The most discriminant characters are shown in Fig. 6. These characters were used to perform the Discriminant Analyses (see below), and the most operative ones to build the key (in conjunction with qualitative characters).

In Discriminant Analysis the four species of sect. *Dissecta* (*G. asphodeloides*, *G. crenophilum*, *G. dissectum*, and *G. sintenisii*) were analyzed and corrected classified in 100% of the cases. The plot of axis 1 against axis 2 shows a large separation for *G. dissectum* OUT's (Fig. 7). *Geranium dissectum* is an annual species supported by quantitative characters such as deeply divided leaves, shorter and narrower petals, and shorter filaments. The characters contributing most to separation of perennial species were petal width and the length of glandular hairs of stem and pedicels. *Geranium sintenisii*, which is more clearly discriminated than *G. asphodeloides* and *G. crenophilum*, has an important qualitative character: a turnip-shaped rootstock.

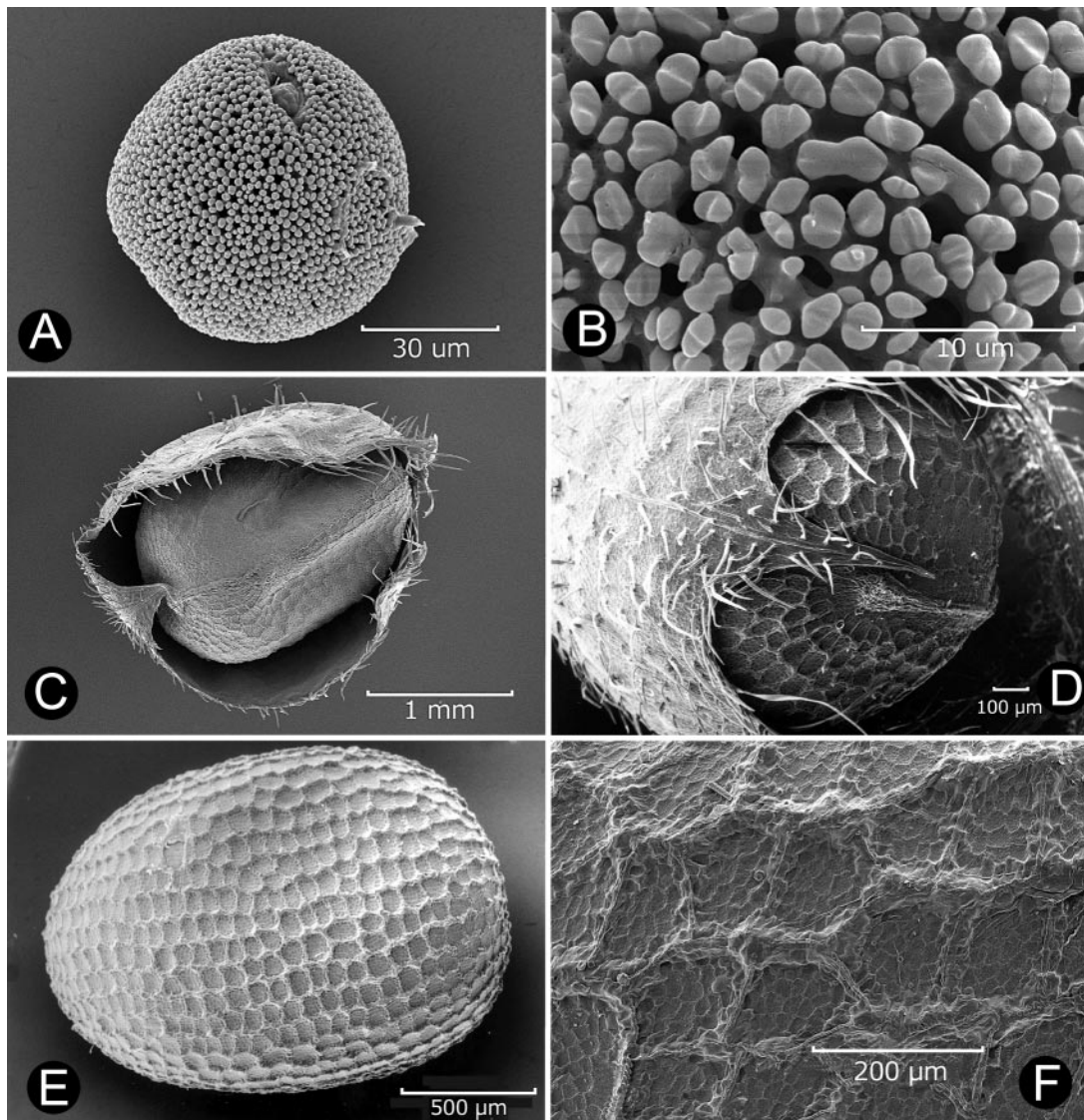


FIG. 5. SEM photographs showing pollen, fruit and seed features of *Geranium* sect. *Dissecta*. A. Pollen grain of *G. asphodeloides* (Castroviejo 15220, MA). B. Pollen ornamentation of *Geranium crenophilum* (Kotschy 346, MA). C. Mericarp of *Geranium asphodeloides* (Castroviejo 15357, MA); D. Basal mericarp prong of *G. dissectum* (Tawira & Tormos s.n., MA); E. Seed of *G. dissectum* (Tawira & Tormos s.n., MA); F. Seed-coat ornamentation of *G. asphodeloides* (Castroviejo 15357, MA).

Phylogenetic Relationships. Phylogenetic analyses using all *trnL-F* sequences available (Table 2) gave two most parsimonious trees of 49 steps (Fig. 8a; C.I. = 1; R.I. = 1; H.I. = 0). The analysis was carried out using *G. palmatum* as the outgroup. Analysis of ITS sequences with the same outgroup yielded two most parsimonious trees of 104 steps (Fig. 8b; C.I. = 0.99; R.I. = 0.80). The monophyly of the four species of sect. *Dissecta* is inferred from both analyses. The *trnL-F* sequence length varies between 385 bp (*G. palmatum* and *G. dissectum*) and 397 bp (*G. crenophilum*, *G. sintenisii* and *G. asphodeloides*). ITS marker has 621 bp in *G. crenophilum*, *G. sintenisii*, and *G. asphodeloides*, 622 bp in *G. dissectum*,

and 623 bp in *G. palmatum* (ITS1: *G. palmatum* 227 bp, all others 226 bp; ITS2: *G. palmatum*, *G. dissectum* 232 bp, all others 231 bp). The variation among species sampled for *trnL-F* ranges from 0% to 1.8%. Sequences of *G. asphodeloides* and *G. crenophilum* are identical, while *G. dissectum* and *G. sintenisii* showed a little divergence (1.8%). On the other hand, sequence divergence between populations of the same species varies from 0% to 0.25%. In fact, sequences of the two populations of *G. asphodeloides* as well as *G. dissectum* are identical, while *G. sintenisii* populations showed a little divergence (0.25%). The variation among species sampled for ITS range from 0.32% (*G. asphodeloides*-*G. sin-*

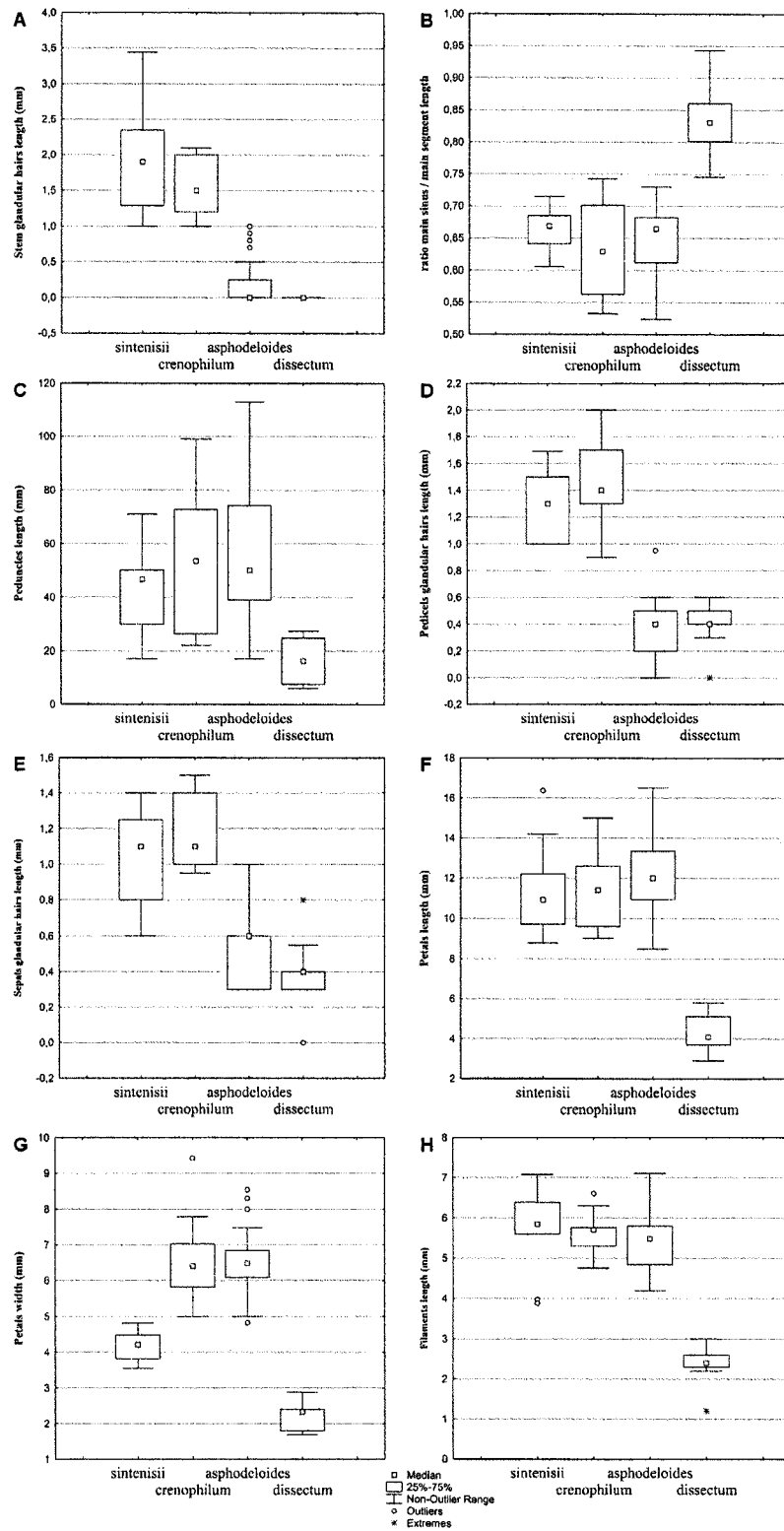


FIG. 6. Box plot of the main discriminant quantitative characters in *Geranium* sect. *Dissecta*.

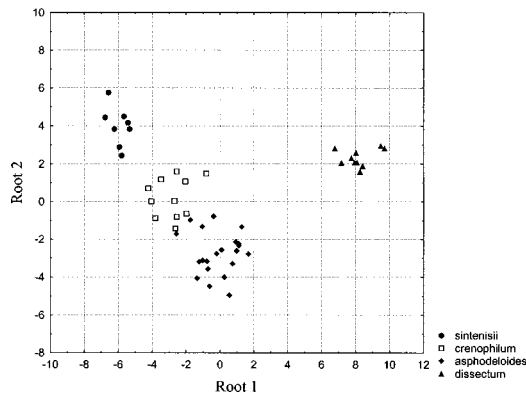


FIG. 7. Plot of the first two axes of Linear Discriminant Analysis of *Geranium* sect. *Dissecta* OTU's.

tenisii) to 3.68% (*G. crenophilum*-*G. dissectum*), while there is no sequence divergence between populations. The cladistic analysis of morphological data (Tables 3, 4) produced a topology similar to that obtained in molecular analyses (Fig. 8C); in all cases *G. dissectum* appeared as sister to the remaining species. In fact, the highest sequence divergence for both markers was found between *G. dissectum* and another ingroup species. Combined analysis resulted in two most parsimonious trees (168 steps; C.I. = 0.98; R.I. = 0.84). All topologies retrieved from heuristic and exhaustive searches were identical, except for combined analyses where the *G. asphodeloides* clade collapsed in the heuristic search (Fig. 8D).

These results indicate that the three allogamous pe-

rennials (*G. asphodeloides*, *G. crenophilum*, and *G. sintensisii*) have an autogamous annual (*G. dissectum*) as basal. Thus, an autogamous annual species can be suggested as ancestor of this group or, alternatively, *G. dissectum* derivate from a perennial ancestor. Preliminary results (ITS and *trnL-F* sequences of several relatives) suggest the first possibility as more feasible, and *G. dissectum* or other annual relatives could have given rise to perennials by changing its reproductive strategy to a facultative or allogamous system.

TAXONOMIC TREATMENT

GERANIUM sect. DISSECTA Yeo, Bot. J. Linn. Soc. 89: 10. 1984.—TYPE: *G. dissectum* L.

Herbs annual or perennial. *Rootstock* (in perennial species) horizontal or vertical, not tuberculate, usually not turnip-shaped, with or without thick fleshy roots. *Stem* erect, leafy, herbaceous. *Leaves* polygonal in outline, cordate, palmatifid, with 5–7 rhombic segments; cauline leaves usually opposite; stipules free. *Inflorescence* a monochasial cyme with solitary cymules; pedicel and peduncle together usually overtopping the subtending leaf. *Sepals* smooth, not accrescent, 3-nerved. *Petals* erect-patent, with claw, glabrous on the adaxial side, ciliate on the basal margin, purplish. *Stamens* 10, both whorls bearing anthers, not exerted. *Nectaries* glabrous or hairy. *Fruit* of seed ejection type; mericarps without a strand of fibres, smooth, without longitudinal rib, without basal beak, without a basal callus, with a prong. *Seeds* reticulate, brownish; hilum 1/8 as long as the perimeter. *Cotyledons* with entire margin.

KEY TO THE SPECIES OF GERANIUM SECTION DISSECTA

1. Plant annual; leaf deeply divided (ratio main sinus length /main segment length = 0.74–0.94); petals 2.9–5.8 mm long 4. *G. dissectum*
1. Plant perennial; leaf not deeply divided (ratio main sinus length /main segment length = 0.52–0.74); petals 8.5–16.5 mm long
2. Rhizome oblique, bearing thick fleshy roots; petals (5.8)6–8.3 mm wide; pedicels with or without glandular hairs
3. Stem with retrorse, eglandular hairs, without glandular hairs, or also with short glandular hairs (0.5)0.7–0.9(1) mm long 1. *G. asphodeloides*
3. Stem with glandular hairs (1)1.2–2(2.1) mm long 2. *G. crenophilum*
2. Rhizome ± vertical, slender, ± turnip shaped, without thick fleshy roots; petals 3.5–4.8 mm wide; pedicels with glandular hairs 1–1.7 mm long 3. *G. sintensisii*

1. GERANIUM ASPHODELOIDES Burm. f., Spec. Bot. Geran.: 28. 1759.—TYPE: Italy. Lucania, Potenza, montis Foi, loco le Dragonare dicto, *Fl. Italica Exsic., Fiori & Beguinot 2725* (neotype, here designated, G!; isoneotypes, P! RO!). Fig. 9.

Geranium orientale Mill., Gard. Dict. ed. 8, no. 10. 1768.—TYPE: unknown locality, cultivated at Chelsea Physic Garden, London, *Miller s.n.* (lectotype, here designated, BM-digital image!).

Geranium pallens M. Bieb., Fl. Taur.-Caucas. 2: 138. 1808. *Geranium asphodeloides* subsp. *pallens* (M. Bieb.)

Woronow in Kusn., N. Busch & Fomin, Fl. Cauc. Crit. 3(7): 27. 1908.—TYPE: GEORGIA. Iberia, *Steven s.n.* (lectotype, designated by Novoselova 1998: 152, LE!).

Geranium nemorosum Ten., Fl. Napol. 1: lxx. 1811–15. *Geranium pyrenaicum* var. *nemorosum* (Ten.) DC., Prodr. 1: 643. 1824. *Geranium asphodeloides* var. *nemorosum* (Ten.) Boiss., Fl. Orient. 1: 878. 1867. *Geranium asphodeloides* subsp. *nemorosum* (Ten.) Fritsch, Mitt. Naturwiss. Vereines Steiermark 50: 380. 1914.—TYPE: ITALY. Basilicata, Balvano, *Te-*

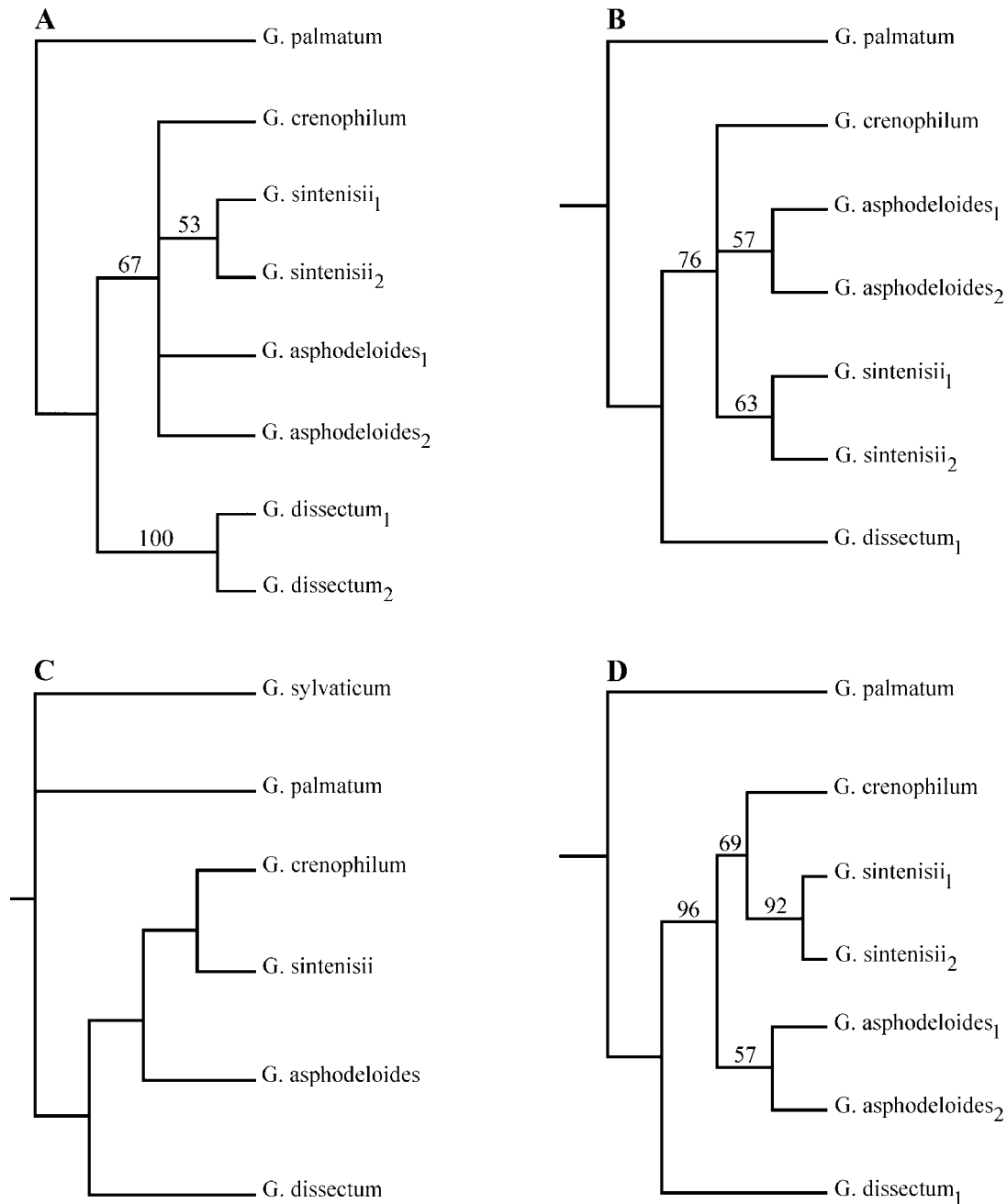


FIG. 8. Strict consensus trees obtained from analyses of DNA and morphological data for species included in *Geranium* sect. *Dissecta*, using *G. palmatum* as outgroup (DNA studies) or both *G. sylvaticum* and *G. palmatum* (morphological studies). A: analysis of *trnL-F* sequences. B: analysis of ITS sequences. C: analysis of morphological data. D: analysis of combined *trnL-F*, ITS, and morphological data set. Bootstrap values above 50% are shown.

nore s.n. (lectotype, here selected, NAP-digital image!).

Geranium fasciculatum Pančić, Verh. Zool.-Bot. Vereins Wien 6: 492. 1856.—TYPE: SERBIA. Kragujevac, 44°00'N, 20°50'E, *Pančić s.n.* (lectotype, here designated, W!).

Geranium tauricum Rupr., Mém. Acad. Imp. Sci. Saint Pétersbourg ser. 7, 15(2): 268. 1869.—TYPE: UKRAINE. Ex Tauria merid., 1810, *Bieberstein s.n.* (lectotype, here designated, LE-digital image!).

Herbs perennial, 20–51 cm tall. *Rootstock* 4–9.8 mm

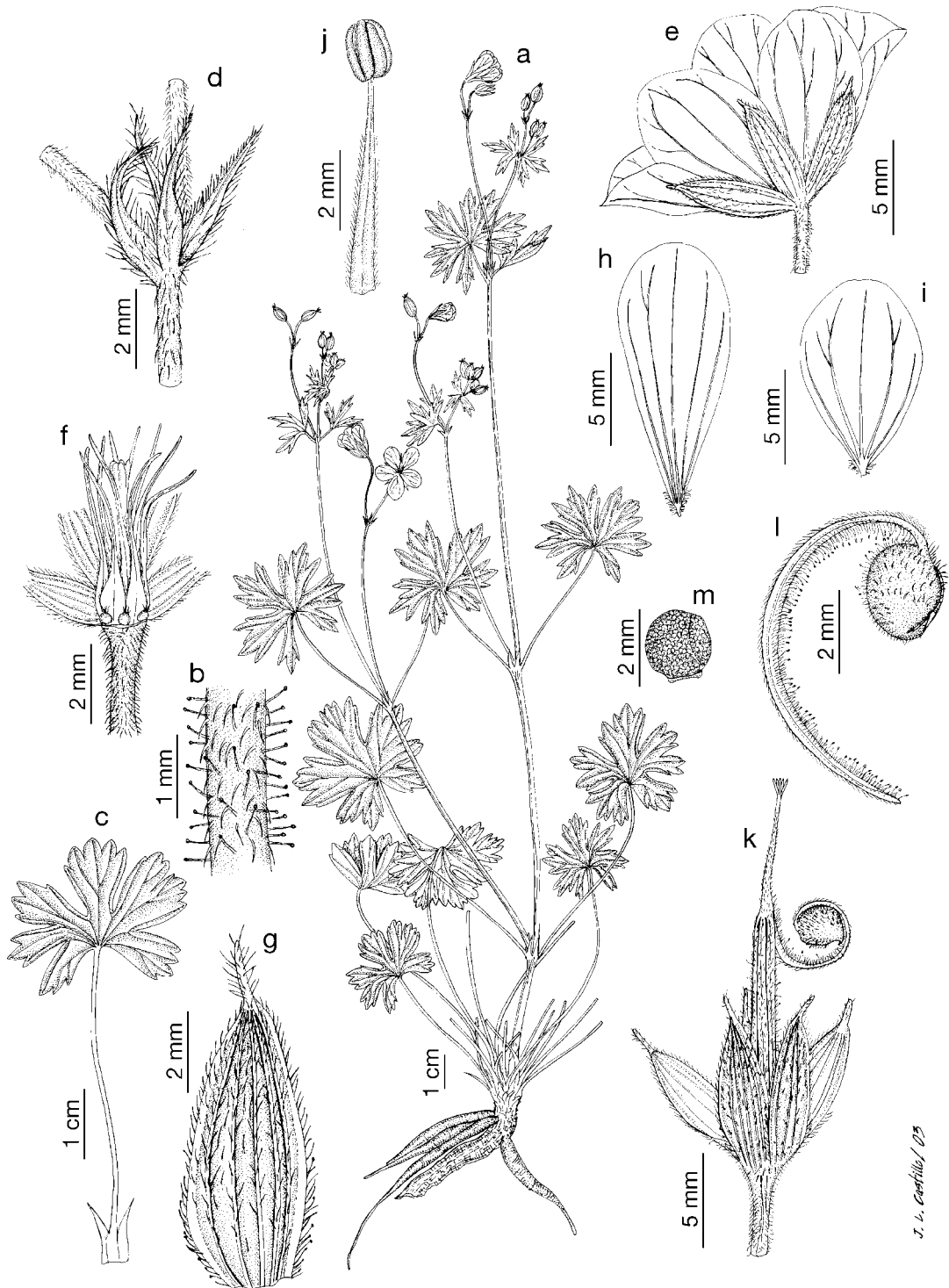


FIG. 9. *Geranium asphodeloides*. a. Habit. b. Stem indumentum. c. Leaf. d. Bracts. e. Flower. f. Androecium and gynoecium. g. Sepal. h-i. Petals. j. Stamen. k. Fruit. l. Mericarp. m. Seed. [based on: a-g, i-j, *Petrova s.n.* (MA-209961); h, *Barbey s.n.* (G); k-m, *Burnat s.n.* (G).]

diam., \pm horizontal, not turnip-shaped, with thick fleshy, fasciculate roots. *Stem* with retrorse, appressed, eglandular hairs 0.2–1.6 mm long, and sometimes glandular hairs (0.5)0.7–0.9(1) mm long. *Basal leaves* in a deciduous rosette; lamina 2–5.5 \times 2.3–7.1 cm, divided for 0.52–0.73 of its length), pilose, with appressed, eglandular hairs; segments 2.8–10.5 mm at the base, 3–12-lobed in distal half (ratio main-sinus length of the middle segment / middle-segment length = 0.2–0.38); cauline leaves opposite; petioles to 16 cm long, with retrorse, appressed, eglandular hairs 0.2–1 mm long, and sometimes patent, glandular hairs 0.2–1.8 mm long; stipules 2.4–8.8 \times 0.9–2.6 mm, lanceolate to acuminate, with eglandular and sometimes glandular hairs on abaxial surface and on the margin, glabrous adaxially. *Peduncles* 1.7–11.3 cm long, with patent to retrorse, eglandular hairs 0.2–1.2 mm long, sometimes with glandular hairs 0.2–0.5(–1) mm long; bracteoles 2.8–6.3 \times 0.4–1.1 mm, linear, with eglandular and sometimes glandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1.35–3.1 cm long, with patent to retrorse, eglandular hairs 0.2–1.2 mm long, and usually with glandular hairs 0.2–0.5(–0.95) mm long (mainly towards the apex); pedicel and peduncle together overtopping the subtending leaf (ratio cymule length / leaf length = 1.1–5.2). *Sepals* 5.1–9.2 \times 1.9–3.5 mm (ratio pedicel length / sepal length = 1.8–5), with mucro 0.7–1.9 mm long, with scarious margins 0.2–0.3 mm wide, with \pm patent, eglandular hairs 0.3–0.8 mm long, and glandular hairs 0.3–1 mm long on the abaxial side, glabrous adaxially (sometimes only with eglandular hairs). *Petals* 8.5–16.5 \times (4.8–)6.1–8.5 mm, entire to retuse, with claw 0.4–0.6 mm long. *Staminal filaments* 4.1–7.1 mm long, lanceolate, ciliate except on the apex, with hairs 0.1–0.2 mm long; anthers 0.9–2.1 \times 0.5–1.2 mm, bluish; pollen bluish. *Nectaries* with a tuft of hairs at the top, dorsally glabrous. *Gynoecium* 3.4–8.8 mm long. *Fruit* 20.2–26 mm long; mericarps 2–3.4 \times 1.3–2.5 mm, with patent, eglandular hairs 0.2–0.6 mm long, and sometimes glandular hairs 0.2–0.8 mm long, brownish; rostrum 15.2–20.9 mm long, with a narrowed apex 3.7–6.9 mm long, with patent, eglandular hairs 0.1–0.3 mm long, and glandular hairs 0.4–0.8 mm long; stigmatic remains 0.9–1.9 mm long, with 5 glabrous lobes. *Seeds* 1.6–2.1 \times 1.2–1.8 mm. Chromosome number: $2n = 24, 26, 28, 30+f$.

Phenology. Flowering specimens from April to August.

Distribution and Habitat. Southeastern Europe to Western Asia; forest, scrub, meadows, banks, between 0 and 1850 m (Fig. 10).

Representative Specimens Examined. ALBANIA: Kruja, Muras, 41°33' N, 19°40' E, *Markgraf* 1180 (B); Mali Thate, 40°11' N, 19°55' E, *Bourcart* s.n. (P); Tomor-Gebirges, östlich Berat, Kloster Abbas Ali, Kalk, 40°42' N, 20°7' E, *Markgraf* 1342 (B). BULGARIA: Strandza, supra Velika, 42°3' N, 27°0' E, *Petrova* s.n. (MA, G). GEORGIA: Kartli, Bakuriani Botanical Garden, 41°55' N, 44°25' E,

Kenularia s.n. (MA); Tiflis, Gori, Bakuriani, 41°45' N, 43°32' E, *Kozlovsky* s.n. (G). GREECE: Arkadia, Kato Kotilion, pr. Karitaina, 37°28' N, 22°0' E, *Rechinger* 25524 (G, B); Arta, Pistiana, 39°18' N, 20°59' E, *Willing* 33646 (B); Chalkidikis, Cholomondas Oros, 40°17' N, 23°31' E, *Snogerup* 9908 (B); Corfu, 39°35' N, 19°50' E, *Aketournin?* s.n. (P); Epirus, Ioánnina, entre col de Katara et Ioánnina, 39°47' N, 21°10' E, *Burdet & Charpin* 10284 (G); Evritania, Nikolaos, 38°54' N, 21°52' E, *Willing* 4554b (B); Fokis, Grigorio, 38°36' N, 21°58' E, *Willing* 14189 (B); Grevena, Dheskati, 39°54' N, 21°46' E, *Willing* 28866 (B); Imathia, Kato Vermion, 40°34' N, 22°2' E, *Willing* 9534 (B); Kalavrita-Patras, 38°15' N, 21°44' E, *Raabe* s.n. (B); Kardhitsu, Moni Koronis, 39°18' N, 21°46' E, *Willing* 82273 (B); Kastoria, Pefkofito, 40°19' N, 20°49' E, *Willing* 6115 (B); Kozanis, Kamvounia Ori, 39°57' N, 21°49' E, *Willing* 9088 (B); Laconia, montes Taygetos, Langada, 37°4' N, 22°25' E, *Rechinger* 24810 (G); Larisa, Elassonos, Loutro, 39°59' N, 21°56' E, *Willing* 28010 (B); Macedonia, Grevenon, W Perivoli, 39°59' N, 21°7' E, *Moller & al.* 1176 (G); Magnisia, Volou, 0.7 km W Portaria, 39°23' N, 23°0' E, *Willing* 26424 (B); Thessalia, in monte Pindo pr. Castania, 39°45' N, 21°30' E, *Pinatzi* 16558 (G); Viotia, Levadhias, 1.4 km WNW Evangelistria, 38°20' N, 23°2' E, *Eichenbald & Willing* 52749 (B). ITALY: Barletta, 41°18' N, 16°16' E (G); Bosoco della Rocca (RO); Calabria, entre Nicastro et Monteleone, 38°58' N, 16°18' E, *Reynier* s.n. (G); Lucania, Potenza, montis Foi, loco le Dragonare dicto, 40°35' N, 15°50' E, *Gavioli* s.n. (P, G, RO); Pignola, loco Puggio Ricciardi? dicto, 40°33' N, 15°46' E, *Gavioli* s.n. (MA); Salerno, monte Alburno, 40°32' N, 15°16' E, *Montelucci* s.n. (RO); Sicilia, 37°50' N, 14°15' E, *Gussonne* s.n. (G); Mistretta, 37°56' N, 14°22' E (RO). MACEDONIA: N Ljirbotan gebirge, 41°40' N, 21°40' E, *Seitter* s.n. (G); Sar-planina, Kobelica, Tetovo, 42°1' N, 20°59' E, *Behr* s.n. (B). SERBIA: Belgrad, Rakowitza, 44°49' N, 20°30' E, *Bornmüller* s.n. (B); ad Topcider, 44°46' N, 20°27' E, *Pančić* s.n. (G); Nisch, montis Souva Planina, 43°18' N, 21°53' E, *Petrovic* s.n. (COI, G, P). SYRIA: Bhamra, 35°37' N, 36°3' E, *Haradjian* 2748 (G); Frolouk, Quenzeul Dag, 35°48' N, 35°48' E, *Pabot* s.n. (G); Kessab, Karadourane, 35°56' N, 35°59' E, *Pabot* s.n. (G); Slenfé, 35°35' N, 36°12' E, *Guittonneau* 73070307 (herb. Guittonneau). TURKEY: Amasya, Akdagh, 40°55' N, 35°55' E, *Manissadjian* 848 (E); Balikesir, Kaz dag, 39°42' N, 26°49' E (E); Bandirma, Erdek, monte Malya Tepeler, 40°27' N, 27°50' E, *Castroviejo* 15201 (MA); Bolu, al S de Abant Golu, 40°35' N, 31°17' E, *Aedo & al.* 6165 (MA); Broussa, Yildiz, 40°11' N, 29°4' E, *Post* s.n. (G); Bursa, Ulu Dag, 40°3' N, 29°13' E, *De Wilde* 4043 (E); Buyukdere, 39°30' N, 27°4' E, *Barbey* s.n. (G); Çankiri, Kastamonu, Ilgaz-Daglari, 35 km S of Kastamonu, 41°8' N, 33°45' E, *Edmondson* 447 (G); Cassius, Jebel Agra, 35°57' N, 35°58' E, *Gombault* 1146 (P); Çoruh, Ardahan-Ardanuç, unterhalb Kutul Yayla, 41°7' N, 47°7' E, *Nydegger* 44524 (G); entre Scutari et Kutekuk, 41°1' N, 29°3' E, *Ayasse* s.n. (G); Eskisehir, Sündiken dağı, Catacik, 39°58' N, 30°55' E, *Ekin* 939 (E); Evciler, Kaz Dagı, mt. Ido, 39°44' N, 26°48' E, *Castroviejo* 15220 (MA); İçel, Gözne, in the mts. Çukurova, 37°0' N, 34°33' E, *Deaver* T195 (E); Istanbul, Aydos dağı, N foot, Aydos kalesi, 40°56' N, 29°15' E, *Demiriz* 4688 (E); Kavale, 41°9' N, 31°49' E, *Post* s.n. (G); Kilyos ad litus Ponti Euxini, 41°15' N, 29°1' E, *Rechinger* 21898 (G, MA); montagnes d'Amanus, pres Marasch, 36°45' N, 36°19' E, *Haradjian* s.n. (P); Samsun, Meseli Düz, 41°0' N, 36°0' E, *Tobey* 536 (E); Sinop, entre Kurucasile y Sinop, 7 km al W de Denizkonak, 41°46' N, 33°6' E, *Valcárcel & al.* 217VV01 (MA); Thracia, NW de Estambul, 5 km Balabán, 41°15' N, 28°35' E, *Castroviejo* 15294 (MA); Trabzon, 41°0' N, 39°43' E, *Stainton* 8001 (E); Zonguldak, above Karabük, Kel Tepe, 41°4' N, 32°27' E, *Davis & Coode* 38820 (E). UKRAINE: Crimea, Yalta, Nikita, 44°30' N, 34°14' E, *Davis* 33154 (G); Tauria, Compiere, 44°37' N, 34°28' E, *Prefrott* s.n. (LE).

Discussion. *Geranium asphodeloides* is the most widespread of the three perennial species of the section. It is easily distinguished from *G. sintenisii* by its \pm horizontal, not turnip-shaped rootstock, with thick,

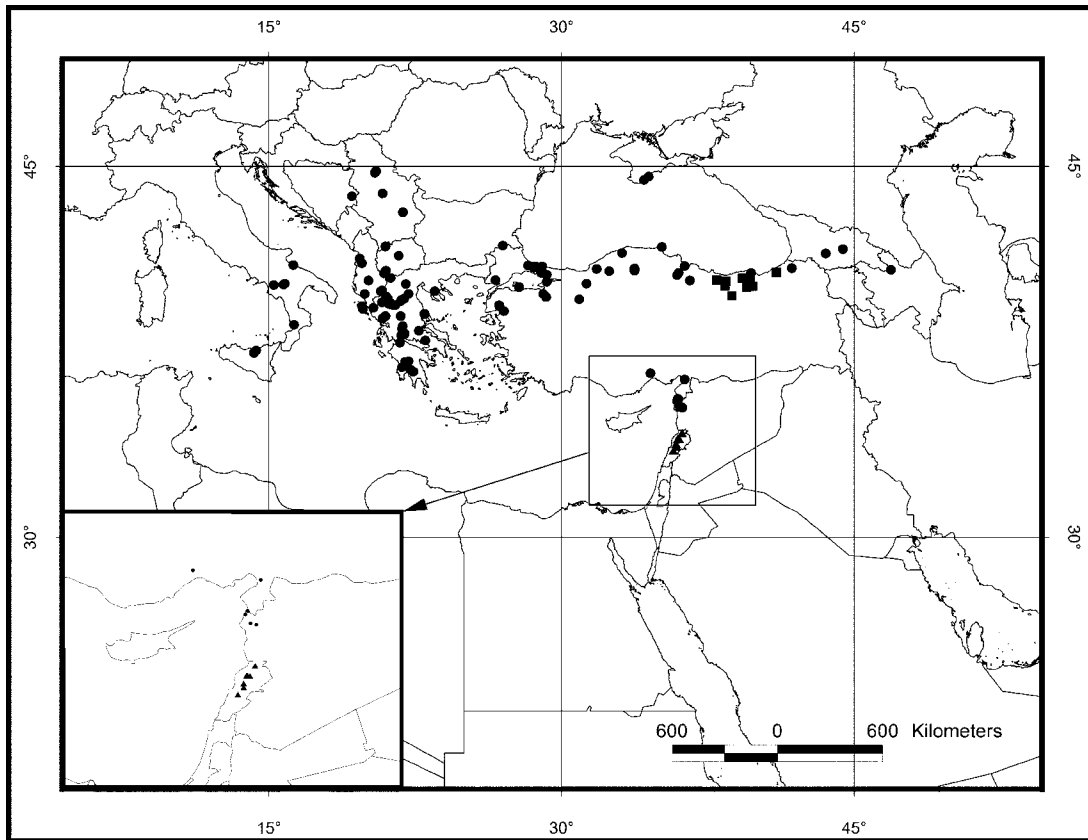


FIG. 10. Distribution of *Geranium asphodeloides* (circles), *G. crenophilum* (triangles), and *G. sintenisii* (open squares).

fleshy, fasciculate roots, and its petals (4.8–)6.1–8.5 mm wide. By contrast, *G. sintenisii* has \pm vertical, turnip-shaped rootstock, without thick, fleshy, fasciculate roots, and narrow petals (3.5–4.8 mm wide). Rare herbarium specimens of *G. asphodeloides* showing relatively narrow petals were collected at the end of July. These specimens also had well developed fruits. Such data suggest that extemporaneous flowering could produce smaller petals, a fact that should be considered when critical specimens are identified (specimens with lower petal width). *Geranium sintenisii* consistently has glandular hairs on the stem, petioles, and inflorescence, whereas in *G. asphodeloides* glandular hairs are not always present. If present, glandular hairs are short and straight in *G. asphodeloides*, whereas they are long and a bit tortuous in *G. sintenisii*. *Geranium crenophilum* is similar to *G. asphodeloides* in rootstock, roots, and petal features, although it shows glandular hairs as described in *G. sintenisii*.

Geranium asphodeloides varies considerably in the presence and distribution of glandular hairs. There are specimens with no glandular hairs, others with scattered glandular hairs restricted to sepal bases, or with more or less copious glandular hairs on stems and inflorescences. In some plants a part of the pedicels have

glandular hairs and elsewhere none or few. Such variability does not show any geographical pattern.

Bobrov (1949) recognized from Russia two independent species related to *G. asphodeloides*: *G. tauricum* endemic to the Crimea and characterized by its indumentum of eglandular hairs, short stipules (4–5 mm long), and long petals (15–17 mm long), and *G. pallens* distributed throughout the Caucasus and characterized by its indumentum of glandular hairs, long stipules (6–8 mm long), and short petals (12–17 mm long). As discussed above, indumentum variability does not support the differentiation of any taxa from *G. asphodeloides*. In the same way, length of stipules and petals of the specimens studied from the Crimea and Caucasus fall into the variability of those characters in *G. asphodeloides*. Novoselova (1998) showed that the previously mentioned characters are quite variable in Caucasian plants, although recognized *G. pallens* as subspecies of *G. asphodeloides*.

No original specimen of *Geranium asphodeloides* has been located at G, where Burman herbarium is kept. Thus, a neotype has been designated from Italy, in accordance with the protologue. We have chosen a specimen from the widely distributed Flora Italica Exsiccatae.

Geranium asphodeloides was recorded from Iran by Parsa (1952). However, Schönbeck-Temesy (1970) included this species in "species incertae" in Iran (and we agree with this opinion), since she did not find any specimen supporting those records.

2. GERANIUM CRENOPHILUM Boiss., Diagn. Pl. Orient. ser. 1, 8: 117. 1849. *Geranium asphodeloides* subsp. *crenophilum* (Boiss.) Bornm., Repert. Spec. Nov. Regni Veg. Beih. 89(3): 134. 1936.—TYPE: LEBANON. Ehden, Boissier s.n. (lectotype, here designated, G-digital image!; isolectotypes, K! P!). Fig. 11.

Geranium asphodeloides var. *hispidum* Boiss., Fl. Orient. 1: 878. 1867.—TYPE: LEBANON. Bcharre, Kotschy 346 (lectotype, here designated, MA!; isolectotypes, MPU! P! W!).

Herbs perennial, 28–80 cm tall. *Rootstock* 4.1–14 mm diam., \pm horizontal, not turnip-shaped, with thick, fleshy roots. *Stem* with patent, eglandular hairs 0.3–0.8 mm long, and glandular hairs (1)1.2–2(2.1) mm long. *Basal leaves* in a deciduous rosette; lamina 1.6–7.2 \times 2.1–8.7 cm, divided for 0.53–0.74 of its length, pilose, with appressed, eglandular and glandular hairs; segments 4.1–14.3 mm at the base, 5–13-lobed in distal half (ratio main-sinus length of the middle segment / middle-segment length = 0.21–0.37); cauline leaves opposite; petioles to 10.7 cm long, with patent, eglandular hairs 0.2–1 mm long, and sometimes patent, glandular hairs 0.2–2.4 mm long; stipules 2.5–9 \times 0.9–3.5 mm, lanceolate to acuminate, with eglandular and sometimes glandular hairs on abaxial surface and on the margin, glabrous adaxially. *Peduncles* 2.2–9.9 cm long, with patent to retrorse, eglandular hairs 0.2–0.9 mm long, and glandular hairs 0.2–1.44 mm long; bracteoles 3.1–6.4 \times 0.4–0.8 mm, linear, with eglandular and sometimes glandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 0.9–3.3 cm long, with patent to retrorse, eglandular hairs 0.2–0.9 mm long, and glandular hairs (0.2)1.3–2 mm long; pedicel and peduncle together overtopping the subtending leaf (ratio cymule length / leaf length = 1.1–4.9). *Sepals* 5.6–8.7 \times 1.9–3.8 mm (ratio pedicel length / sepal length = 1.3–4.4), with mucro 0.7–1.8 mm long, with scarios margins 0.2–0.3 mm wide, with \pm patent, eglandular hairs 0.2–1 mm long, and glandular hairs 0.3–1.5 mm long on the abaxial side, glabrous adaxially (sometimes only with eglandular hairs). *Petals* 9–15 \times 5–9.4 mm, entire, with claw 0.4–0.6 mm long. *Staminal filaments* 4.7–6.6 mm long, lanceolate, ciliate except on the apex, with hairs 0.1–0.2 mm long; anthers 1.4–2.1 \times 0.5–1 mm, color unknown; pollen color unknown. *Nectaries* with a tuft of hairs at the top, dorsally glabrous. *Gynoecium* 4.2–6 mm long. *Fruit* 20–26 mm long; mericarps 2.3–3 \times 1.7–2.3 mm, with patent, eglandular hairs 0.3–0.7 mm long, and glandular

hairs 0.5–1.2 mm long, brownish; rostrum 15.2–22.2 mm long, with a narrowed apex 3.7–5.7 mm long, with patent, eglandular hairs 0.2–0.8 mm long, and glandular hairs 0.6–1.7 mm long; stigmatic remains 1–1.8 mm long, with 5 glabrous lobes. *Seeds* 2–2.3 \times 1.5–1.7 mm. Chromosome number: unknown.

Phenology. Flowering specimens from May to August.

Distribution and Habitat. Endemic to Lebanon; meadows, stream and channel shores, between 1450 and 1900 m (Fig. 10).

Specimens Examined LEBANON: Dimane, 34°15' N, 35°57' E (P); Hasroum, 34°15' N, 35°56' E (P); Afka, 34°3' N, 35°52' E, Peyron 627 (G); Ehden, 34°16' N, 35°58' E, Bornmüller 11542 (E, G); jugi Sanin, Bornmüller 273 (P); Khan Sannin, 33°57' N, 35°52' E, Mouterde 3093b (G); Sannin, 33°57' N, 35°52' E, Peyron 627b (G).

Discussion. *Geranium crenophilum* shares with *G. asphodeloides* two important characters: a) \pm horizontal, not turnip-shaped rootstock, with thick, fleshy, fasciculate roots, and b) wider petals. However, this species has constantly glandular hairs on the stem, petioles, and inflorescence, whereas in *G. asphodeloides* glandular hairs are not always present. As stated above, glandular hairs of *G. asphodeloides* are short and straight, whereas they are long and a bit tortuous in *G. crenophilum*.

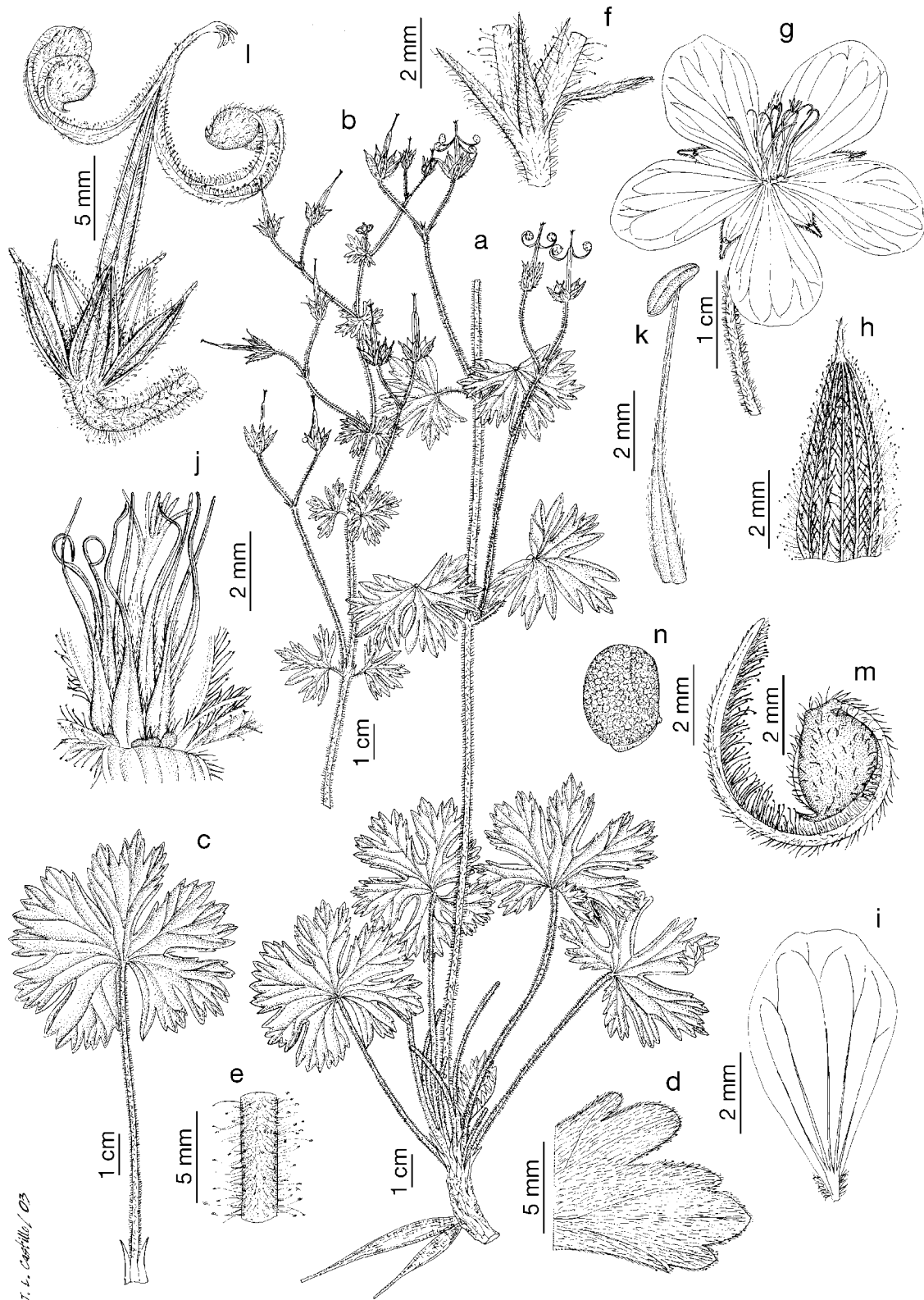
Mouterde (1966) recorded *G. crenophilum* from Syria. However, the specimen supporting this record (Bhamra, Haradjian 2748, G) is *G. asphodeloides*.

3. GERANIUM SINTENISII Freyn, Bull. Herb. Boissier 3: 104. 1895. *Geranium asphodeloides* subsp. *sintenisi* (Freyn) P.H. Davis, Notes Roy. Bot. Gard. Edinburgh 28: 36. 1967.—TYPE: TURKEY. Gümüşkhane, Karagölldagh, in valle Schadachlar, 3 Aug. 1894, *Sintenis* 7050 (lectotype, designated by Knuth 1912: 156, B†; isolectotypes, BM! E! F! G! K! P! W!). Fig. 12.

Geranium ibericum var. *parviflorum* Boiss., Fl. Orient. 1: 876. 1867. *Geranium parviflorum* (Boiss.) Hand-Mazz., Ann. K.K. Naturhist. Hofmus. 23: 161. 1909, nom. illeg., non Curtis 1782. *Geranium wiedemannii* P.H. Davis, Notes Roy. Bot. Gard. Edinburgh 22: 25. 1955, nom. nov.—TYPE: TURKEY. Hab. in monte Jyldisdagh, *Wiedeman* s.n. (lectotype, here designated, LE!).

Geranium davisianum Peşmen & Güner, Notes Roy. Bot. Gard. Edinburgh 38(3): 436. 1980.—TYPE: TURKEY. Rize, Çamlıhemşin, Amlakit Ya. Arkavit to Husayd, 24 July 1974, *Güner* 1182 (holotype HUB; isotype, E!).

Geranium chelikii Kit Tan & Yildiz, Notes Roy. Bot. Gard. Edinburgh 45(3): 440. 1989.—TYPE: TURKEY. Sivas, Şerefiye, Köse Dağı, Cehennem dere, *Yildiz & Çelik* 4994 (holotype, E not located; isotype, CUFH not located).



J. L. Carrillo / 023

FIG. 11. *Geranium crenophilum*. a-b. Habit. c. Leaf. d. Leaf indumentum. e. Stem indumentum. f. Bracts. g. Flower. h. Sepal. i. Petal. j. Androecium and gynoecium. k. Stamen. l. Fruit. m. Mericarp. n. Seed. [based on: a-n, *Pabot s.n.* (G).]

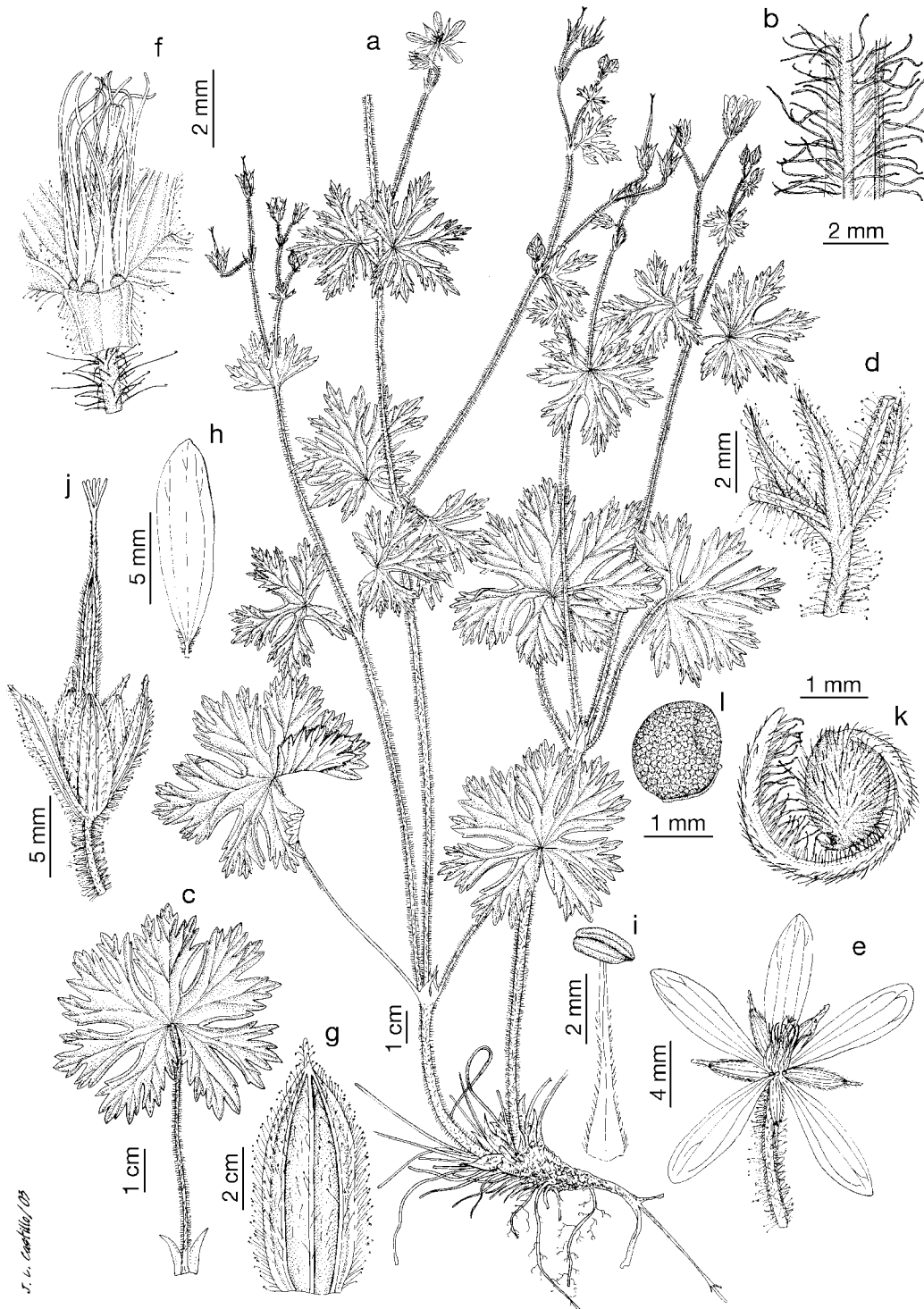


FIG. 12. *Geranium sintenisii*. a. Habit. b. Stem indumentum. c. Leaf. d. Bracts. e. Flower. f. Androecium and gynoecium. g. Sepal. h. Petal. i. Stamen. j. Fruit. k. Mericarp. l. Seed. [based on: a-l, *Nisa* 712 (MA-687191).]

Herbs perennial, 26–64 cm tall. *Rootstock* 4.4–9.2 mm diam., \pm vertical, turnip-shaped, without thick, fleshy roots. *Stem* with patent, glandular hairs 1–3.4 mm long. *Basal leaves* in a deciduous rosette; lamina 2.1–6.9 \times 2.6–8.8 cm, divided for 0.60–0.71 of its length, pilose, with appressed, eglandular and glandular hairs; segments 4.1–9.5 mm at the base, 7–18-lobed in distal half (ratio main-sinus length of the middle segment / middle-segment length = 0.17–0.27); cauline leaves opposite; petioles to 24 cm long, with patent, glandular hairs 0.9–2.5 mm long, and sometimes with patent, eglandular hairs c. 0.4 mm long; stipules 4.4–11.1 \times 1.8–4 mm, lanceolate to acuminate, with eglandular and sometimes glandular hairs on the margin, glabrous on both sides. *Peduncles* 1.7–7.1 cm long, with patent to retrorse, eglandular hairs 0.3–0.6 mm long, and glandular hairs 1–1.6 mm long; bracteoles 2.2–5.4 \times 0.4–1.2 mm, linear, with eglandular and glandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 0.8–2.5 cm long, with patent to retrorse, eglandular hairs 0.2–0.6 mm long, and glandular hairs 1–1.7 mm long; pedicel and peduncle together overtopping the subtending leaf (ratio cymule length / leaf length = 1.5–2.5). *Sepals* 5.6–7.2 \times 1.8–3.1 mm (ratio pedicel length / sepal length = 1.1–3.7), with mucro 0.8–1.8 mm long, with scarious margins 0.2–0.3 mm wide, with \pm patent, eglandular hairs 0.3–0.6 mm long, and glandular hairs 0.3–1.4 mm long on the abaxial side, glabrous adaxially (sometimes only with eglandular hairs). *Petals* 9.1–16.3 \times 3.5–4.8 mm, entire, with claw 0.4–0.6 mm long. *Staminal filaments* 3.8–7 mm long, lanceolate, ciliate except on the apex, with hairs 0.1–0.2 mm long; anthers 1.2–2 \times 0.5–1 mm, bluish; pollen bluish. *Nectaries* with a tuft of hairs at the top, dorsally glabrous. *Gynoecium* 4.5–6.9 mm long. *Fruit* 19.6–26.5 mm long; mericarps 2.3–3.1 \times 1.4–2 mm, with patent, eglandular hairs 0.2–0.5 mm long, and glandular hairs 0.6–1.1 mm long, brownish; rostrum 14.7–20.3 mm long, with a narrowed apex 3.7–6.2 mm long, with patent, eglandular hairs 0.2–0.6 mm long, and glandular hairs 0.6–1.3 mm long; stigmatic remains 1–2.1 mm long, with 5 glabrous lobes. *Seeds* 1.5–2.3 \times 1.3–2.3 mm. Chromosome number: unknown.

Phenology. Flowering specimens from June to August.

Distribution and Habitat. Endemic to Turkey; meadows, by streams, rocky slopes, between 600 and 2100 m (Fig. 10).

Specimens Examined TURKEY: Giresun, Balabandaglari above Tamdere, 40°30' N, 38°22' E, *Davis & al.* 20471 (E); Gümüşhane, carretera de Yeniol a Yagmurdere, subida al puerto de Kostandagi, vertiente S, 40°29' N, 39°47' E, *Herrero & al.* 1402 (MA); Lazistan, Djimil, 39°40' N, 40°40' E, *Balansa s.n.* (P, G); Ordu, Canik Daglari, carretera de Ordu a Çambasi, c. 10 km de Çambasi, 40°43' N, 37°56' E, *Herrero & al.* 1169 (MA); Trabzon, carretera de Torul a Trabzon, vertiente N, porto Zigana, 40°40' N, 38°25' E, *Nissa &*

al. 712 (MA); Trabzon, Hamsikoy, 40°41' N, 39°28' E, *Stainton & Henderson* 6329 (E); in monte Ulugoba pr. vicum Fol, ad alpem Zowon, 40°07' N, 38°43' E, *Handel-Mazzetti* 647 (W); in ditone vici Fol Koei, 40°47' N, 39°16' E, *Handel-Mazzetti* 413 (W).

Discussion. Like *Geranium crenophilum*, *G. sintenisii* has constantly long, glandular hairs on stem, petioles, and inflorescence, similar both in shape and size. However, *G. sintenisii* can be distinguished by its \pm vertical, turnip-shaped rootstock, without thick fleshy, fasciculate roots, and by its narrow petals.

Geranium chelikii was described by Kit Tan and Yildiz (1989) as endemic to the Sivas region of Turkey (the same area as *G. sintenisii*). It has been impossible to examine the type or any collection from the type locality of this species. The holotype was apparently sent to E. There, H. Hoy kindly made two exhaustive searches without success. Our friend, Dr. Askoy (from Istanbul) has contacted to staff at CUFH where the isotype was deposited, also without success. Kit Tan and Yildiz (1989) described *G. chelikii* as bearing "roots slender" rather than "fleshy, fusiform roots" as in *G. asphodeloides*. They also indicated that *G. chelikii* has narrow petals (4–5 mm wide). All these data strongly suggest that *G. chelikii* should be considered as synonym of *G. sintenisii*.

Geranium sintenisii was recorded from Iran by Köie (1945). Later, Parsa (1952) mentioned the same collection. Schönbeck-Temesy (1970) included this species in "species incertae" in Iran, since she did not find any specimen supporting those records. However, the specimens supporting this record (Köie 339, C, and Köie s.n., C) are *G. rotundifolium* L.

4. GERANIUM DISSECTUM L., Cent. Pl. I: 21. 1755.—TYPE: "Habitat in Europa australiori" (lectotype, designated by Carolin 1965: 336, LINN 858.82, microfiche!). Fig. 13.

Geranium dissectum var. *minimum* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 122. 1837.—TYPE: FRANCE. Manchecourt, *Picard s.n.* (no original material located).

Geranium dissectum var. *palmatum* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 122. 1837.—TYPE: FRANCE. Marcadet, *Picard s.n.* (no original material located).

Geranium dissectum var. *pumilum* Peterm., Fl. Lips. Excurs.: 512. 1838.—TYPE: GERMANY. ante portam Aeusseres-Petersthor, ad pagos Konnewitz, Schönfeld, Eutritzs, Möckern, Kl.-Zschocher etc, *Petermann s.n.* (no original material located).

Geranium dissectum var. *byzantinum* Griseb., Spic. Fl. Rumel. 1: 123. 1843. *Geranium dissectum* [b] *byzantinum* (Griseb.) Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913. *Geranium dissectum* f. *byzantinum* (Griseb.) Borza, Consp. Fl. Roman. 2: 174. 1949.—TYPE: TURKEY. Bithynia, ins. Principo, pr. Hersek, *Grisebach s.n.* (no original material lo-

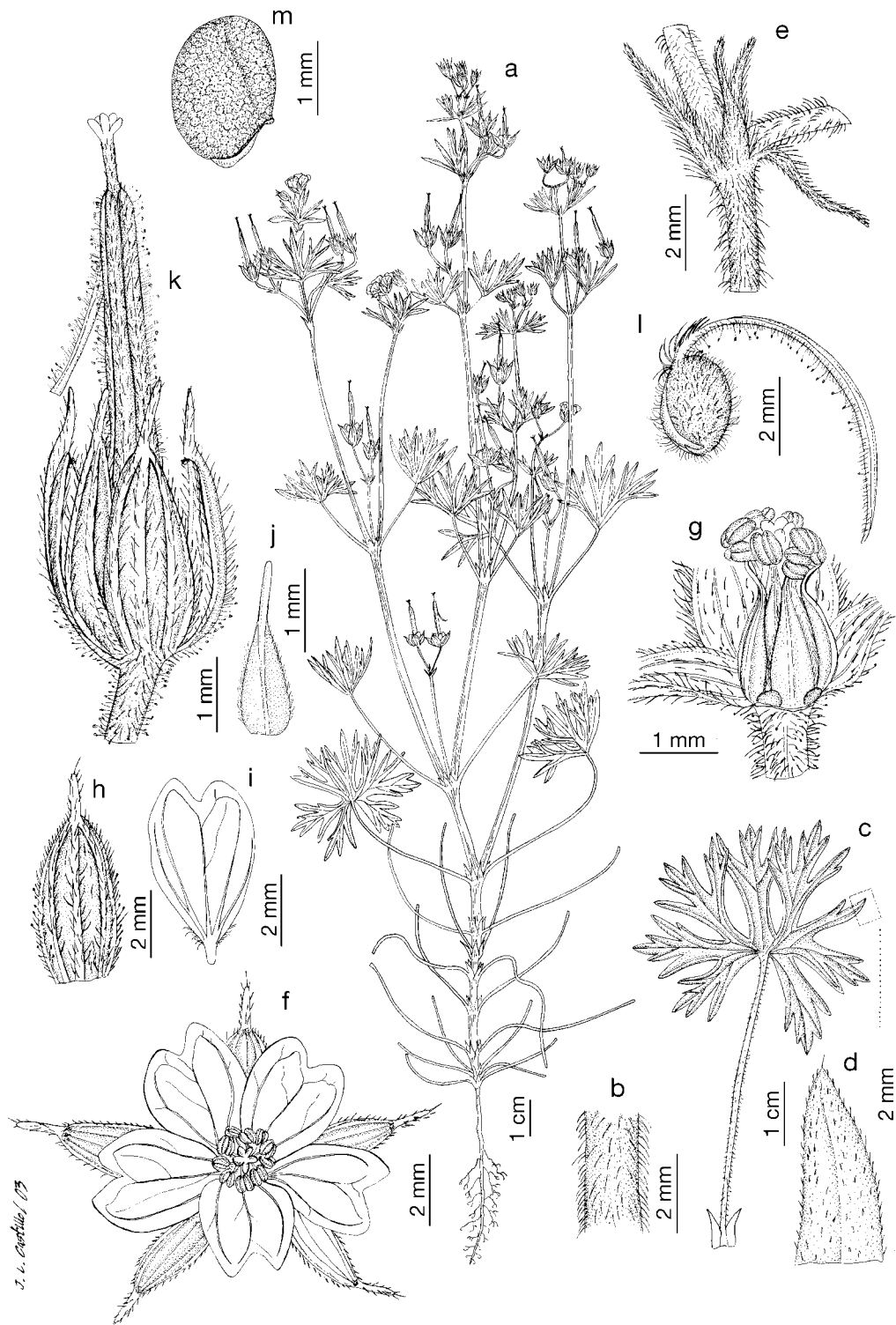


FIG. 13. *Geranium dissectum*. a. Habit. b. Stem indumentum. c. Leaf. d. Leaf indumentum. e. Bracts. f. Flower. g. Androecium and gynoecium. h. Sepal. i. Petal. j. Stamen. k. Fruit. l. Mericarp. m. Seed. [based on: a-j, *Aedo* 3492 (MA-557520); k-m, *Aedo* 2087 (MA-529265).]

- cated; according to Strid 2000: 294, no material at GOET).
- Geranium dissectum* var. *subintegrilobatum* Godet, Fl. Jura: 128. 1852. *Geranium dissectum* f. *subintegrilobatum* (Godet) Gams in Hegi, Ill. Fl. Mitt.-Eur. 4(3): 1682. 1924.—TYPE: SWITZERLAND. Neuchâtel, Chantier, Roulet, Aug. 1850, Godet s.n. (lectotype, here designated, NEU!).
- Geranium dissectum* var. *furcatum* Schur, Enum. Pl. Transsilv.: 138. 1866. *Geranium dissectum* [B] *furcatum* (Schur) Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913. *Geranium dissectum* f. *furcatum* (Schur) Gams in Hegi, Ill. Fl. Mitt.-Eur. 4(3): 1682. 1924.—TYPE: ROMANIA. Hermannstadt, Schur s.n. (no original material located).
- Geranium pusillum* var. *malviflorum* Baumg. ex Schur, Enum. Pl. Transsilv.: 138. 1866. *Geranium dissectum* [C] *baumgartenianum* Schur ex Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913. *Geranium dissectum* f. *erectum* Patze ex Gams in Hegi, Ill. Fl. Mitt.-Eur. 4(3): 1682. 1924.—TYPE: ROMANIA. Hermannstadt, Schur s.n. (no original material located).
- Geranium dissectum* var. *purpureum* Kuntze, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 176. 1887. *Geranium dissectum* [1] *purpureum* (Kuntze) Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913. *Geranium dissectum* f. *purpureum* (Kuntze) Gams in Hegi, Ill. Fl. Mitt.-Eur. 4(3): 1682. 1924.—TYPE: GEORGIA. Batum, Kuntze s.n. (no original material located).
- Geranium dissectum* var. *roseum* Kuntze, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 176. 1887. *Geranium dissectum* [1] *roseum* (Kuntze) Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913. *Geranium dissectum* f. *roseum* (Kuntze) Gams in Hegi, Ill. Fl. Mitt.-Eur. 4(3): 1682. 1924.—TYPE: IRAN. Talysch, Kuntze s.n. (no original material located).
- Geranium dissectum* var. *albidum* Kuntze, Trudy Imp. S.-Peterburgsk. Bot. Sada 10: 176. 1887. *Geranium dissectum* [1] *albidum* (Kuntze) Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913.—TYPE: IRAN. Talysch, May 1886, O. Kuntze s.n. (lectotype, here selected, LE!).
- Geranium dissectum* var. *villosum* N. Terracc., Nuov. Giorn. Bot. Ital. ser. 2, 14: 138. 1907. *Geranium dissectum* [II] *villosum* (N. Terracc.) Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913.—TYPE: ITALY. Pisterola, N. Terracciano s.n. (no original material located).
- Geranium dissectum* var. *glutinosum* N. Terracc., Nuov. Giorn. Bot. Ital. ser. 2, 14: 138. 1907. *Geranium dissectum* [III] *glutinosum* (N. Terracc.) Graebn. in Asch. & Graebn., Syn. Mitteleur. Fl. 7(1): 44. 1913.—TYPE: ITALY. Costa della Rocca, N. Terracciano s.n. (no original material located).
- Geranium laxum* Hanks ex Hanks & Small in Underw. & Britton (eds.), N. Amer. Fl. 25(1): 9. 1907.—TYPE: U.S.A. Washington, Chehalis Co., Oyhut, 7 Aug. 1897, Lamb 1263 (lectotype, designated by Aedo 2000: 64, MO!; UC-fragment!).
- Geranium dissectum* f. *albiflorum* R. Fern., Bol. Soc. Brot. ser. 2, 22: 69. 1948.—TYPE: PORTUGAL. Serra de Ossa, Herdade da Coelheira, 7 May 1947, Fernandes & Sousa 1686 (holotype, COI photocopy!).
- Herbs* annual, (7-)15–69 cm tall. *Stem* with retrorse, not appressed, eglandular hairs 0.5–1.2 mm long. *Basal leaves* in a ± persistent rosette; lamina 2.4–8 × 2.5–5.4 cm, divided for 0.74–0.94 of its length, pilose, with appressed, eglandular (and sometimes glandular) hairs; segments 2–5 mm at the base, 3–9-lobed in distal half (ratio main-sinus length of the middle segment / middle-segment length = 0.32–0.62); cauline leaves usually opposite, sometimes basal ones alternate; petioles to 16 cm long, with retrorse or subpatent, usually eglandular hairs 0.4–1.2 mm long; stipules 3.4–9.7 × 1–3 mm, lanceolate, sometimes lobed, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. Peduncles 0.6–5 cm long, with patent, mainly eglandular hairs 0.2–0.9 mm long (sometimes only with glandular hairs); bracteoles 2–4.8 × 0.4–0.9 mm, lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 0.6–1.3 cm long, with patent, glandular 0.2–0.6 mm long, and eglandular hairs 0.2–0.9 mm long (sometimes only with eglandular hairs); pedicel and peduncle together not overtopping the subtending leaf (ratio cymule length / leaf length = 0.42–0.82). *Sepals* 4.2–7.1 × 1.8–3.6 mm (ratio pedicel length / sepal length = 1.1–2.4), with mucro 0.85–2 mm long, with scarios margins 0.1–0.2 mm wide, with ± patent, glandular hairs 0.2–0.8 mm long, and eglandular hairs 0.3–0.7 mm long on the abaxial side, glabrous adaxially (sometimes only with eglandular hairs). *Petals* 2.9–5.8 × 1.7–2.8 mm, emarginate (notch 0.5 mm deep), with claw 1 mm long. *Staminal* filaments 1.2–3 mm long, lanceolate with an abruptly narrowed apex, ciliate on all its length, with hairs c. 0.1 mm long; anthers 0.32–0.55 × 0.25–0.5 mm, purplish; pollen bluish. *Nectaries* glabrous. *Gynoecium* 1.1–3 mm long. *Fruit* 15.1–18.5 mm long; mericarps 2.3–2.9 × 1.7–2.2 mm, with patent, eglandular hairs 0.2–0.7 mm long, and sometimes glandular hairs 0.1–0.5 mm long, brownish; rostrum 11.1–13.5 mm long, with a narrowed apex 1.6–2.7 mm long, with patent, eglandular hairs 0.1–0.6 mm long, and glandular hairs 0.3–0.6 mm long; stigmatic remains 0.6–1 mm long, with 5 hairy lobes. *Seeds* 1.7–2.2 × 1.2–2 mm. Chromosome number: $2n = 22$.
- Phenology.** Flowering specimens from January to December.
- Distribution and Habitat.** Europe, Western and

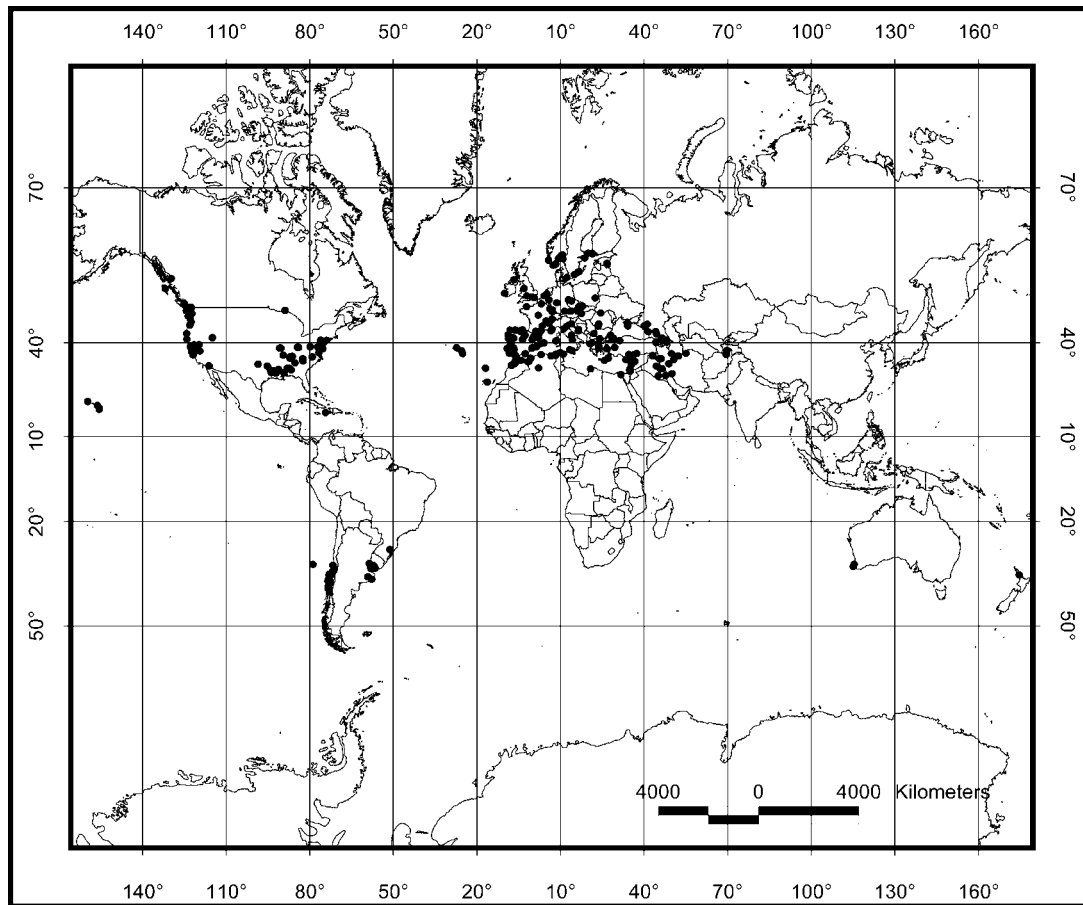


FIG. 14. Distribution of *Geranium dissectum*.

Central Asia, Macaronesia, and Northern Africa (introduced in North America, Caribbean, South America, Southern Africa, Australia, Hawaii, and Eastern Asia); edge of forest, prairies, fields, and disturbed areas, between 0 and 2000 m (Fig. 14).

Representative Specimens Examined ALGERIA: Constantine, 36°21' N, 6°36' E, *Joly s.n.* (MPU). ARGENTINA: Buenos Aires, General Pueyrredon, Laguna de los Padres, 38°0' S, 57°45' W, *Ruiz Leal 22295* (CORD). ARMENIA: steppa Mugan, 40°10' N, 44°16' E, *Zacharjan s.n.* (LE, M). AUSTRALIA: Western Australia, Kudardup, 34°16' S, 115°5' E, 12-XI-1955, *Royce 5187* (PERTH). AUSTRIA: near Aistersheim, Upper Austria, 48°11' N, 13°45' E, *Kerk s.n.* (MO). AZERBAIJAN: Baku, Geokczai, ad Mususli, 40°39' N, 47°44' E, *Alexeenko 7413* (LE). BELGIUM: Teuven, 50°45' N, 5°52' E, *Larsen s.n.* (COI). BRAZIL: Rio Grande do Sul, Kappesberg, pr. Caxias, 29°10' S, 51°11' W, *Rambo 43463* (F, P). BULGARIA: pr. Ahtopol, 42°6' N, 27°57' E, *Petrova & Ivanova 937* (MA). CANADA: British Columbia, Esquimalt, 48°27' N, 123°25' W, *Groh s.n.* (DAO). CHILE: La Araucanía, 8 km al N de Yupehue, 38°28' S, 73°30' W, *Aedo 7175* (MA); Juan Fernández I, Más a Tierra, 33°38' S, 78°52' W, *Angulo 114* (CONC). CROATIA: Dalmatia, Stobrec, 43°31' N, 16°31' E, *Duytjcs & al. 692* (LE). CYPRUS: Leonarisso, 35°28' N, 34°8' E, *Economides 1089* (W). CZECH REPUBLIC: pr. Velemín, 50°32' N, 13°58' E, *Vitous s.n.* (P). DENMARK: Hundige Strand, SW of Copenhagen, 55°36' N, 12°20' E, *Hansen 12305* (MA). EGYPT: Basse-Egypte, Abou Kebir, 30°44' N, 31°40' E, *Letourneux*

s.n. (P). ESTONIA: Tartu, 58°21' N, 26°44' E, *Kapp s.n.* (TAA). FINLAND: Alandia, Geta, Bonäs, 60°8' N, 21°32' E, *Klingstedt s.n.* (MO, P). FRANCE: Aude, Ligean a Sainte Croix, 43°8' N, 1°10' E, *Sennen s.n.* (MA). GEORGIA: Kaischaur, 42°26' N, 44°30' E, *Owerin s.n.* (LE). GERMANY: Chemnitz, 50°50' N, 12°55' E, *Weiker 1592* (LE, P). GREAT BRITAIN: Coates, pr. Cirencester, 51°42' N, 2°2' W, *Aedo 3857* (MA). GREECE: Epiros, ad versuras S Joannina, 39°45' N, 20°40' E, *Rechinger 25553* (W); Kriti, Hierapetra, pr. Males, 35°1' N, 25°45' E, *Leonis 15* (W). HAITI: Mare Boeuf, Mornes des Commissaires, 18°26' N, 74°18' W, *Holdridge 937* (F). HUNGARY: Koronczó, 47°35' N, 17°32' E, *Ebenhösch s.n.* (LE). IRAN: Daland, Gurgaon, 37°2' N, 55°3' E, *Wooney 6574* (W). IRAQ: Baghdad, 33°20' N, 44°23' E, *Escalera s.n.* (MA). IRELAND: Castle Roch, near Coleraine, 55°7' N, 6°40' W, *Yschiting 119* (K). ISRAEL: between Petah-Tikwa and Herzlia, 32°5' N, 34°52' E, *Eig & al. s.n.* (MA, LE, P). ITALY: Abruzzo, L'Aquila, Santa Eufemia, 42°7' N, 14°1' E, *Aldasoro & al. 3396* (MA); Sardegna, rio Monumtones, 40°33' N, 8°19' E, *Valsecchi s.n.* (SS); Sicilia, Palermo, Portela Mandarini, 37°51' N, 14°6' E, *García & al. 1402* (MA). LEBANON: Hadeth, 33°49' N, 35°31' E, *Mouterde 2265* (P). LIBYA: Cyrenaica, inter Tauchiram et Barcem, 32°30' N, 20°54' E, *Maire & Weiller 329* (MPU). MOROCCO: Beni-Said, Aguada de Dar-Kebdani, 35°44' N, 5°50' W, *Sennen & Mauricio s.n.* (BC). NETHERLANDS: pr. Oude Tonge, isl. Goeree-Overflakkee, 51°42' N, 4°12' E, *Florschütz & al. 506* (MA). NEW ZEALAND: Waitemata Co., Mairangi Bay, 36°44' S, 174°46' E, *Bangarter 5209* (MO). NORWAY: Akershus, Asker, 59°49' N, 10°25' E, *Thomle s.n.* (O). POLAND: Lublin, pr. Parchatka, 51°15'

N, 22°30' E, *Zinger s.n.* (MO, K). PORTUGAL: Algarve, Loulé, Sao Brás de Alpostel, 37°8' N, 8°20' W, *Malato Beliz & Guerra 15432* (MA); Azores, Santa Maria, 36°58' N, 25°6' W, *Pombo 92* (COI); Madeira, Faja da Nogueira, 32°44' N, 16°54' W, *Nacarro 3079* (MA). ROMANIA: Oltenia, Dolj, pr. Fratostita, 44°35' N, 23°35' W, *Cirtu 988* (G). RUSSIA: Krasnodar, Circassiae, Tschernomore, 44°59' N, 41°10' E, *Steup s.n.* (LE). SERBIA: ad Vranpka Banja, 42°32' N, 22°0' E, *Adamovic s.n.* (P). SLOVENIA: Istria, in valle fl. Dragonja, 45°0' N, 14°0' E, *Wraber 547* (LE). SPAIN: Cantabria, Serna, 43°1' N, 4°13' W, *Aedo & Aldasoro 3492* (MA); Baleares, Mallorca, Almedrà, 39°46' N, 2°49' E, *Aedo & al. 4594* (MA); Canary I., Tenerife, Santa Cruz, 28°27' N, 16°14' W, *Pitard 445* (MO). SWEDEN: Blekinge, Aryd, 56°12' N, 15°2' E, *Lagerkranz s.n.* (W). SWITZERLAND: au Chantier, Roulet, 47°77' N, 6°58' E, *Godet s.n.* (NEU). SYRIA: Homs, 34°44' N, 36°43' E, *Gombault 2264* (P). TADZHIKISTAN: Bujarskia vlad, Kuliabskoie vekstvo, 37°55' N, 69°47' E, *Dubnoiorskia 165* (LE). TUNISIA: foret de Sraia, Ouchteta, 36°28' N, 8°15' E, *Cosson s.n.* (P). TURKEY: Balaban, Terkos lake, 41°12' N, 28°35' E, *Castroviejo 15309* (MA). UKRAINA: Yalta, 44°30' N, 34°10' E, *Gold s.n.* (LE). URUGUAY: Flores, Santa Adelaida, 33°58' S, 57°6' W, *Gallinal & al. 922* (F). USA: Kentucky, Pendleton Ballast, 38°47' N, 84°22' W, *Buddell II & Thieret 1032* (NY); Hawaii National Park, Mauna Loa, 19°28' N, 155°36' W, *Fagerlund & Mitchell 1068* (BISH).

Discussion. *Geranium dissectum* is the most common and widespread species treated in this revision. It is easily distinguished from all other species of sect. *Dissecta* by deeply divided leaves, short petals, and annual life-span. This species shows cymules shorter than the adjacent leaf, whereas in the three perennial species of the section cymules are longer than the adjacent leaf. *Geranium dissectum* has been frequently confused with *G. columbinum* L., which is characterized by seed-ejection with callus fruit (not prong). Additionally, *G. dissectum* has cymules not overtopping the subtending leaf whereas in *G. columbinum* pedicel and peduncle together clearly overtop the subtending leaf.

Sometimes it is possible to find depauperate plants of *G. dissectum*, fertile but with the leaves not fully developed. Some such specimens have leaves with undivided segments, and have been named var. *subintegrilobatum*. However, no other character state is associated with this size reduction, which suggests that this form also does not deserve taxonomic recognition.

Geranium dissectum has been recorded from Afghanistan (Schönbeck-Temesy 1970), Japan (Akiyama 2001), and South Africa (Hilliard and Burt 1985). Unfortunately, it has been impossible to examine the specimens supporting these records.

The specimen supporting the record of *G. dissectum* in Peru (Taylor 1993) is an unidentified species of sect. *Geranium*. *Geranium dissectum* was also recorded from the Dominican Republic (Moscoso 1943), although no specimen was mentioned. The specimens kept at the National Herbarium (JBSD) as *G. dissectum* are *G. carolinianum* L.

EXCLUDED NAMES

Geranium angustifolium Gilib., Fl. Lit. Inch. 2: 176 (1782), nom. inval. (ICBN, Appendix V).

Geranium asphodeloides var. *genuinum* Boiss., Fl. Orient. 1: 878 (1867), nom. inval. (ICBN, art. 24.3).

Geranium asphodeloides f. *parviflora* Sint. ex R. Knuth in Engl., Pflanzenr. IV.129 (Heft 53): 156 (1912), nom. nud., pro syn. (ICBN, art. 34.1).

Geranium baumgartenianum Schur, Sert. Fl. Transs.: 16 (1853), nom. nud.

Geranium calabricum, nom. nud., in sched. (K!)

Geranium dissectum var. *alba* A. Huet ex Nyman, Consp. Fl. Eur. 1: 138 (1878), nom. nud., pro syn. (ICBN, art. 34.1).

Geranium dissectum var. *baumgartenianum* Schur ex Nyman, Consp. Fl. Eur.: 138 (1878), nom. nud.

Geranium dissectum var. *latilobum* Sennen, nom. nud., in sched. (BC!)

Geranium dissectum var. *marianica* Rivas Goday & Bellet, nom. nud., in sched. [MAF-25271!]

Geranium dissectum var. *procumbens* Sennen, nom. nud., in sched. (MPU!)

Geranium dissectum var. *typicum* R. Knuth in Engl., Pflanzenr. IV.129 (Heft 53): 51 (1912), nom. inval. (ICBN, art. 24.3).

Geranium furcatum Schur ex R. Knuth in Engl., Pflanzenr. IV.129 (Heft 53): 51 (1912), nom. nud., pro syn.

Geranium haemanthum Willd. ex Spreng., Syst. Veg. 3: 74 (1826), nom. nud., pro syn. (ICBN, art. 34.1).

Geranium malvifolium Baumg. ex R. Knuth, Pflanzenr. IV.129 (Heft 53): 51 (1912), nom. nud., pro syn. (ICBN, art. 34.1).

Geranium minimum Picard ex B.D. Jacks., Index Kew. 2: 1020 (1893), nom. nud., pro syn. (ICBN, art. 34.1).

Geranium navieri Jord. ex Gren., nom. nud., in sched. (P!)

Geranium palmatum Picard ex B.D. Jacks., Index Kew. 2: 1020 (1893), nom. nud., pro syn. (ICBN, art. 34.1).

Geranium pusillum Labram & Hegetschw. ex R. Knuth, Pflanzenr. IV.129 (Heft 53): 51 (1912), nom. nud., pro syn. (ICBN, art. 34.1).

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LITERATURE CITED

- AEDO, C. 1996. Revision of *Geranium* subgenus *Erodioidea* (Geraniaceae). *Systematic Botany Monographs* 49: 1–104.
 ———. 2000. The genus *Geranium* L. (Geraniaceae) in North Amer-

- ica. I. Annual species. *Anales del Real Jardín Botánico de Madrid* 58: 39–82.
- . 2001. Taxonomic revision of *Geranium* sect. *Brasiliensia* (Geraniaceae). *Systematic Botany* 26: 205–215.
- . 2003. Taxonomic revision of *Geranium* sect. *Trygonium* (Geraniaceae). *Botanicheskii Zhurnal. Moscow & Leningrad* 88: 124–131.
- , F. MUÑOZ GARMENDIA, and F. PANDO. 1998a. World checklist of *Geranium* L. (Geraniaceae). *Anales del Real Jardín Botánico de Madrid* 56: 211–252.
- , J. J. ALDASORO, and C. NAVARRO. 1998b. Taxonomic revision of *Geranium* L., sections *Divaricata* Rouy and *Batrachioidea* W.D.J. Koch (Geraniaceae). *Annals of the Missouri Botanical Garden* 85: 594–630.
- , ———, and ———. 2002. Revision of *Geranium* sections *Azorelloida*, *Neoandina*, and *Paramensia* (Geraniaceae). *Blumea* 47: 205–297.
- , ———, LL. SÁEZ, and C. NAVARRO. 2003. Taxonomic revision of *Geranium* sect. *Gracilia* (Geraniaceae). *Brittonia* 55: 93–126.
- AKIYAMA, S. 2001. *Geranium* L. Pp. 287–293 in *Flora of Japan* vol. 2b, K. Iwatsuki, D. E. Boufford, and H. Ohba, eds. Tokyo: Kodansha.
- ALVES, M. C. and M. T. LEITÃO. 1976. Contribuição para o conhecimento citotaxonomico des Spermatophyta de Portugal XIII. *Boletim da Sociedade Broteriana serie 2*, 50: 231–245.
- BALDWIN, B. G. 1992. Phylogenetic utility of the internal transcribed spacer of nuclear ribosomal DNA in plants: an example from the Compositae. *Molecular Phylogenetics and Evolution* 1: 3–16.
- BALTISBERGER, M. 1991. Cytological investigations of some Greek plants. *Flora Mediterranea* 1: 157–173.
- BELL, G. 1985. On the function of flowers. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 224: 223–265.
- BERTIN, R. I. and C. M. NEWMAN. 1993. Dichogamy in angiosperms. *Botanical Review* 59: 112–152.
- BOBROV, E. G. 1949. *Geranium* L. Pp. 2–62 (pp. 3–49 in the English ed.) in *Flora of the U.S.S.R.*, vol. 14, B. K. Shishkin, and E. G. Bobrov, eds. Koenigstein: Koeltz Scientific Books.
- CAROLIN, R. C. 1965. The genus *Geranium* L. in the south western Pacific area. *Proceedings of the Linnean Society of New South Wales* 89: 326–361, plates VI–VII.
- CARLQUIST, S. and D. R. BISSING. 1976. Leaf anatomy of Hawaiian Geraniums in relation to ecology and taxonomy. *Biotropica* 8: 248–259.
- CRUDEN, R.W. 1976. Intraspecific variation in pollen-ovule ratios and nectar secretion—preliminary evidence of ecotypic adaptation. *Annals of the Missouri Botanical Garden* 63: 277–289.
- . 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.
- DAVIS, P. H. 1967. *Geranium* L. Pp. 451–474 in *Flora of Turkey* vol. 2, P. H. Davis, J. Cullen, and J. E. Coode, eds. Edinburgh: Edinburgh University Press.
- . 1970. *Geranium* sect. *Tuberosa*, revision and evolutionary interpretation. *Israel Journal of Botany* 19: 91–113.
- DE LEONARDIS, W., P. PAVONE, M. C. TERRASI, and A. ZIZZA. 1981. Numeri cromosomici per la Flora Italiana: 814–830. *Informatore Botanico Italiano* 13: 158–167.
- DÍAZ LIFANTE, Z., T. LUQUE, and C. SANTA BÁRBARA. 1992. Chromosome numbers of plants collected during Iter Mediterraneum II in Israel. *Bocconea* 3: 229–250.
- FIZ O, V. VALCARCEL, and P. VARGAS. 2002. Phylogenetic position of Mediterranean Astereae and character evolution of daisies (*Bellis*, Asteraceae) inferred from nrDNA ITS sequences. *Molecular Phylogenetics and Evolution* 25: 157–171.
- GADELLA, T. W. J. and E. KLIPHUIS. 1966. Chromosome numbers of flowering plants in the Netherlands II. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen: Series C* 69: 541–556.
- GAUGER, W. 1937. Ergebnisse einer zytologischen Untersuchung der Familie der Geraniaceae. I. *Planta* 26: 529–531.
- GUITTONNEAU, G. G. 1975. Contribution à l'étude caryosystématique et phylogénétique des Géraniacées dans le bassin méditerranéen. *Colloques Internationaux du Centre National de la Recherche Scientifique* 235: 195–205.
- HILLIARD, O. M. and B. L. BURTT. 1985. A revision of *Geranium* in Africa south of the Limpopo. *Notes from the Royal Botanic Garden, Edinburgh* 42: 171–225.
- HOLLINGSWORTH, P. M., R. J. GORNALL, and J. P. BAILEY. 1992. Contributions to a cytological catalogue of the British and Irish flora, 2. *Watsonia* 19: 134–137.
- KIMURA, M. 1980. A simple method for estimating evolutionary rate of base substitution through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 11–120.
- KIRSCHNER, J., J. ŠTĚPÁNEK, and J. ŠTĚPÁNKOVÁ. 1982. In Á. Löve, (ed.). IOPB chromosome number reports LXXVI. *Taxon* 31: 574–575.
- KIT TAN, B. and K. YILDIZ. 1989. Thirteen new species from Turkey. *Notes from the Royal Botanic Garden, Edinburgh* 45: 439–541.
- KNUTH, R. 1912. *Geranium* L. Pp. 43–221, 575–583 in *Das Pflanzenreich* IV.129 (Heft 53), A. Engler, ed. Leipzig: Wilhelm Engelmann.
- . 1931. Geraniaceae. Pp.43–66 in *Die natürlichen Pflanzenfamilien*, ed. 2, 19a, A. Engler and H. Harms. Leipzig: Wilhelm Engelmann.
- KOIE, M. E. 1945. Beitrag zur Flora Südwest-Irans I. Pp. 9–55 in *Danish scientific investigations in Iran* IV, K. Jessen and R. Spärek, eds. Copenhagen: E. Munksgaard.
- LÖVE, Á. and E. KJELLQVIST. 1974. Cytotaxonomy of Spanish plants. IV. Dicotyledons: Caesalpinaceae–Asteraceae. *Lagascalia* 4: 153–211.
- and D. LÖVE. 1945. Cyto-taxonomical studies on boreal plants. III. Some new chromosome numbers of Scandinavian plants. *Arkiv for Botanik* 31A(12): 1–22.
- LÖVKVIST, B. and U. HULTGARD. 1999. Chromosome numbers in south Swedish vascular plants. *Opera Botanica* 137: 1–42.
- MÁJOVSKÝ, J. (ed.). 1974. Index of chromosome numbers of Slovakian flora (Part 3). *Acta Facultatis Rerum Naturalium Universitatis Comenianae. Botanica* 22: 1–20.
- MOSCOSO, R. M. 1943. *Catalogus Florae Domingensis*. New York: L & S. Printing Co., Inc.
- MOUTERDE, P. 1966. *Nouvelle flore du Liban et de la Syrie*, vol. 2: 434–440. Beyrouth, France: Éditions de L'Imprimerie Catholique.
- NOVOSELOVA, M. 1998. Vidy roda *Geranium* L. (Geraniaceae) podroda *Geranium* flory Kavkaza [Generis *Geranium* L. (Geraniaceae) subgeneris *Geranium* species florae Caucasi]. *Novosti Sistematiki Vysshikh Rastenii* 31: 143–158. [in Russian].
- PARSA, A. 1952. *Flore de l'Iran*, vol. 1(2). Teheran: Imprimerie Danesh.
- PAYNE, W. W. 1978. A glossary of plant hair terminology. *Brittonia* 30: 239–255.
- PEŞMEN, H. 1980. Six new species from Anatolia. *Notes from the Royal Botanic Garden, Edinburgh* 38: 435–441.
- PHILLIP, M. 1985. Reproductive biology of *Geranium sessiliflorum*, 1. Flower and flowering biology. *New Zealand Journal of Botany* 23: 567–589.
- PHILLIP, M. and T. HANSEN. 1999. The influence of plant and corolla size on pollen deposition and seed set in *Geranium sanguineum* (Geraniaceae). *Nordic Journal of Botany* 20: 129–140.
- PRICE, R. A. and J. D. PALMER. 1993. Phylogenetic relationships of the Geraniaceae and Geraniales from *rbcL* sequence comparisons. *Annals of the Missouri Botanical Garden* 80: 661–671.
- SAITOU, N. and M. NEI. 1987 The Neighbor-Joining method: a new

- method for reconstructing phylogenetic trees. *Molecular Phylogenetics and Evolution* 4: 406–425.
- SCHÖNBECK-TEMESY, E. 1970. Geraniaceae. Pp. 1–67 in *Flora Iranica*, vol. 69, K. H. Rechinger, ed. Graz: Akademische Druck.
- SHINOZAKI, K., M. OHME, M. TANAKA, T. WAKASUGI, N. HAYASHIDA, T. MATSUBAYASHI, N. ZAITA, J. CHUNWONGSE, J. OBOKATA, K. YAMAGUCHI-SHINOZAKI, C. OHTO, K. TORAZAWA, B. Y. MENG, M. SUGITA, H. DENO, T. KAMOGASHIRA, K. YAMADA, J. KUSUDA, F. TAKAIWA, A. KATO, N. TOHDOH, H. SHIMADA, and M. SUGIURA. 1986. The complete nucleotide sequence of the tobacco chloroplast genome: its gene organization and expression. *The EMBO Journal* 5: 2043–2049.
- SKALIŃSKA, M., J. JANKUM, and H. WCISLO (eds.). 1976. Further studies in chromosome numbers of Polish angiosperms. Eleventh contribution. *Acta Biologica Cracoviensia. Series Botanica* 19: 107–148.
- SNEATH, P. H. and R. R. SOKAL. 1973. *Numerical taxonomy*. San Francisco: W. H. Freeman.
- STAFFORD, P. J. and S. BLACKMORE. 1991. Geraniaceae. Pp. 49–78 in *The northwest European pollen flora*, VI, W. Punt and S. Blackmore, eds. Amsterdam, London, New York & Tokyo: Elsevier.
- STRID, A. 2000. New taxa described in Grisebach's "Spicilegium Florae Rumelicae et Bithynicae" (1843–46). *Preslia* 72: 241–321.
- STRID, A. and R. FRANZÉN. 1981. In IOPB chromosome number reports LXXIII, ed. Å. Löve. *Taxon* 30: 829–842.
- SWOFFORD, D. L. 2001. PAUP*. Phylogenetic analysis using parsimony (* and other methods), version 4.0. Sunderland: Sinauer Associates, Inc.
- TABERLET P., L. GIELLY, G. PAUTOU, and J. BOUVET. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
- TAYLOR, M. S. 1993. Geranium L. Pp. 545–548 in *Catálogo de las Angiospermas y Gimnospermas del Perú* (Monographs in Systematic Botany from the Missouri Botanical Garden 45), ed. L. Brako and J. L. Zarucchi. St. Louis: Missouri Botanical Garden.
- THEOBALD, W. L., J. L. KRAHULIK, and R. C. ROLLINS. 1979. Trichome description and classification. Pp. 40–53 in *Anatomy of the dicotyledons*, edition 2, vol. 1, C. R. Metcalfe and L. Chalk, eds. Oxford: Clarendon Press.
- TOLIVIA, D. and J. TOLIVIA. 1987. Farga: a new polychromatic method for simultaneous and differential staining of plant tissues. *Journal of Microscopy* 148: 113–117.
- VAN LOON, J. C. 1984a. Chromosome numbers in *Geranium* from Europe. I. The perennial species. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen: Series C* 87: 263–277.
- . 1984b. Chromosome numbers in *Geranium* from Europe. II. The annual species. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen: Series C* 87: 279–296.
- . and J. J. M. H. OUDEMANS. 1982. In IOPB chromosome number reports LXXXV, ed. Å. Löve. *Taxon* 31: 343–344.
- WARBURG, E. F. 1938. Taxonomy and relationship in the Geraniales in the light of their cytology. *New Phytologist* 37: 130–159.
- WEBER, M. 1996. The existence of a special exine coating in *Geranium robertianum* pollen. *International Journal of Plant Sciences* 157: 195–202.
- WHITE, T. J., T. BRUNS, S. LEE, and J. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in *PCR protocols: a guide to methods and applications*, M. Innis, D. Gelfand, J. Sninsky, and T. White, eds. San Diego: Academic Press.
- YEO, P. F. 1973. The biology and systematics of *Geranium*, sections *Anemonifolia* Knuth and *Ruberta* Dum. *Botanical Journal of the Linnean Society* 67: 285–346.
- . 1984. Fruit-discharge-type in *Geranium* (Geraniaceae): its use in classification and its evolutionary implications. *Botanical Journal of the Linnean Society* 89: 1–36.
- . 1992. A revision of *Geranium* L. in south-west China. *Edinburgh Journal of Botany* 49: 123–211.

APPENDIX 1

Index to numbered collections cited. The numbers in parentheses refer to the corresponding species in the text.

Aedo 2018 (4), 2035 (4), 2039 (4), 2046 (4), 2087 (4), 2377 (4), 3857 (4), 4464 (4), 6724 (4), 7175 (4), 7513 (4); *Aedo* & al. 4594 (4), 5077 (4), 6165 (1), 6241 (4), CN-91 (4); *Aedo* & *Aldasoro* 3492 (4); *Ahart* 6434 (4); *Ahles* 53286 (4); *Aldasoro* & al. 3396 (4); *Alexander* & *Kellogg* 3668 (4); *Alexeenko* 15711 (4), 7413 (4); *Alexson* 30 (4); *Allard* 19904 (4); *Allen* 8737 (4); *Allen* & al. 7716 (4); *Álvarez* & al. 1175 (4); *Anders* 1218 (4); *Anderson* 11977 (4); *Angulo* 114 (4); *Aragón* & *Martínez* GA 0192 (4); *Aznavor* 492 (1); *Bacigalupo* & *Fortunato* 1413 (4); *Baker* 5314 (4); *Bangerter* 5209 (4); *Barbosa* & al. 13726 (4); *Barkley* 7538 (4); *Barros* 24689 (4); *Baytop* 10946 (1); *Baytop* & *Atila* 10969 (1); *Beliz* 762 (4); *Bent* & al. 427–109 (4); *Bliss* 830 (4); *Bornmüller* 144 (4), 273 (2), 11542 (2); *Bourgeau* 62 (1); *Buddell* II & *Thieret* 1032 (4); *Burdet* & *Charpin* 10284 (1); *Cabrera* 5366 (4); *Calder* & *MacKay* 29978 (4), 30508A (4), 31469A (4); *Calder* & *Taylor* 35329 (4); *Carreiro* 262 (4); *Castroviejo* 15201 (1), 15220 (1), 15275 (4), 15294 (1), 15308 (1), 15309 (4), 15357 (1); *Cirtu* 988 (4); *Cirtu* & *Cirtu* 989 (4); *Coman* 2662b (4); *Coode* & *Jones* 73 (1); *Correll* 37119 (4), 37228 (4); *Correll* & *Ogden* 25189 (4); *Culbertson* 36 (4); *Daumail* 4140 (4); *Davis* 12113 (4), 33154 (1), 33604 (4); *Davis* & al. 20471 (3), 38346 (1); *Davis* & *Coode* 37166 (1), 37437 (1), 38820 (1); *Davis* & *Hedge* 29713 (1); *De Wilde* 4043 (1); *Deaver* T195 (1); *Demiriz* 4315 (1), 4688 (1); *Diamond* 12999 (4), 13036 (4), 13038 (4), 13111 (4); *Dubnoiskia* 165 (4); *Dunk* & al. 32 (4); *Duytjes* & al. 692 (4); *Earle* 2007 (4); *Economides* 1089 (4); *Edmondson* 447 (1); *Ehrenberg* 1875 (2); *Eichenbald* 33966 (1); *Eichenbald* & *Willing* 52749 (1); *Eig* & al. 347 (4); *Ekim* 939 (1); *Elmer* 4730 (4); *Ewan* 19053 (4); *Fagerlund* & *Mitchell* 1068 (4); *Felix* 687 (4); *Fernández* Alonso 178JF (4), 179JF (4), 2105JF (4), 823JF (4); *Fernández* Casas 114 (4); *Fitz* & *Spitzenberger* 17 (4); *Florschütz* & al. 506 (4); *Flynn* 1464 (4); *Folarszky* 290 (4); *Fraser* *Jenkins* 2188 (1); *Furse* 1933 (4); *Gallinal* & al. 1232 (4), 922 (4); *Gamble* 20004 (4); *García* & al. 1402 (4); *Gillman* 62 (4); *Gombault* 1146 (1), 2264 (4); *Grant* 145 (4); *Greuter* 14427 (1), 5441 (4); *Grimes* 3469 (4); *Groh* 359 (4); *Guerra* 621 (4); *Guinea* 271 (4), 812 (4); *Guittonneau* 73070307 (1); *Güner* 1182 (3); *Handel-Mazzetti* 413 (3), 647 (3); *Hansen* 12305 (4); *Haradjian* 885 (4), 2748 (1), 2820 (4); *Harcombe* & *Wille* 60303 (4); *Harrison* 1111 (4); *Hartvig* & al. 5828 (1); *Heller* 3949 (4); *Herrero* & al. 1169 (3), 1402 (3); *Herter* 94 951 (4); *Hibon* 772 (4); *Higgins* 10021 (4); *Hill* 16506 (4); *Holdridge* 937 (4); *Hosaka* 2477 (4), 3589 (4); *Hurrell* & al. 1187 (4); *Izuzquiza* & al. 2535 (4); *Izuzquiza* & *Sánchez* 297 AI (4); *Jackson* & *Jackson* 123 (4); *Jacobs* 6580 (4); *Keighery* 14871 (4); *Khan* & al. 656A (1); *Koelz* 17321 (4); *Koie* 943 (4); *Kotschy* 346 (2); *Kral* 26621B (4); *Kral* 38463 (4), 49722 (4), 52470 (4); *Lamb* 1263 (4); *Leonis* 15 (4); *Lexalle* 9242 (4), 11998 (4); *López* & al. 1248GF (4); *Maire* & *Meiller* 328 (4), 329 (4); *Malato* *Beliz* 739 (4), 2673 (4), 6343 (4), 6564 (4), 9948 (4), 10382 (4), 10450 (4), 10752 (4), 15432 (4); *Mamble* 26–69 (4); *Manissadjian* 848 (1); *Markgraf* 1180 (1), 1342 (1); *Mathei* & *Quezada* 1133 (4), 1156 (4), 1215 (4); *McCormac* 468 (4); *Mellerio* 128 (4); *Michelson* 53 (4); *Miller* & al. 864 (4); *Moller* & al. 1176 (1); *Montero* 5669 (4); *Moura* 3543 (4); *Mouterde* 2265 (4), 3093b (2), 5578 (2), 6079 (2), 8985b (2); *Muenscher* 9995 (4); *Muñoz* & *Sierra* 7335 (4); *Navarro* 3079 (4); *Nissa* & al. 712 (3); *Nydegger* 44524 (1); *Orphanides* 623 (1); *Pabot* 807 (1); *Parks* & *Parks* 24118 (4); *Pedrol* 125 (4), 545 (4); *Pedrol* & al. 2752b (4); *Petrova* & *Ivanova* 937 (4); *Peyron* 627 (2); *Philippi* 270 (4); *Pinatzi* 16558 (1); *Piper* 41 (4); *Pitard* 445 (4); *Podlech* 10315 (4); *Polunin* & *Naib* 64 (4); *Pombo* 92 (4); *Porter* 1650 (4); *Rambo* 43463 (4); *Raulin* 566 (4); *Raven* 6879 (4); *Rechinger* 8372g (4), 8604 (4), 8957 (4), 16392 (4), 21876 (4), 21898 (1), 22697 (1), 23088 (4), 24810 (1), 25524 (1), 25553 (4), 39867a (4); *Rodgers* & *Mullens* 7692 (4); *Rogers* 6113 (4); *Rose* 42029 (4); *Royce* 5187 (4); *Rubtzoff* 2332 (4); *Ruiz* *Leal* 22295 (4); *Salcedo* 802 (4); *Schuur* 764b (4); *Sealy*, *Burt* & *Ross-Craig* 886 (4); *Selma* 24169 (4); *Sheldahl* 19 (4); *Sheldon* 10980 (4); *Sintenis* 340 (1), 2069 (1), 952 (1), 4416 (1),

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