# Taxonomic Revision of Geranium Subsect. Mediterranea (Geraniaceae) 

Carlos Aedo, ${ }^{1,3}$ Miguel Á. García, ${ }^{1}$ María L. Alarcón, ${ }^{1}$ Juan J. Aldasoro, ${ }^{1}$ and Carmen Navarro ${ }^{2}$<br>${ }^{1}$ Real Jardín Botánico, Consejo Superior de Investigaciones Científicas, Plaza de Murillo 2, 28014 Madrid, Spain;<br>${ }^{2}$ Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, 28040 Madrid, Spain<br>${ }^{3}$ Author for correspondence (aedo@ma-rjb.csic.es)

Communicating Editor: Gregory M. Plunkett


#### Abstract

Geranium subsect. Mediterranea (Geraniaceae) consists of ten species. The highest diversity of the group is located in the Caucasus and neighbouring areas of Turkey and Iran, with five endemic species. Other species reach western Europe and northwestern Africa. In contrast to the current literature, we consider G. montanum and G. ibericum subsp. jubatum to be synonyms of G. ibericum. A univariate morphometric study revealed some valuable quantitative characters useful for the identification of these species. Micromorphological features of pollen, stigmas, seeds, and mericarps were investigated by SEM. A new key is provided, as well as new and detailed descriptions. Geranium kurdicum is here illustrated for the first time. Eleven lectotypes are designated, and distribution maps are presented. Maximum parsimony and Bayesian analyses of chloroplastic $\operatorname{trnL}$ - $t r n F$ and ribosomal nuclear ITS regions suggest that sect. Mediterranea is monophyletic. Two clades are recovered, one including the annual species and other with the perennials, in which G. tuberosum (subsect. Tuberosa) emerges within a paraphyletic subsect. Mediterranea.


Resumen. Geranium subsect. Mediterranea (Geraniaceae) está formada por diez especies. El Cáucaso es la región más rica con cinco especies endémicas, pero alguna alcanza incluso el oeste de Europa y noroeste de África. En este estudio consideramos G. montanum, y G. ibericum subsp. jubatum como sinónimos de G. ibericum. Un análisis morfométrico permitió evaluar los caracteres cuantitativos y seleccionar los más adecuados para la clave de identificación. Se investigaron también las características micromorfológicas del polen, el estigma, la semilla y el mericarpo. Se presenta una nueva clave, así como nuevas y detalladas descripciones y mapas de distribución para cada una de las especies y se eligen once lectótipos. Geranium kurdicum es aquí dibujado por primera vez. Análisis de máxima parsimonia y bayesianos de las regiones ITS ribosómica nuclear y trnL-trnF cloroplástica sugieren que la sect. Mediterranea es monofilética. Se recuperan dos clados principales, uno con las especies anuales y otro con las perennes entre las que se incluye G. tuberosum (subsect. Tuberosa) dentro de una subsect. Mediterranea parafilética.

Keywords: biogeography, ITS, morphology, phylogeny, taxonomic revision, trnL-trnF.

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), and a key to the subgenera and sections can be found in Aedo et al. (1998a, b). 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. Subgen. Geranium, the largest, comprises over 370 species grouped in at least 10 sections. It is characterized by fruit of the seedejection type, in which the explosive recurvature of the awn carries the mericarp upwards in an arc, throwing the seed out. Yeo (1984) included section Tuberosa (Boiss.) Reiche in subgenus Geranium, indicating that it differs from the general model of this subgenus in two ways: (1) the awn (with attached mericarps) falls away from the columella, and (2) there is no structure for retaining the seed in the pre-explosive interval. These important fruit characters seem to support the idea that sect.

Tuberosa is a natural group, in which two subgroups can be differentiated: subsect. Tuberosa (Boiss.) Yeo, with tuberose rootstock and palmatisect leaves, and subsect. Mediterranea, which lacks both of these features (Yeo 1984).
Knuth's (1912) monograph of Geranium, which was based on the limited material available at that time, classified the species of subsect. Mediterranea in four different groups. Geranium bohemicum was included in sect. Columbina W. D. J. Koch, which was an aggregate of annual species now considered to belong to several different groups. Geranium gracile was included in sect. Striata R. Knuth, and G. kurdicum in sect. Sanguinea R. Knuth. The remaining species were classified in subsect. Mediterranea, in which he also included G. atlanticum Boiss. and G. psilostemon Ledeb. These two last species are currently classified in sect. Geranium. Knuth (1912) synonymized G. lanuginosum to $G$. bohemicum, but did not provide any explanation for this decision. As an unavoidable consequence of a scarcity of material, the taxonomic treatment was incomplete and descriptions lacked some important features, including inflorescence, petals, fruits,
and indumentum. Thus, Knuth's key has some ambiguous leads (e.g., G. gymnocaulon and G. libani are identified as having "Pedicelli glandulosi"). Additionally, Knuth's (1912) distributions were preliminary (without maps) and no drawings were provided.

Major floras of the eastern Mediterranean area and the Caucasus provided different treatments for G. ibericum and related species. For instance, Bobrov (1949) and Schönbeck-Temesy (1970) accepted G. montanum as endemic from the Caucasus, and Davis (1967) considered G. ibericum subsp. jubatum as endemic from the Black Sea area. Here, these taxa are considered as synonyms of $G$. ibericum (see below).

Following our recent revisions of several sections of Geranium (Aedo 1996, 2001, 2003; Aedo et al. 1998b, 2002, 2003, 2005), and with the goal of comprehensively monographing the genus, we present here a revision of subsection Mediterranea.

## Materials and Methods

This revision is based on more than 650 herbarium specimens from the following herbaria: $B C, B M, B R, C, E$, F, FI, G, GOET, H, HBG, ISTE, JACA, JE, K, KRA, L, LD, LE, LISE, M, MA, MAF, MO, MPU, NMW, O, P, PR, S, SEV, SOM, UPA, V, W, WA, WAG, WU, and Z (A comprehensive list of studied specimens is available at http:// www.rjb.csic.es/Geranium/Index_geranium.html). Microfiche, color slides, digital photographs, and other data have also been examined from B, FI, G, LINN, and UPS. Curators from CL, GB, GH, KSU, KWAH, LJM, and LY kindly answered our petition, but they did not find any of the requested specimens in their herbaria, or could not send them.

Unfortunately, we had difficulties in obtaining loans of some types. 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 opinion was found, these names are included in the "Excluded Names" section.

For scanning electron microscopy (SEM), samples were glued to aluminium stubs, coated with $40-50 \mathrm{~nm}$ gold, and examined with a JEOL-TSM T330A scanning electron microscope at 15 kV . Pollen was counted for at least four specimens (eight to 15 anthers) in each species and P/O was calculated according to Cruden $(1976,1977)$. The number of viable ovules in Geranium is five, one for each mericarp. Each ovary initially has ten ovules, but five degenerate during flower development. Thus, we have calculated the ratio P/O considering only the viable ovules (i.e., the number of pollen grains of one anther $\times 10$ anthers $/ 5$ ovules).

Fifty-seven quantitative characters were measured and recorded using a Mitutoyo CD-15CD digital caliper. To represent the variability of each descriptor within species, box-plots containing medians and percentiles were prepared using the Statistica sofware package. 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 causing some difficulties for their use. To avoid these problems, ranges are included in brackets in the key. The most frequent and useful values are done by percentiles and


FIG. 1. Diagram of characters used to describe the leaf lamina and the fruit. A. lamina length; B. lamina width; C. segment length; D. main sinus length; E. secondary sinus length; F. maximum width; G. segment width at the base. H. fruit length; I. rostrum length; J. rostrum narrowed apex length; K. stigmatic remains length; L. mericarp length; M. mericarp width.
are shown without brackets. Standarized approaches used to describe leaf lamina and fruit are illustrated in Fig. 1.

Voucher information for the samples used in the molecular study are listed in Appendix 1. All DNA samples were obtained from approximately 20 mg of leaf tissue from herbarium specimens. DNA extractions followed the E.Z.N.A. Plant MiniPrep Kit (Omega-Biotech, Doraville, USA). ITS sequences of four additional species available from GenBank were used in all analyses. These four species (G. retrorsum L'Hér. ex DC., G. solanderi Carolin, G. homeanum Turcz., and G. brevicaule Hook. f.) belong to different sections of Geranium subgen. Geranium. According to Aedo et al. (2005), the specimens of G. sessiliflorum Cav. from New Zealand and Australia should be considered G. brevicaule. Additionally, we obtained an ITS sequence of G. robertianum L. (subgen. Robertium), and together with the four species of subg. Geranium, these samples were selected as the outgroup to test the monophyly of subsect. Mediterranea.

The primer pair 18 S 1830for and 26S 40rev (Nickrent et al. 2004) was used for polymerase chain reaction (PCR) amplification and sequencing of the ITS region. To amplify the ITS-2 region from G. bohemicum, internal primers ITS2
and ITS3 (White et al. 1990), located at the 5.8 S region, were used. The PCR amplification of the $\operatorname{trnL} L-t r n F$ region ( $\operatorname{trnL}$ intron, trnL 3' exon, trnL-trnF intergenic spacer and trnF gene) was accomplished using the primers described in Taberlet et al. (1991). For the PCR amplification reactions, we used Ready-to-Go PCR Beads (Amersham Biosciences). The cycling parameters for ITS amplifications were 5 min at $94^{\circ} \mathrm{C}$ followed by 40 cycles at $94^{\circ} \mathrm{C}$ for $30 \mathrm{~s}, 52^{\circ} \mathrm{C}$ for 30 s , and $72^{\circ} \mathrm{C}$ for 1 min , and a final extension at $72^{\circ} \mathrm{C}$ for 10 min . Parameters for $\operatorname{trnL}-\operatorname{trnF}$ amplifications were 5 min at $94^{\circ} \mathrm{C}$ followed by 5 cycles at $94^{\circ} \mathrm{C}$ for $30 \mathrm{~s}, 55^{\circ} \mathrm{C}$ for 30 s , and $72^{\circ} \mathrm{C}$ for $1 \mathrm{~min}, 33$ cycles at $94^{\circ} \mathrm{C}$ for $30 \mathrm{~s}, 48^{\circ} \mathrm{C}$ for 30 s , and $72^{\circ} \mathrm{C}$ for 1 min , and a final extension at $72^{\circ} \mathrm{C}$ for 10 min .

Amplification products were cleaned from agarose gels using the QIAquick Gel Extraction Kit (Qiagen). When light PCR products were visualized, cloning was conducted using the pGEM-T Easy-Vector II cloning kit (Promega). Cycle sequencing reactions were conducted using primers specific to ITS and trnL region or universal primers specific to the plasmid (T7 and SP6). The program Sequence Navigator (Applied Biosystems) was used to edit the resulting electropherograms and to assemble contiguous sequences. Sequences were then imported into SeqApp (Gilbert 1993) and aligned manually. The ITS and $\operatorname{trnL}-\operatorname{trnF}$ sequences have been submitted to the EMBL Nucleotide Sequence Database (accession numbers provided in Appendix 1). The data matrices have been deposited in TreeBASE (study number S1667).

Gaps, including indels, were coded as missing data. Minimum length Fitch trees were constructed with maximum parsimony (MP) using heuristic searches with TBR branch-swapping and MULPARS options in PAUP* 4.0b10 (Swofford 2002). Branch robustness was estimated by bootstrap analyses (Felsenstein 1985) with a full heuristic search of 100 replicates in PAUP*. Bayesian analyses were conducted using MrBayes 3.0b4 (Ronquist and Huelsenbeck 2003). The analyses were performed assuming the GTR $+\Gamma$ substitution model as was determined by the maximum likelihood ratio test implemented by ModelTest 3.06 (Posada and Crandall 1998) according to the Akaike Information Criterion (AIC). To determine the posterior probability distribution of trees, two independent runs were executed; a preliminary analysis of 300,000 generations and a second one of $1,000,000$ generations, both with four parallel chains and trees sampled every 100 generations. Both runs showed similar estimates of substitution-model parameters, topology and branch lengths. The results reported here are based on the chains of the 1,000,000-generation run. The point of stationarity was determined by examining the posterior probability distribution. The initial 1,000 trees were discarded as burn-in before stationarity was reached. Both the majority-rule consensus tree and the posterior probability of the nodes were calculated from the 9,001 remaining trees using PAUP*.

Ancestral areas were reconstructed using dispersal-vicariance analysis (DIVA version 1.1; Ronquist 1997). In DIVA, dispersal events are counted as one step, but vicariance is considered the default mode of speciation. We constrained our search to a maximum of three areas. Seven areas of endemism were considered: (a) Western Mediterranean, (b) Central and Northern Europe, (c) Southern Balkan Peninsula, (d) Caucasus, (e) Lebanon mountains, (f) Kurdistan mountains, and (g) Elburz mountains. (Fig. 2).

## Results

Morphology. Duration and Habit. All species of Geranium subsect. Mediterranea except G.


Fig. 2. Areas of the biogeographic analysis of Geranium subsect. Mediterranea: A. Western Mediterranean. B. Central and northern Europe. C. Southern Balkan Peninsula. D. Caucasus. E. Lebanon mountains. F. Kurdistan mountains. G. Elburz mountains. Taxa number per area are shown in parentheses.
bohemicum and G. lanuginosum are perennial herbaceous plants. The perennial species share $\pm$ horizontal and cylindric rootstocks that are not tuberculated and have thin roots. All species of subsect. Mediterranea have erect, leafy stems that can reach 80 cm in height.

Indumentum. In the species studied here, three trichome types can be found, all of which are simple and uniseriate (Theobald et al. 1979). (a) Eglandular, unicellular hairs, smooth or with a papillose surface (Fig. 3B). According to Payne (1978) these could be included in the "subulate" type. They have been found in all species and are widespread on almost all organs of the plant. Two subtypes can be distinguished: (a1) patent to retrorse hairs, 0.1-5.4 mm long (Fig. 3C; 4E); and (a2) uncinate hairs $0.1-0.3 \mathrm{~mm}$ long, which can be found on petioles, peduncles, or pedicels of all species (Fig. 3A) but G. kurdicum. (b) Glandular hairs, $0.2-1.8 \mathrm{~mm}$ long, with $2-4$ cells, smooth, the foot consisting of cylindric or decussated cells (Fig. 3C). These hairs are found in all species but G. gymnocaulon, G. kurdicum, and G. libani. (c) Short glandular hairs ( $<55 \mu \mathrm{~m}$ long), smooth, usually consisting of by two cells, but sometimes with a bicellular foot (Fig. 3D). They are present in all species here studied, but since they are only evident at high magnification, they will not be considered in the descriptions.

Leaves. The leaves in all species of subsect. Mediterranea are polygonal in outline, cordate, palmatifid, with (3-)5-7 segments. Basal leaves frequently form a persistent rosette, whereas cauline ones are opposite (usually one pair, except


FIg. 3. SEM photographs showing hair types found in Geranium subsect. Mediterranea. A. Pedicel of G. gracile showing uncinate eglandular hairs (Schönswetter \& Tribsch s.n., 15 July 1997, WU). B. Papillose surface of an eglandular hair of G. libani (Samuelsson 2016, S). C. Pedicel of G. ibericum showing: (1) long glandular hair with a foot of decussated cells, and (2) patent eglandular hair (Herrero \& al. 1550, MA). D. Pedicel of G. gracile showing a short glandular hair (Schönswetter \& Tribsch s.n., 15 July 1997, WU).
G. gracile, which has 2-3 pairs). In G. bohemicum and G. lanuginosum, however, the lowest cauline leaves are alternate. All species have palmatifid leaves, but in G. kurdicum the leaves are more deeply divided, almost palmatisect (Fig. 4a). The secondary division is deep in both G. kurdicum and G. gymnocaulon, but shallow in G. gracile (Fig. 4b). The central segment of the leaf is rhombic in all species, but $\pm$ obtriangular in G. platypetalum and G. renardii (Fig. 4c). The number of lobes per segment (central segment) varies from 5 to 34 . This character tends to overlap in almost all species, but occasionally may be useful to discriminate some pairs of species (Fig. 4d).

Inflorescence. The inflorescence in most species of subsect. Mediterranea is dichasial, with dichotomous branching and a long pedunculate cymule at the primary branch. Terminal cymules are usually aggregated at the top of the branches resembling umbels, sometimes with short or without peduncles. Among the perennials, only G. gracile has a monochasial cyme, with solitary cymules (not aggregated at the top of the
branches). Finally, the two annuals (G. bohemicum and G. lanuginosum) have dichasial cymes with monochasial branching. The cymules are twoflowered in all species of subsect. Mediterranea. The bracteoles are distinctly longer in G. platypetalum, providing a good character to distinguish this species (Fig. 4f).

Calyx. Sepals are smooth and not accrescent in most species of subsect. Mediterranea. Only in the two annuals are they noticeably accrescent. The number of nerves varies from 3 to 5 in G. gracile, G. kurdicum, G. libani, and G. peloponnesiacum, and from 5 to 7 in G. gymnocaulon, G. ibericum, G. platypetalum, and G. renardii. Finally, the sepals of G. bohemicum and G. lanuginosum have 5 nerves.

COROLLA. The flowers are actinomorphic, with patent petals in G. gymnocaulon, G. ibericum, G. libani, G. peloponnesiacum, G. platypetalum, and G. renardii, or erect-patent in the remaining species. Most species of this section have bluish petals. Only G. gracile, G. kurdicum, and G. peloponnesiacum have purplish petals, and G. renardii white ones. In all species, the petals have a notched apex and


FIG. 4. Box plot showing leaf and inflorescence key quantitative characters. A. ratio main sinus/main segment length; B. ratio second sinus/middle segment length; C. ratio maximum width/segment length; D . lobes number of the leaf central segment. E. length of the eglandular hairs of the peduncle (mm); F. bracteoles length (mm).


Fig. 5. Box plot showing: A. petal length (mm); B. ratio petal width/petal length. C. flowering period; D. Log Pollen/ ovule ratio.
some cilia on the basal margin. However, some differences in indumentum distribution have been detected. In G. gymnocaulon, G. ibericum, G. lanuginosum, and G. platypetalum, both sides are glabrous, whereas in G. bohemicum, G. gracile, and G. kurdicum the petals are pubescent on the base of adaxial side and glabrous on the abaxial side. In G. libani, G. peloponnesiacum, and G. renardii the opposite condition is found. Only the apex of the petal is pubescent in G. bohemicum and sometimes in G. gymnocaulon. The eight perennial species have longer petals ( $10.4-28.4 \mathrm{~mm}$ long) than $G$. bohemiсит and G. lanuginosum (5.4-9.4 mm long) (Fig. 5a). The petals of G. gracile are remarkably narrow in relation with their length (Fig. 5b).
As expected, the annual species (G. bohemicum and G. lanuginosum) have more extended flowering periods. These species occur on an extensive area (mainly G. bohemicum) with many different habitats and climatic conditions. The core of the flowering
period is, for most species, between June and August, although G. lanuginosum, G. libani, and G. peloponnesiacum flower mainly during spring. In $G$. lanuginosum, this trend is clearer if specimens from Sweden (where it has been introduced) are excluded. These three species have a southern distribution, mainly in the Mediterranean region, which could explain phenological differences (Fig. 5a).

Stamens, Pollen, and Nectaries. In all species of subsect. Mediterranea there are ten stamens disposed in two whorls of different lengths, which mostly mature successively, beginning with those of the external whorl. However, in G. bohemicum and G. lanuginosum, both whorls usually mature at the same time. The filaments of subsect. Mediterranea are lanceolate and both whorls are included inside the flower. The hairs of the filaments are relatively short in G. gracile, G. kurdicum, and the two annuals, while in G. platypetalum they are remarkably longer.


Fig. 6. SEM photographs showing pollen features of Geranium subsect. Mediterranea. A. Pollen grain of G. renardii (Arnold s.n., 1998, JE). B. Pollen ornamentation of G. libani (Samuelsson 1216, S). C. Pollen grain of G. bohemicum (Hansen s.n., 4 July 1967, C). D. Pollen ornamentation of G. bohemicum (Hansen s.n., 4 July 1967, C).

The pollen is characterized by the reticulate exine ornamentation with distinctly baculate, clavate, or gemmate supratectal elements as in the rest of the genus (Weber 1996). In the perennial species, there is little variation in the size of supratectal elements (Fig. 6A, B), whereas the two annuals show great variation in their size (Fig. 6C, D), bearing gemmate elements that may protrude further from the reticulum giving and the grain an irregular outline. According to Stafford and Blackmore (1991), some other unrelated species such as G. macrorhizum L. (subg. Robertium) and G. phaeum L. (subg. Erodioidea) have similar variation.

Gynoecium. Geranium bohemicum and G. lanuginosum have a shorter gynoecium (3.1-4 mm) than the perennial species of the subsection (4.311.2 mm ). The abaxial side of the stigma is glabrous in the eight perennials, while in the annuals it is hairy, with eglandular, antrorse hairs that could favor capture of pollen grains dispersed by flower movements. According to Heslop-Harrison and Shivanna (1977), Geranium has dry stigmas, which should be classified in the group II, characterized by receptive cells concentrated in distinct zones. These stigmas have
multicellular and uniseriate papillae on adaxial side, only evident at high magnification. All these features have been verified in species of subsect. Mediterranea.

Fruit. Geranium subsect. Mediterranea is assigned to subgenus Geranium, which exhibits the "seed ejection-type" of fruit discharge (Yeo 1984). In this fruit type a single seed is actively discharged by the explosive recurvature of the awn. The awn and the mericarp wall remain 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 during the pre-explosive interval. In subsect. Mediterranea, there is no structure for retaining the seed in this interval (Fig. 7A). Instead, the mericarp is twisted at its attachment to the awn and, consequently, the orifice faces almost horizontally. The top of the mericarp is longitudinally compressed (Fig. 7B), probably strengthening the connection between the awn and the mericarp and favoring the twisting of the mericarp. Mericarps have a similar size, and are smooth (Fig. 7C) and brownish in all species. The rostrum has a nar-


FIG. 7. SEM photographs showing mericarp features of Geranium subsect. Mediterranea. A. Mericarp of G. bohemicum (López s.n., MA-213282); B. Top of the mericarp of G. ibericum showing the area of longitudinal compression (unknown collector, BR-825853); C. Mericarp surface of G. libani (Samuelsson 2016, S).
rowed apex ( $1-6.7 \mathrm{~mm}$ long) in the perennials, a feature not present in the annuals.

Seeds. The seeds are $\pm$ ellipsoid, with scattered stomata (Fig. 8B). The seed-coat is finely reticulate at a magnification of 30 , but in all species, SEM shows that the reticulate surface is due to the prominence of outer and middle layers of the outer integument (Fig. 8A, B). Only G. lanuginosum shows a foveolate seed-coat (Fig. 8C, D). The seeds are usually uniformly reddish in all species except in G. bohemicum, which has mottled seeds (brown-
ish with more clear areas). The size is similar in the ten species, and usually with a hilum one-fourth as long as the seed perimeter. Only in the two annual species the hilum is shorter, about one-sixth as long as the perimeter of the seed.

According to Corner (1976), seeds of Geraniaceae have cells that contain solitary crystals and tannin in the inner layer of the outer integument. These crystal cells are also present in the endotesta of Hypseocharis Remy and Oxalidaceae (Boesewinkel 1988). According to Boesewinkel and Been (1979), crystals extend as small protusions beyond the socalled light-line, reaching the coat surface of the seed. They form bipyramidal figures produced by calcium oxalate trihydric crystals (Netolitzky 1926). In Geranium subsect. Mediterranea we have found crystals on the seed-coat of G. ibericum and G. lanuginosum (Fig. 8E, F).
The cotyledons are always conduplicate, one half of each cotyledon lying in the primary fold of the opposite one. They are pale green, and have entire margins (except G. bohemicum, which has a notch on each side), subcordate bases, and short petioles, as found in sect. Batrachioidea (Aedo et al. 1998b).

Chromosome Numbers. All chromosome counts carried out to date in G. bohemicum gave $2 n=28$. By contrast, there is a controversy regarding the chromosome number of G. lanuginosum. Warburg (1938) reported $2 n=42$ (sub G. deprehesum), while Dahlgren (1952) and Van Loon (1984b) found $2 n=$ 48. The latter authors considered Warburg's count mistaken. According to Van Loon (1984b), the chromosome number of G. lanuginosum may have originated from a dysploid change.

Among the remaining eight species of the group, all perennials, only three have been counted. Both G. gymnocaulon and G. ibericum have diploids and tetraploids ( $2 n=28$, or 56 ), while G. platypetalum has only diploids $(2 n=28)$. According to Yeo (2002), the triploid number $(2 n=42)$ attributed by Warburg (1938) to G. platypetalum with some doubts, should be assigned to G. $\times$ magnificum. Van Loon (1984a, b) considered $x=14$ as the basic number for all species of subsect. Mediterranea.
Breeding System and Flower Features. The species studied here show Log P/O ratios between 2.29 and 3.19 (Table 1; Fig. 5d). In the two annual species, both considerably lower Log P/O ratios and smaller petals suggest facultative autogamy. Cruden $(1976,1977)$ observed that the pollen-ovule ratios ( $\mathrm{P} / \mathrm{O}$ ) are related to the breeding system. A substantial decrease in $\mathrm{P} / \mathrm{O}$ is associated with a pass from xenogamy to facultative xenogamy or to autogamy.

There is a significant positive correlation between either petal length or gynoecium length


FIG. 8. SEM photographs showing seed features of Geranium subsect. Mediterranea. A. Seed of G. gracile (Rikli s.n., 25 Aug 1912, Z); B. Seed-coat of G. libani with a stomata (Samuelsson 2016, S); C. Seed of G. lanuginosum (Delvosalle s.n., June 1884, BR); D. Seed-coat of G. lanuginosum (Delvosalle s.n., June 1884, BR). E. Seed-coat of G. lanuginosum showing calcium oxalate crystals (Delvosalle s.n., June 1884, BR); F. Seed-coat of G. ibericum showing calcium oxalate crystals (Davis \& Hedge 32137, E).

Table 1. Pollen-ovule ratio of Geranium subsect. Mediterranea (Ss: Sample size; sd.: standard deviation).

| Species | Pollen/anther |  |  |  |  |
| :--- | ---: | :--- | :---: | :---: | :---: |
|  | Ss | mean | sd | P/O | Log P/O |
| G. bohemicum | 8 | 107.75 | 14.6 | 216 | 2.333 |
| G. gracile | 10 | 334.6 | 20.1 | 669 | 2.826 |
| G. gymnocaulon | 9 | 473.11 | 33.3 | 946 | 2.976 |
| G. ibericum | 15 | 548.2 | 66.7 | 1096 | 3.04 |
| G. lanuginosum | 10 | 97.833 | 7.8 | 196 | 2.292 |
| G. libani | 11 | 780 | 74.7 | 1560 | 3.193 |
| G. peloponnesiacum | 8 | 592.5 | 26.7 | 1185 | 3.074 |
| G. platypetalum | 8 | 685.5 | 32.1 | 1371 | 3.137 |
| G. renardii | 9 | 714.89 | 36.9 | 1430 | 3.155 |

and Log P/O (petal length $-\log \mathrm{P} / \mathrm{O}: \mathrm{r}=0,822 ; \mathrm{p}$ $<0.0064$; gynoecium length $-\log \mathrm{P} / \mathrm{O}: \mathrm{r}=0,795$; $\mathrm{p}<0.0104$ ). This is congruent with protandry observed in herbarium specimens of all species but G. bohemicum and G. lanuginosum, which show lack of dichogamy. Petal size is correlated with reproductive type in Geranium and in many other genera (Bell 1985; Phillip and Hansen 1999). Consequently, longer petals are expected in allogamous taxa. According to Philipp (1985), most perennial species of Geranium produce large and protandrous flowers, while a slight or null protandry is accompanied by an increased selfing and a reduction in flower size. Selfing is here related to annual or colonizer strategies, which occur in many other taxa (Baker 1955, 1967; Stebbins 1957, 1970; Ambruster 1993).

Hybrids. Yeo (2002: 214) indicated that artificial hybrids between many species of subsect. Mediterranea (including G. ibericum and G. platypetalum) have been produced by A. Bremner. However, no names for these hybrids are available except Geranium $\times$ magnificum.

Geranium $\times$ magnificum Hyl., Lustgården 42: 114, fig. 1. 1961. [TYPE: Sweden. cultivated at Uppsala Botanical Garden, 17 June 1960 (holotype: UPS color slide!)] is usually considered a hybrid between G. ibericum (without glandular hairs) and G. platypetalum (with glandular hairs). Hylander (1961) did not cross parental species but suspected its hybrid status because of the intermediate characters and the sterility of his plant. In our opinion, the type and many specimens identified as G. $\times$ magnificum are indistinguishable from glandular forms of G. ibericum. On the other hand, one species of subsect. Mediterranea [G. renardii: Aedo 4478 (MA)] cultivated at Madrid Botanical Garden seems to be infertile with its own pollen. This characteristic has been reported in subsect. Tuberosa (Yeo 2002). If auto-incompatibility could be demonstrated in G. ibericum, a new interpretation of $G . \times$ magnificum could be given. Thus, plants identified as G. $\times$ magnificum could be considered as garden clones obtained from glandular forms of G. ibericum, which do not deserve taxonomic recognition.

Phylogenetic Relationships. The trnL-trnF region was amplified and sequenced from the seven species indicated in Appendix 1. Sequences of $G$. robertianum and G. pusillum L. obtained from GenBank were also incorporated into the data matrix. The total length of the region analyzed was 983 positions, with 76 variable characters, of which only four were parsimony-informative. The MP analysis, with G. robertianum as outgroup, resulted in a single tree of 83 steps (tree not shown). The
species of subsect. Mediterranea arise in an unresolved clade with moderate bootstrap support ( $74 \%$ ). The topology of this clade is a polytomy with both G. libani and G. peloponnesiacum placed in an internal clade with low bootstrap value ( $63 \%$ ). These data support the monophyly of subsect. Mediterranea, but the low number of informative characters does not allow further consideration of the phylogeny of the group.

ITS amplification using 1830 f and 40 r primers was straightforward for all the species except $G$. bohemicum. Up to six different accessions of $G$. bohemiсиm were extracted and PCR-amplified, but in all cases the yield was low and the resulting products were of a smaller size than the other species. After cloning these products, we obtained several sequences of fungal origin, some of them endophytic parasites. We amplified ITS in two parts, using primers ITS1 and ITS2 to get the 18S5.8 S region, and ITS3 and ITS4 to get the 5.8S-26S region. We obtained bright bands for the ITS-2 region but not for ITS-1, indicating a primer hybridization problem at the $3^{\prime}$ end of the 18 S gene. Attempts to amplify the $3^{\prime}$ end of 18 S with other primers also failed. Therefore, the ITS1 region of $G$. bohemicum was coded as missing data.

The aligned length of the ITS matrix was 677 positions, of which 180 were variable and 124 were parsimony informative. MP analysis of the ITS matrix resulted in 72 optimal trees (length $=257$; CI $=0.830 ;$ RI $=0.9097$; tree not shown). The parsimony strict consensus and the Bayesian majority-rule trees showed identical topology. The tree resulting from the Bayesian analysis is illustrated in Fig. 9. Using G. robertianum as outgroup, two monophyletic groups arise with bootstrap (BS) and Bayesian posterior probability (BPP) values of $100 \%$ and 1.00 , respectively. The first clade comprises four species from New Zealand and shows the phylogenetic relationship of $G$. retrorsum and G. solanderi, both placed in sect. Chilensia R. Knuth. The other clade includes all species of subsect. Mediterranea and G. tuberosum L. (subsect. Tuberosa). Within this clade, two internal groups were recovered, one including the two annual species (G. lanuginosum and G. bohemicum) with 1.0 BPP and $100 \%$ BS, and a second one including all the perennial species, but only weakly supported ( 0.67 BPP and $58 \%$ BS).

Habitat and Biogeography. Geranium bohemicum is broadly distributed across a longitudinal range of 4200 km and a latitudinal range of 2400 km . The distribution of the other annual species (G. lanuginosum) is not so large, ranging 3000 km longitudinally and 1000 km latitudinally. The two species are only sympatric in the Iberian


Fig. 9. Majority-rule consensus tree based on 9,000 trees from a Bayesian inference analysis. Posterior probabilities followed by the bootstrap value from the MP analysis are indicated on the branches.

Peninsula and France. Both G. bohemicum and G. lanuginosum grow in forests, from the sea level to 1800 m , on limestone and acidic rocks, and generally on recently burned sites.
The group reaches its highest diversity in the Caucasus and neighbouring areas of Turkey and Iran, where five endemic perennials and the annual G. bohemicum grow. The other three perennials are endemic to Greece (G. peloponnesiacum), SE Turkey and Iraq (G. kurdicum), and Lebanon and neighbouring areas (G. libani). They grow on alpine meadows or montane forests from 500 to 3500 m . Among them, G. libani and G. peloponnesiacum occur at intermediate elevations, while G. kurdicum grows at higher elevations. Geranium ibericum, G. gymnocaulon, and G. platypetalum are usually found growing on acidic rocks, while G. libani and G. peloponnesiacum grow on limestone substrates. We have no information about the substrates for $G$. gracile, G. kurdicum or G. renardii.
The biogeographic analysis using DIVA and the phylogenetic tree (Fig. 9) resulted in a single optimal reconstruction requiring 13 dispersal events (Fig. 10). The ancestral area for the entire group is a composite formed by all areas of endemism.


FIG. 10. Biogeographic reconstruction of Geranium subsect. Mediterranea using DIVA on the phylogenetic tree. Areas of the biogeographic analysis (see fig. 3): a. Western Mediterranean; b. Central and northern Europe; c. Southern Balkan Peninsula; d. Caucasus; e. Lebanon mountains; f. Kurdistan mountains; g. Elburz mountains.

## Discussion on Phylogeny and Biogeography

The two main clades resolved with the ITS data indicate that the annual species form a distinctive group within the species of subsect. Mediterranea. This group is also supported by a number of morphological characters, as accrescent sepals, inflorescences in dichasial cymes with monochasial branches and blackish mericarps (discussed under G. bohemicum). Among the perennial species, well supported clades are formed by different populations of the same species, except for the G. ibericum clade, which also includes the only accession of $G$. gymnocaulon that was successfully amplified. Additional specimens of G. gymnocaulon are needed to clarify its relationship with G. ibericum. The tree also indicates a relationship between G. platypetalum and G. gracile. However, among the characters analyzed in this study, we have not found any morphological synapomorphies that support this relationship. Morphologically, G. platypelalum appears to be more closely related to G. ibericum, but they are not placed together in the molecular tree. Geranium renardii is well characterized as a species by its reticulate leaves and white petals, but its relationship to the other perennial species is left unresolved. Geranium tuberosum (subsect. Tuberosa) is included within the perennial species of subsect. Mediterranea, rendering the latter paraphyletic. Further molecular analyses that include sequences from other species of subsect. Tuberosa are needed to elucidate the monophyly of subsection Tuberosa itself. Otherwise, the presence of tuberose rootstocks and palmatisect
leaves may have arisen independently several times as an adaptation to drier habitats.
Geranium bohemicum and G. lanuginosum, which are the earliest-diverging clade in this tree, are annuals spread across a large geographic area. The remaining species are perennials endemic to narrower areas. As in many groups of angiosperms (Stebbins 1957, 1970; Baker 1955, 1967) and in several other Geranium taxa (unpublished data), facultative or autogamous annuals, specialized in disturbed habitats, can spread over large areas.
The ancestors of the central subclade of the tree are assigned to the Caucasus area. The terminal taxa of this clade (composed by G. tuberosum, G. libani, G. kurdicum, and G. peloponnesiacum) are endemics located in mountain ranges close to the Caucasus or in the Eastern Mediterranean. This pattern is not easy to explain, but it could have occurred after extinction in the western Mediterranean and several dispersals around the Caucasus.

## Taxonomic Treatment

Geranium subsect. Mediterranea R. Knuth in Engl., Pflanzenr. 53: 107. 1912.-TYPE: G. platypetalum Fisch. \& C.A. Mey. (designated by Yeo 1984: 12).

Geranium sect. Lanuginosa Rouy in Rouy \& Fouc., Fl. France 4: 87. 1897.-TYPE: G. lanuginosum Lam.
Geranium sect. Bohemica Tzvelev in Nov. Syst. Pl. Vasc. 29: 95. 1993.—TYPE: G. bohemicum L.

Herbs annual or perennial. Rootstock (in perennial species) not tuberculate, usually turnip-shaped, without thick fleshy roots. Stem erect, leafy, herbaceous. Leaves polygonal in outline, cordate, palmatifid, with (3)5-7 rhombic segments; cauline leaves alternate or opposite; stipules free. Inflorescence in a monochasial or dichasial cyme with cymules 2-flowered, solitary or in aggregates at the top of each branch; pedicel and peduncle together overtopping the subtending leaf. Sepals smooth, accrescent or not, 3-7-nerved. Petals patent to erectpatent, emarginate, without claw, purplish to bluish, sometimes white. Stamens 10, both whorls bearing anthers, not exserted. Nectaries glabrous or hairy. Fruit of seed-ejection type; mericarps smooth, compressed at apex, lacking longitudinal rib, basal beak, basal callus, and prong. Seeds reticulate to foveolate, brownish or reddish; hilum $1 / 6-1 / 4$ as long as the perimeter. Cotyledons entire or notched.

## Key to the Species of Geranium Subsection Mediterranea

1. Plants annual . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
2. Seeds brownish, mottled; cotyledons with a notch on each side; petals with ciliae at the apex; nectaries with a tuft of
hairs at the top . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . bohemicum
3. Seeds uniformly reddish; cotyledons entire; petals glabrous at the apex; nectaries glabrous . . . . 2. G. lanuginosum
4. Plants perennial
5. Leaves reticulate
6. G. renardii
7. Leaves without reticulate nervation . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
8. Pedicels bearing only eglandular hairs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
9. Leaves deeply palmatifid [ratio main sinus/main segment length $=0.71-0.84(0.9)$ ]; stems and petioles glabrous or with sparse eglandular hairs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10. G. kurdicum
10. Leaves not deeply palmatifid [ratio main sinus/main segment length $=(0.49) 0.55-0.65(0.76)$ ]; stem and petioles usually hairy $\qquad$
11. Peduncles with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, without long patent hairs 9. G. gymnocaulon
12. Peduncles with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long and patent eglandular hairs $0.4-3.3 \mathrm{~mm}$ long
13. Peduncles with patent eglandular hairs $0.4-0.7(0.8) \mathrm{mm}$ long; petals (10.4)12.9-16.9(18.3) mm long; leaf central segment with (8)9-13(16) lobes
14. G. libani
15. Peduncles with patent eglandular hairs (1)2.1-2.5(3.3) mm long; petals (15.4)19.5-24.9(28.4) mm long; leaf central segment with (14)16-24(39) lobes
16. G. ibericum
17. Pedicels bearing glandular and eglandular hairs . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8
18. Leaves with short secondary lobes (ratio second sinus/middle segment length $=0.04-0.09$ ); petals narrow (ratio petal width/petal length $=0.30-0.45$ ) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3. G. gracile
19. Leaves with deeper secondary lobes (ratio second sinus/middle segment length $=0.15-0.35$ ); petals broader (ratio petal width/petal length $=0.56-0.86$ )
20. Peduncles with patent eglandular hairs $0.6-1(1.2) \mathrm{mm}$ long; petals hairy on the base of abaxial side, glabrous on the adaxial side, ciliate on the basal margin . . . . . . . . . . . . . . . . 7. G. peloponnesiacum
21. Peduncles with patent eglandular hairs (1)2.3-3.1(4.8) mm long; petals glabrous on both sides, ciliate on the basal margin
ent $(0.58) 0.61-0.68(0.74)]$ bracteoles (3.2)5.2-6.4(8.2) mm length
22. G. ibericum
23. Main leaf segment obtriangular [ratio maximum width/segment length $=(0.75) 0.76-0.79(0.84)$ ]; bracteoles (8.4)9.6-14.1(18.8) mm length
24. G. platypetalum
25. Geranium bohemicum L., Cent. Pl. II: 25. 1756. Geranium caeruleum Moench, Methodus: 284. 1794, nom. illeg.-TYPE: CZECH REPUBLIC. Bohemia, Miller s.n. (lectotype: designated by Novoselova 1998: 150, LINN 585.69 colour slide!). Fig. 11.

Herbs annual, $20-73 \mathrm{~cm}$ tall. Stem erect, leafy, herbaceous, with patent eglandular hairs 1.22.9 mm long and patent glandular hairs $0.5-$ 0.8 mm long. Basal leaves in a $\pm$ persistent rosette; lamina $2.2-6.8 \times 3.1-8.8 \mathrm{~cm}$, palmatifid (ratio main-sinus length/middle-segment length $=$ $0.47-0.57$ ), pilose, with eglandular (and sometimes glandular), appressed hairs, not reticulate, not projected; segments $5-7$, rhombic [ratio maximum width/middle-segment length $=$ (0.59)0.64$0.70(0.71)], 4-11.4 \mathrm{~mm}$ wide at the base, $7-27$-lobed in distal half (ratio second-sinus length/middlesegment length $=0.15-0.21$ ); cauline leaves alternate (1-3), upper opposite; petioles to 15 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $1.4-2.7 \mathrm{~mm}$ long, and patent glandular hairs $0.4-1.2 \mathrm{~mm}$ long; stipules $5.8-11.5 \times 0.7-2.4 \mathrm{~mm}$, lanceolate, with eglandular and glandular hairs on abaxial surface and on the margin, glabrous adaxially. Inflorescence a dichasial cyme with monochasial branches; cymules 2flowered, solitary; peduncles $1.1-6.8 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $2-3 \mathrm{~mm}$ long and patent glandular hairs 0.3-0.6 mm long; bracteoles 1.4-5.5 $\times 0.3-$ 0.8 mm , linear-lanceolate, with usually eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels $0.4-3 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $1.6-2.6 \mathrm{~mm}$ long and patent glandular hairs $0.3-0.6 \mathrm{~mm}$ long. Sepals $5.2-12.4$ $\times 2.2-6.9 \mathrm{~mm}$, accrescent, 5-nerved, with mucro $1.1-3.4 \mathrm{~mm}$ long, with scarious margins $0.1-$ 0.2 mm wide, with patent, eglandular hairs $1.8-$ 2.6 mm long, and patent, glandular hairs $0.4-$ 0.7 mm long. Petals (5.5)5.8-7.7(11.4) $\times 3.5-9 \mathrm{~mm}$ (ratio petal width/petal length $=0.55-0.79$ ), erectpatent, emarginate (notch 0.6-1.9 mm deep), hairy on the base of adaxial side, glabrous on the abaxial side, ciliate on the basal and apical margin, bluish. Staminal filaments $2.8-4.7 \mathrm{~mm}$ long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $0.4-1 \mathrm{~mm}$ long; anthers $0.7-1.3 \times$ $0.6-0.8 \mathrm{~mm}$, yellow; pollen yellow. Nectaries with a tuft of hairs at the top, dorsally glabrous. Gynoecium 3-4 mm long, purplish. Fruit 2429.9 mm long; mericarps 4.9-6.1 $\times 1.7-2.9 \mathrm{~mm}$, with $\pm$ patent, eglandular hairs $1.2-2.4 \mathrm{~mm}$ long, and some glandular hairs $0.4-0.8 \mathrm{~mm}$ long at the apex, blackish; rostrum 17.3-23.2 mm long, with-
out a narrowed apex, with patent, eglandular 0.51.7 mm long, and patent glandular hairs $0.3-$ 0.7 mm long; stigmatic remains $0.8-2.2 \mathrm{~mm}$ long, with 5 hairy lobes. Seeds $2.8-4.4 \times 1.5-2 \mathrm{~mm}$, finely reticulate, brownish, mottled; hilum $1 / 6$ as long as the perimeter. Cotyledons with a notch on each side.

Additional Illustrations. Cavanilles (1787, tab. 81 fig. 2);Reichenbach (1841,tab. 188); Gams (1924:1697).

Chromosome Number. $2 n=28$ (Dahlgren 1952: 315; Van Loon 1984b: 294).

Phenology. Flowering specimens from April to November.

Distribution and Habitat. Europe (from Finland to Spain and Greece), and western Asia (Caucasus and N Turkey); open areas of Quercus, Fagus, Abies, Picea or Pinus forest, on limestone or acidic rocks, usually on recently burned sites, between 20 and 1800 m (Fig. 12). Geranium bohemicum has been recorded from Austria (Janchen 1959: 949), Hungary (Soó 1966: 580), and Baltic states (Bobrov 1949: 59). Unfortunately, it has been impossible to examine the specimens supporting these records. Additional maps: Meusel et al. (1978: 261); Hultén and Fries (1986: 633).

Representative Specimens Examined. ALBANIA: Greca ultra fines Kuci, $40^{\circ} 39^{\prime} \mathrm{N}, 20^{\circ} 49^{\prime} \mathrm{E}, 25$ Jul 1900, Baldaci 211 (BM, G, MO, W). BELORUSSIYA: Minsk, $53^{\circ} 54^{\prime} \mathrm{N}, 27^{\circ} 34^{\prime} \mathrm{E}$, 11 Apr 1901, Bordzilowski s.n. (LE). BOSNIA-HERZEGOVINA: Bara-Pale, $43^{\circ} 48^{\prime} \mathrm{N}, 18^{\circ} 33^{\prime} \mathrm{E}, 25$ Aug 1907, Maly s.n. (LD). BULGARIA: Rila, supra monaster, $42^{\circ} 8^{\prime} \mathrm{N}, 23^{\circ} 21^{\prime} \mathrm{E}$, 1939, Lindberg s.n. (H, LD). CZECH REPUBLIC: Carlsbad, $50^{\circ}$ $14^{\prime}$ N, $12^{\circ} 52^{\prime}$ E, (HBG). FINLAND: Abo Skargard, Vijshront, $60^{\circ} 9^{\prime} \mathrm{N}, 21^{\circ} 36^{\prime} \mathrm{E}, 4 \mathrm{Jul}$ 1967, Hansen s.n. (C). FRANCE: Alpes-Maritimes, environs de Villars du Var, au Pic des Quatre-Cantons, $43^{\circ} 58^{\prime} \mathrm{N}, 7^{\circ} 4^{\prime} \mathrm{E}, 29$ Jun 1909, Briquet $\mathcal{E}$ al. 2021 (F, MPU, Z). GEORGIA: Batumskaya oblats, $41^{\circ} 38^{\prime}$ N, $41^{\circ} 40^{\prime}$ E, 1911, Woronow 4388 (LE). GERMANY: Baden, Friburg, $47^{\circ} 59^{\prime}$ N, $7^{\circ} 50^{\prime}$ E, Jul 1891 (MPU). GREECE: Florinis, mt. Boutsi, pr. Vatochorion, $40^{\circ} 42^{\prime} \mathrm{N}, 21^{\circ} 8^{\prime} \mathrm{E}, 9 \mathrm{Jul}$ 1981, Strid \& al. 18843 (B, G). ITALY: Tirolia meridionali media, Gummer, $46^{\circ} 30^{\prime} \mathrm{N}, 11^{\circ} 30^{\prime} \mathrm{E}$, Ambrosi s.n. (E). MACEDONIA: Strmno pl., $42^{\circ} 0^{\prime} \mathrm{N}, 20^{\circ} 51^{\prime} \mathrm{E}$, Aug 1899, Formánek s.n. (PR). NORWAY: Buskerud, Ringerike, Stubal, under Ingeborg, $59^{\circ} 52^{\prime} \mathrm{N}, 9^{\circ} 52^{\prime} \mathrm{E}, 28$ Aug 1988, Engelskjon $\mathcal{E}$ Steilnes s.n. (C). POLAND: Braslaw, Grodziszki, $49^{\circ} 42^{\prime} \mathrm{N}, 19^{\circ}$ $4^{\prime}$ E, 4 Aug 1937, Dabkowska s.n. (F). ROMANIA: Oltenia, distr. Mehedinti, in silva montis Macropriciu, pr. Vîrciorova, $45^{\circ} 18^{\prime} \mathrm{N}, 22^{\circ} 21^{\prime} \mathrm{E}, 17 \mathrm{Jul}$ 1948, Morariu s.n. (C, G, H, JE, M, MAF, O, S, W, Z). RUSSIA: Rostov, Millerovo, $46^{\circ} 39^{\prime} \mathrm{N}, 40^{\circ}$ $30^{\prime}$ E, 20 Jun 1939, Nurljuskin s.n. (LE). SPAIN: Zamora, Ribadelago, Galende, barranco del Fornillo, $42^{\circ} 6^{\prime} \mathrm{N}, 6^{\circ} 40^{\prime}$ W, Jun 1948, Montserrat s.n. (C, G, MA). SWEDEN: Närke, Svennevad, Sjölunda, $59^{\circ} 2^{\prime}$ N, $15^{\circ} 23^{\prime}$ E, 7 Aug 1950, Gösta Kjellmert s.n. (MA). SWITZERLAND: Valais, vallée d'Anniviers, entre Vercorin et Pensec, $46^{\circ} 15^{\prime}$ N, $7^{\circ} 32^{\prime}$ E, 10 Aug 1879, Burnat s.n. (FI). TURKEY: Paphagonia, Wilajet Kastambuli, Tossia, Giaurdagh, $40^{\circ} 54^{\prime}$ N, $33^{\circ} 53^{\prime}$ E, 29 Jul 1892, Sintenis 4863 (BM, FI, G, JE, LD, P, PR, S, Z). UKRAINA: Tauria, $44^{\circ} 34^{\prime} \mathrm{N}, 34^{\circ} 11^{\prime} \mathrm{E}, 31$ Jun 1906, Junge s.n. (LE). YUGOSLAVIA: Montenegro, 8 km E of Rozaj, $42^{\circ} 52^{\prime} \mathrm{N}, 20^{\circ}$ 11' E, 10 Sep 1972, Kukkonen 8616 (H, PR).

Discussion. Geranium bohemicum is recognised by its cotyledons, which are notched on each side,


Fig. 11. Geranium bohemicum L. a. Habit; b. Cotyledons; c. Indumentum of the peduncle; d. Sepal; e. Petal; f. Staminal filament; g. Fruit; h-i. Mericarp; j. Seed. G. lanuginosum Lam. k. Cotyledons; 1. Leaf; m. Petal; n. Seed. [a: Montserrat s.n. (MA359961); b, c: Aedo 2440 (MA-534865); d, e, f: Sesé 198.1312 (JACA-131292); g: Montserrat s.n. (MA-252442); h-j: López s.n. (MA213282); k-m: Montserrat s.n. (BC 99741); n: Fontes \& al. 1115 (LISE-17735)].


FIG. 12. Area of distribution of Geranium bohemicum (dots) and G. lanuginosum (triangles).
its brownish seeds with clearer areas, its petals with ciliae on the apical margin, and its hairy nectaries. It has usually been considered closely related to G. lanuginosum. However, the latter species has entire cotyledons, uniformly reddish seeds, petals without ciliae at the apex, and glabrous nectaries. Additionally, in G. bohemicum the leaves are not as deeply divided (the ratios main-sinus length/middle-segment length, and second-sinus length/middle-segment length are lower), and the eglandular hairs of peduncles and pedicels are longer than in G. lanuginosum.

Geranium bohemicum shares with G. lanuginosum some character states not present in the remaining species of subsect. Mediterranea. Both are annuals, with accrescent sepals, inflorescence in dichasial cyme with monochasial branches, and blackish mericarps. Additionally, they have shorter petals, staminal filaments, anthers, and gymnoecia than the perennials species of the section. The fruits are also shorter, without narrowed apices in the rostra, and the abaxial side of the stigmatic remains is hairy instead of glabrous, as in the perennial species.
According to Dahlgren (1952) and Milberg (1994), the seeds remain viable over long time periods (at least 129 years). If not subjected to heat, the seeds do not easily germinate. This species often appears suddenly after forest fires, as can be confirmed from many herbarium labels. Thus, G. bohemicum seems to be well adapted to occasional natural forest fires that may occur after long time lags. This could partially explain its scattered distribution and temporal disappearance in some localities.
2. Geranium lanuginosum Lam., Encycl. 2: 655. 1788. Geranium bohemicum subsp. lanuginosum (Lam.) O. Bolòs \& Vigo, Butll. Inst. Catalana Hist. Nat. 38: 81. 1974.-TYPE: ALGERIA. Numidie, Poiret s.n. (lectotype: here designated, P!). Fig. 11.
Geranium perreymondii Shuttleworth \& Huet in H. Roux, Bull. Soc. Bot. Hort. Prov. 1880: 139. 1880.-TYPE: FRANCE. Collobrières, 14 May 1873, Huet s.n. (neotype: here designated, BC!; isoneotypes: FI! G! Z!).
Geranium bohemicum subsp. depraehensum E.G. Almq., Svensk Bot. Tidskr. 10: 411, fig. 1A, 2b. 1916. Geranium deprehensum (E.G. Almq.) Lindm., Bot. Soc. Exch. Club Brit. Isles 7: 765. 1925.-TYPE: SWEDEN. Ad Ekvik prope Segersgärde paroeciae Lofta Smolandiae, Almquist s.n. (lectotype: here designated, Svensk Bot. Tidskr. 10: 2 fig. 1A).

Herbs annual, $29-61 \mathrm{~cm}$ tall. Stem erect, leafy, herbaceous, with patent eglandular hairs 1.22.1 mm long and patent glandular hairs $0.2-$ 0.9 mm long. Basal leaves in a $\pm$ persistent rosette; lamina 3.2-8.6 $\times 3.8-10.5 \mathrm{~cm}$, palmatifid (ratio main-sinus length/middle-segment length $=$ $0.58-0.68$ ), pilose, with appressed, eglandular (and sometimes glandular) hairs, not reticulate, not projected; segments 5-7, rhombic [ratio maximum width $/$ middle-segment length $=(0.66) 0.68-$ $0.75(0.76)], 3.3-8.1 \mathrm{~mm}$ wide at the base, $10-18-$ lobed in distal half (ratio second-sinus length/ middle-segment length $=0.21-0.36$ ); cauline leaves alternate (1-3), upper opposite; petioles to 20 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $1.1-2.2 \mathrm{~mm}$ long and patent glandular hairs $0.3-0.7 \mathrm{~mm}$ long; stipules $5.3-13.9 \times 1-2.1 \mathrm{~mm}$, linear-lanceolate, sometimes lobed, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. Inflorescence in dichasial cyme with monochasial branches; cymules 2-flowered, solitary; peduncles $0.4-5.9 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $0.3-1.9 \mathrm{~mm}$ long and patent glandular hairs $0.4-0.6 \mathrm{~mm}$ long; bracteoles 1.8-4.7 $\times 0.4-0.9 \mathrm{~mm}$, linear-lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels $0.3-2.4 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $0.2-1.6 \mathrm{~mm}$ long, and patent glandular hairs $0.4-0.7 \mathrm{~mm}$ long. Sepals $5-$ $9.9 \times 1.9-5.4 \mathrm{~mm}$, accrescent, 5-nerved, with mucro $0.9-2.5 \mathrm{~mm}$ long, with scarious margins $0.1-0.2 \mathrm{~mm}$ wide, with patent, eglandular hairs $0.9-3.3 \mathrm{~mm}$ long, and patent, glandular hairs $0.6-$ 1 mm long. Petals (5.4)6.3-6.9(8.3) $\times 3.1-6.1 \mathrm{~mm}$ (ratio petal width/petal length $=0.52-0.74$ ), erect-
patent, emarginate (notch $0.4-1.2 \mathrm{~mm}$ deep), glabrous on both sides, ciliate on the basal margin, bluish. Staminal filaments $3.1-4 \mathrm{~mm}$ long, lanceolate, pilose on the abaxial side, ciliate on all of its length, with hairs $0.5-1.3 \mathrm{~mm}$ long; anthers 0.6-1.1 $\times 0.4-0.9 \mathrm{~mm}$, yellow; pollen yellow. Nectaries glabrous. Gynoecium 3.1-4 mm long, purplish. Fruit 18-29.5 mm long; mericarps 4.1-5.5 $\times 1.5-2.6 \mathrm{~mm}$, with $\pm$ patent, eglandular hairs $1.5-2.8 \mathrm{~mm}$ long, and some glandular hairs $0.4-0.9 \mathrm{~mm}$ long at the apex, blackish; rostrum $12.1-20.5 \mathrm{~mm}$ long, without a narrowed apex, with patent, eglandular 0.20.9 mm long, and patent glandular hairs $0.5-$ 0.8 mm long; stigmatic remains $1-1.8 \mathrm{~mm}$ long, with 5 hairy lobes. Seeds $2.5-3.4 \times 1.3-2.1 \mathrm{~mm}$, foveolate, uniformly reddish; hilum $1 / 6$ as long as the perimeter. Cotyledons entire.

Additional Illustrations. Fiori and Paoletti (1901: 292).

Chromosome Number. $2 n=48$ (Dahlgren 1952: 316; Van Loon 1984b: 281); $2 n=42$ ? (Warburg 1938: 142).

Phenology. Flowering specimens from March to September.

Distribution and Habitat. Southern Europe and northwestern Africa (introduced in Sweden); open areas of Castanea, Corylus or Quercus forest, on limestone or acidic rocks, usually on recently burned sites, between sea level and 1600 m (Fig. 12). Geranium lanuginosum has been recorded from Albania (Qosja 1992: 209), but it has been impossible to examine the specimen supporting this record. Additional maps: Meusel et al. (1978: 261); Hultén and Fries (1986: 634).

Representative Specimens Examined. ALGERIA: Alger, Tamgout d'Azazga, $36^{\circ} 43^{\prime}$ E, $4^{\circ} 21^{\prime}$ E, 21 May 1952, Faurel s.n. (MPU). FRANCE: Alpes Maritimes, Grasse, $43^{\circ} 40^{\prime} \mathrm{N}, 6^{\circ}$ $54^{\prime} \mathrm{E}, 19$ Jun 1923, Rodié s.n. (MPU); Corse, 3 km 2 W van Casta, $42^{\circ} 40^{\prime}$ N, $9^{\circ} 12^{\prime}$ E, 16 Jul 1956, Segal 289 (WAG). GREECE: Thessalia, Agrapha, in regione inferiori m. Pindi circa monasterium Koróna, $39^{\circ} 18^{\prime}$ N, $21^{\circ} 47^{\prime}$ E, 20 Jun 1895, Heldreich s.n. (E, JE, LD, W). ITALY: Abruzzo, Acquaro, Villavallelonga, $41^{\circ} 52^{\prime}$ N, $13^{\circ} 37^{\prime} \mathrm{E}, 11$ 1904, Fiori s.n. (FI); Sardegna, Tempio, Monte Limbardo, $40^{\circ} 51^{\prime} \mathrm{N}, 9^{\circ} 9^{\prime} \mathrm{E}, 16$ May 1882, Reverchon 253 (BM, BR, E,JE, K, LD, MPU, PR, Z); Sicilia, Palermo, Ficuzza, Godrano, Gungo di Cerro, $37^{\circ} 51^{\prime}$ N, $13^{\circ} 25^{\prime}$ E, 11 Jun 1960, Segelberg 11660 (S). MOROCCO: Atlante rifano, Ketama, $34^{\circ} 54^{\prime} \mathrm{N}, 4^{\circ} 33^{\prime}$ W, 15 Jun 1929, Maire s.n. (MPU). PORTUGAL: Minho, Ponte da Barca, Lindoso, vale do Cabril, prox. da ponte da Varzea, $41^{\circ} 51^{\prime} \mathrm{N}, 8^{\circ} 11^{\prime} \mathrm{W}$, 15 Jun 1945, Fontes \& al. 1115 (LISE). SPAIN: Barcelona, Macizo del Corredor, en la Sierra Litoral, sobre Mataró, $41^{\circ}$ $37^{\prime} \mathrm{N}, 2^{\circ} 28^{\prime} \mathrm{E}, 5$ Dec 1951, Montserrat s.n. (BCN, MA). SWEDEN: Smaland, Lofta, Ekvik, pr. villam Segersgarde, $57^{\circ}$ $51^{\prime} \mathrm{N}, 16^{\circ} 32^{\prime} \mathrm{E}, 19$ Jun 1926, Almquist 1112 (BM, C, F, G, H). TUNISIA: Aïn-Draham, $36^{\circ} 45^{\prime} \mathrm{N}, 8^{\circ} 45^{\prime} \mathrm{E}, 8$ Jun 1903, Murbeck s.n. (LD). TURKEY: Constantinople, au dessous de Lazkeuy, $41^{\circ} 6^{\prime} \mathrm{N}, 28^{\circ} 54^{\prime} \mathrm{E}, 11$ Jun 1893, Aznavour $503 b$ (G).

Discussion. Differences between G. lanuginosum and G. bohemicum are addressed in the discussion
under the latter species. It is interesting to note that glandular hairs on the mericarp are restricted to the apex as well as in G. bohemicum, G. gracile, and G. renardii.

Geranium perreymondii was validly published (Roux 1880) by reference to the Godron's (1847) description of G. bohemicum. According to the Code (art. 7.7), the type should be selected among the specimens mentioned by Godron (1847). Unfortunately, not one of those specimens has been traced. Thus, a specimen mentioned by Roux (1880) has been selected as type, which must then be considered to be a neotype.
Since no original material of G. bohemicum subsp. depraehensum was located, this name was typified on an illustration. It should be indicated that specimens collected later by Almquist (labelled by himself as "depraehensum") are unequivocally $G$. lanuginosum.

According to Dahlgren (1952), G. lanuginosum seeds are similar to those of G. bohemicum in germination features. The ranges of both species overlap only in the Iberian Peninsula and southern France, but there is no evidence of sympatric populations.
3. Geranium gracile Ledeb. in Nordm., Bull. Sci. Acad. Imp. Sci. Saint-Pétersbourg 2(20): 314. 1837.-TYPE: GEORGIA. Awhasien, auf dem Gebirge Hirtscha, Nordmann s.n. (lectotype: designated by Novoselova 1998: 155, LE!; isolectotype: H!). Fig. 13.
Geranium gracile var. glabriusculum Albov, Prodr. Fl. Colchic.: 45. 1895.—TYPE: GEORGIA. Mingrelia, m. Kwira, 1894, Albov s.n. (no original material located).
Geranium trilobum K. Koch, Linnaea 15: 716. 1841, nom. illeg., non Thunb. 1800; Geranium gracile var. trilobum (K. Koch) Boiss., Fl. Orient. 1: 876. 1867.-TYPE: GEORGIA. In Radscha et in monte Nakarala (in Imeretia), 1836, Koch 970 (lectotype: here designated, LE!).
Herbs perennial, $19-80 \mathrm{~cm}$ tall. Rootstock 5.19.7 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, with patent to retrorse eglandular hairs $0.3-1.7 \mathrm{~mm}$ long. Basal leaves in a deciduous rosette; lamina 3.3-13.1 $\times 4.5-20.1 \mathrm{~cm}$, palmatifid (ratio main-sinus length/middle-segment length $=$ $0.69-0.78)$, pilose, with appressed, eglandular hairs, not reticulate, not projected; segments (3)5, rhombic [ratio maximum width/middle-segment length $=(0.48) 0.54-0.57(0.70)], 6.7-26.7 \mathrm{~mm}$ wide at the base, (14)20-23(34)-lobed in distal half (ratio second-sinus length/middle-segment length $=$ $0.04-0.09$ ); cauline leaves opposite ( $2-3$ pairs);


Fig. 13. Geranium gracile Ledeb. a. Habit; b. Inflorescence; c. Bracteoles; d. Indumentum of the peduncle; e. Indumentum of the pedicel; f. Flower; g. Sepal; h. Petal; i-j. Staminal filaments; k. Fruit; 1. Mericarp; m. Seed [a, c-f, h-j: Valcárcel \& al. 370 VV01 (MA); b: Schönswetter \& Tribsch s.n., 15 July 1997 (WU); g, k-m: Tobey 1292 (E)].
petioles to 27.5 cm long, with patent to retrorse eglandular hairs $0.5-1.6 \mathrm{~mm}$ long; stipules 6.7-20.2 $\times 1.6-4.4 \mathrm{~mm}$, lanceolate, with eglandular hairs on both surfaces and on the margin. Inflorescence in
monochasial cyme; cymules 2-flowered, solitary; peduncles $2.4-8.4 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $0.5-1.1 \mathrm{~mm}$ long and patent glandular hairs $0.2-$
0.5 mm long; bracteoles (2.5)3.5-4.3(6.1) $\times 0.5-$ 3.5 mm , linear-lanceolate, with eglandular hairs on both surfaces and on the margin; pedicels 1.53.8 cm long, with $\pm$ uncinate eglandular hairs $0.1-$ 0.3 mm long, and patent glandular hairs $0.2-$ 0.5 mm long. Sepals $6.2-8.3 \times 2.5-4.7 \mathrm{~mm}$, not accrescent, $3-5$-nerved, with mucro $1-2.6 \mathrm{~mm}$ long, with scarious margins $0.07-0.2 \mathrm{~mm}$ wide, with $\pm$ patent, eglandular hairs $1.2-2.9 \mathrm{~mm}$ long, and patent, glandular hairs $0.3-0.65 \mathrm{~mm}$ long. Petals (13.6)17.7-20.5(27.3) $\times 5.4-10.6 \mathrm{~mm}$ (ratio petal width/petal length $=0.30-0.45)$, erect-patent, emarginate (notch $0.8-4.2 \mathrm{~mm}$ deep), hairy on the base of adaxial side, glabrous on the abaxial side, ciliate on the basal margin, purplish. Staminal filaments $7.8-11.9 \mathrm{~mm}$ long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $0.1-1.7 \mathrm{~mm}$ long; anthers $1.1-2.1 \times 0.6-$ 1.3 mm , yellow; pollen yellow. Nectaries glabrous. Gyпоесіит 7.8-10.8 mm long, purplish. Fruit 29.744.3 mm long; mericarps $3.7-5.9 \times 1.8-2.4 \mathrm{~mm}$, with $\pm$ patent eglandular hairs $0.5-1.2 \mathrm{~mm}$ long, and some glandular hairs $0.1-0.5 \mathrm{~mm}$ long at the apex, brownish; rostrum $22-35 \mathrm{~mm}$ long, with a narrowed apex 1.8-4.4 mm long, with $\pm$ patent eglandular hairs $0.1-1.9 \mathrm{~mm}$ long, and patent glandular hairs 0.3-0.7 mm long; stigmatic remains $1.9-3.6 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $2.8-$ $3.3 \times 1.5-2.1 \mathrm{~mm}$, finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons entire.

Additional Illustrations. Grossheim (1962: 13); Mobayen (1996).

Chromosome Number. Unknown.
Phenology. Flowering specimens from May to October.

Distribution and Habitat. Northeastern Turkey, Caucasus, and northern Iran; forests of Fagus, Picea or Abies, or scrubland with Rhododendron, between 700 and 2360 m (Fig. 14). Additional map: Grossheim (1962, map 4).

Representative Specimens Examined. GEORGIA: Abchazia, Gudauty, pr. lacum Ritza, $43^{\circ} 27^{\prime} \mathrm{N}, 40^{\circ} 32^{\prime} \mathrm{E}, 4$ Sep 1936, Kolakovsky 3219 (C, H, KRA, S, W, WA); Samegrela, M. Okhachkuye, $42^{\circ} 46^{\prime} \mathrm{N}, 41^{\circ} 55^{\prime} \mathrm{E}, 7$ Aug 1959, Kemularia \& al. s.n. (MA); Tiflis, Gori, pr. Bakuriani, $41^{\circ} 45^{\prime} \mathrm{N}, 43^{\circ} 33^{\prime} \mathrm{E}, 11$ Jul 1923, Kozlowsky 188 (LD, LE, PR, S, Z). IRAN: Gilan, mountain above Damesh-east of Rudbar, $36^{\circ} 48^{\prime} \mathrm{N}, 49^{\circ} 22^{\prime} \mathrm{E}$, 21 Jun 1975, Wendelbo \& Ala 18170 (E, W); Kandavan, $36^{\circ} 8^{\prime}$ N, $51^{\circ} 18^{\prime}$ E, 31 May 1938, Gauba 1454 (B); Mazanderan, Kalar Dasht, $36^{\circ} 34^{\prime}$ N, $51^{\circ} 15^{\prime}$ E, 30 May 1938, Gauba K 1225-b (W). TURKEY: Armenia turcica, Sipikordagh, ad ripas Szadaghtschai pr. Szadagh, $39^{\circ} 52^{\prime}$ N, $39^{\circ} 35^{\prime}$ E, 19 Aug 1890, Sintenis $2514 b$ (LD); Giresun, 3 km SO Kümbet, $40^{\circ} 33^{\prime} \mathrm{N}, 38^{\circ} 25^{\prime} \mathrm{E}, 7$ Jul 1969, Sorger 69-27-24b (W); Ordu, below Cambasi, $40^{\circ} 39^{\prime}$ N, $37^{\circ} 58^{\prime}$ E, 14 Jul 1965, Tobey 1292 (E); Trabzon, 2 km S of Hamsiköy, $40^{\circ} 41^{\prime} \mathrm{N}, 39^{\circ} 28^{\prime} \mathrm{E}, 23$ Aug 1972, Uotila 19724 (H).

Discussion. Geranium gracile shows some features not present in other species of subsect. Mediterranea. This taxon usually has more than


Fig. 14. Area of distribution of Geranium gracile.
one pair of opposite leaves on the stem, the inflorescence is a monochasial cyme, and the cymules are solitary (not in aggregates at the top of the branches). Additionally, its petals are the narrowest of the group. Among the perennial species, G. gracile shares with G. ibericum, G. peloponnesiacum, G. platypetalum, and G. renardii the presence of glandular hairs on the inflorescence.
Superficially, G. gracile is similar to G. nodosum L. in flower appearance and particularly in leaf form. Leaves of both species have marked rhombic segments, with the wider part near the base, and with less deeply divided secondary divisions. Yeo (2002) suggested that this similarity could be related with the analogous forestry habitat of both species. Knuth (1912) includes G. gracile and G. nodosum in sect. Striata R. Knuth, overlooking the fact that fruit structure unequivocally approaches G. gracile of subsect. Mediterranea.
4. Geranium renardii Trautv. in Trautv., Regel, Maxim. \& C. Winkl., Decas Pl. Nov.: 5. 1882.TYPE: GEORGIA. Ossetia, in alpe Brutsabseli, ad fl. Didi Liachva, 16 July 1881, A.H. Brotherus $\mathcal{E}$ V.F. Brotherus 215 (lectotype: designated by Knuth 1912: 110, LE!; isolectotypes: BM! G! H!). Fig. 15.
Herbs perennial, $14-35 \mathrm{~cm}$ tall. Rootstock 7.614.2 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, with patent to retrorse eglandular hairs $0.3-0.8 \mathrm{~mm}$ long. Basal leaves in a $\pm$ persistent rosette; lamina $2.3-7.2 \times 2.6-8.5 \mathrm{~cm}$, palmatifid (ratio main-sinus length $/$ middle-segment length $=$ $0.26-0.59$ ), pilose above and sericeous beneath, with $\pm$ patent eglandular hairs, nervation reticulate, projected on the abaxial side, sunken adaxi-


Fig. 15. Geranium renardii Trautv. a. Habit; b. Leaf; c. Detail of the leaf adaxial side; d. Detail of the leaf abaxial side; e. Bracteoles; f. Indumentum of the pedicel; g. Flower without petals and sepals; h. Sepal; i. Petal; j. Staminal filaments; k. Fruit; 1. Mericarp; m. Seed [a-j: Busch s.n., May 1907 (LE); k-m: Busch 775 (LE)].
ally; segments $5-7, \pm$ obtriangular [ratio maximum width/middle-segment length $=(0.65) 0.70-$ $0.77(0.80)$ ], $5.6-23 \mathrm{~mm}$ wide at the base, (12)16-21(29)-lobed in distal half (ratio second-sinus length/middle-segment length $=0.07-0.20$ ); cauline leaves opposite; petioles to 22 cm long, with patent to retrorse eglandular hairs $0.3-0.6 \mathrm{~mm}$ long; stipules $6.2-11.1 \times 1.3-4.2 \mathrm{~mm}$, lanceolate, with eglandular hairs on both surfaces and on the margin. Inflorescence in dichasial cyme; cymules 2 flowered, solitary or in aggregates at the top of each branch; peduncles (0)0.5-6.2 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $0.4-1.2 \mathrm{~mm}$ long, and rarely patent, glandular hairs $0.2-0.4 \mathrm{~mm}$ long; bracteoles (3.4)4.7-6.1(10.4) $\times 0.7-1.9 \mathrm{~mm}$, linear-lanceolate, with eglandular hairs on both surfaces and on the margin; pedicels $0.6-2.3 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $0.6-1.5 \mathrm{~mm}$ long, and usually patent glandular hairs $0.2-0.9 \mathrm{~mm}$ long. Sepals $7.4-10.9 \times$ $3.2-5.1 \mathrm{~mm}$, not accrescent, 5-7-nerved, with mucro $0.6-1.4 \mathrm{~mm}$ long, with scarious margins $0.1-0.2 \mathrm{~mm}$ wide, with $\pm$ patent eglandular hairs ( 0.3 ) $1-3.4 \mathrm{~mm}$ long, and usually patent, glandular hairs 0.30.9 mm long. Petals (15.1)16.8-20.3(23) $\times 10-$ 14.8 mm (ratio petal width/petal length $=0.57-$ 0.73 ), patent, emarginate (notch $1-5.5 \mathrm{~mm}$ deep), hairy on the base of abaxial side, glabrous on the adaxial side, ciliate on the basal margin, white with violet veins. Staminal filaments $7.2-12.9 \mathrm{~mm}$ long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $1-2.8 \mathrm{~mm}$ long; anthers $1.9-3.3 \times 0.8-1.3 \mathrm{~mm}$, yellow; pollen yellow. Nectaries glabrous. Gynoecium 5.8-9.9 mm long, pinkish. Fruit 23-34.5 mm long; mericarps 5-6.6 $\times 2-$ 2.8 mm , with $\pm$ patent eglandular hairs 0.8 1.8 mm long, and sometimes scattered glandular hairs $0.4-0.8 \mathrm{~mm}$ long at the apex, brownish; rostrum $15.9-26 \mathrm{~mm}$ long, with a narrowed apex $3.4-5.2 \mathrm{~mm}$ long, with $\pm$ patent eglandular hairs $0.5-2.4 \mathrm{~mm}$ long, and rarely patent glandular hairs $0.3-0.7 \mathrm{~mm}$ long; stigmatic remains $1.4-3.1 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $3-3.6 \times 1.4-$ 2.1 mm , finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons entire.
Additional Illustrations. Bobrov (1949, plate 1); Grossheim (1962: 15); Yeo (2002, photograph 38).

Chromosome Number. Unknown.
Phenology. Flowering specimens from May to August.
Distribution and Habitat. Western and central Caucasus; alpine meadows or scrubland with Rhododendron and Juniperus, between 2000 and 3300 m (Fig. 16). Additional map: Grossheim (1962, map 8).


FIg. 16. Area of distribution of Geranium renardii.

Representative Specimens Examined. GEORGIA: Abkhasia in valle fluminis Kliutseh infra jugum Klukhor, $43^{\circ} 14^{\prime} \mathrm{N}$, $41^{\circ} 52^{\prime}, 27$ Aug 1890, Sommier \& Levier s.n. (FI); Racha, upper part riv. Tsckhra?ya, $42^{\circ} 30^{\prime}, 43^{\circ} 30^{\prime}, 22$ Jul 1966, Gagnidze s.n. (MA); river Chernaya, Aragvi, village Bakurkhevi, $42^{\circ} 28^{\prime} \mathrm{N}$, $44^{\circ} 47^{\prime}$ E, 20 Jul 1973, Menitsky s.n. (LE); South Ossetia, Ermani, mount Fidar-khokh, $42^{\circ} 28^{\prime}$ N, $44^{\circ} 14^{\prime}$ E, 25 Aug 1958, Gochina s.n. (LE). RUSSIA: Kabardino-Balkaria, Baksan, in declivibus austro-occidentalibus montis Cheget, $43^{\circ} 28^{\prime} \mathrm{N}$, $41^{\circ} 16^{\prime}$ E, 15 Aug 1978, Vasák s.n. (WU); KarachayevoCherkasskaiya, Zapadnuiy Kavkaz, Teberdinskiy zapovednik g. Malaia Jatipara, $43^{\circ} 22^{\prime} \mathrm{N}, 41^{\circ} 42^{\prime}$ E, 2 Jul 1963, Pavlov s.n. (MA, MPU); Stavropol, Stavropolvskij kray., Teberdinskiy gos. sapovedni, Cucjurskiy pereval, $43^{\circ} 22^{\prime} \mathrm{N}, 41^{\circ} 42^{\prime} \mathrm{E}$, 14 Jul 1974, Makridin E Kirjman s.n. (G).

Discussion. The leaves of this species are distinctive, permitting G. renardii to be distinguished even in vegetative state. They have a noticeable reticulate nervation projected on the abaxial side, and sunken adaxially. The leaf lamina is green but pilose on the abaxial side (mainly on the nerves), and densely covered with a patent, sericeous indumentum beneath which is both on the nerves and the sunken surface between them.
The inflorescence is dichotomously branched with a long pedunculate cymule at the main fork. Terminal cymules are usually in aggregates (sometimes with short or without peduncles) at the top of the branches, resembling umbels. This type of inflorescence is shared with the following species of subsect. Mediterranea (G. ibericum, G. platypetalum, G. peloponnesiacum, G. libani, G. gymnocaulon, and G. kurdicum).
The indumentum shows some variability in $G$. renardii. On the inflorescence, glandular hairs are usually restricted to pedicels and sepals, and in a few cases can be observed on peduncles. However, in some specimens only eglandular hairs are present. Petals are hairy on the base of abaxial side, and on the basal margin, but in exceptional
cases, they can be present all the entire margin, from the base to the notch.
5. GERANIUM IBERICUM Cav., Diss. 4: 209, tab. 124 fig. 1. 1787. nom. cons. prop.-TYPE: GEORGIA. Bakuriani, Tskhra Tskaro, 10 Aug. 1997, Gagnidze E Nakhutsrishvili 918 (type cons. prop. by Aedo (2005), MA-626647!). Fig. 17.
Geranium montanum Hablitz ex Pall., Neue Nord. Beytr. Phys. Geogr. Erd-Völkerbeschreib. 4: 51. 1784. nom. rej. prop.-TYPE: IRAN. In alpib. Samamisius, Aug., Hablizl s.n. (lectotype: designated by Novoselova 1998: 157, LE!).
Geranium ibericum var. subglandulosum Rupr., Mém. Acad. Imp. Sci. Saint Pétersbourg ser. 7, 15(2): 269. 1869.-TYPE: described from several Caucasian specimens (no original material found).
Geranium ibericum var. hyrcanum Woronow in Kusn., N. Busch \& Fomin, Fl. Cauc. Crit. 3(7): 31. 1908.-TYPE: AZERBAIJAN. Gub. Baku, Talysch, ad rivulum Sangada haud procul m. Bolo-band, 3 Aug. 1897, Th. Alexeenko 7347 (lectotype: here designated, LE!).
Geranium ibericum var. album Lauman in L.H. Bailey, Cycl. Amer. Hort.: 640. 1900.—TYPE: probably cultivated (no original material located).
Geranium jubatum Hand.-Mazz., Ann. K.K. Naturhist. Hofmus. 23: 160, Taf. 9 Fig. 2. 1909. Geranium ibericum subsp. jubatum (Hand.Mazz.) P.H. Davis, Notes Roy. Bot. Gard. Edinburgh 22: 24. 1955.—TYPE: TURKEY. Trapezunti, Aladja Dagh, 15 Jul 1907, HandelMazzetti 1129 (lectotype: here designated, W!; isolectotype: MA!).

Herbs perennial, $18-48 \mathrm{~cm}$ tall. Rootstock $6.8-$ 11.5 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, with patent eglandular hairs $0.2-$ 3.6 mm long and, rarely, patent glandular hairs $0.3-0.4 \mathrm{~mm}$ long. Basal leaves in a $\pm$ persistent rosette; lamina $4.7-8.6 \times 5.6-10.5 \mathrm{~cm}$, palmatifid (ratio main-sinus length/middle-segment length $=$ $0.50-0.68$ ), pilose, with appressed, eglandular (and sometimes glandular) hairs, nervation not reticulate, not projected; segments 5-7, rhombic [ratio maximum width/middle-segment length $=$ (0.58)0.61-0.68(0.74)], $5.4-13.7 \mathrm{~mm}$ wide at the base, (14)16-24(39)-lobed in distal half (ratio second-sinus length/middle-segment length = $0.23-0.35)$; cauline leaves opposite; petioles to 25 cm long, with patent eglandular hairs 0.2 3 mm long and, rarely, patent glandular hairs $0.2-0.3 \mathrm{~mm}$ long; stipules $6.6-17.1 \times 1.3-4.8 \mathrm{~mm}$,
lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. Inflorescence in dichasial cyme; cymules 2-flowered, solitary or in aggregates at the top of each branch; peduncles (0)0.4-6.3 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs (1)2.12.5(3.3) mm long and, sometimes, patent glandular hairs $0.2-1.5 \mathrm{~mm}$ long; bracteoles (3.2)5.2-6.4(8.2) $\times 0.6-1.4 \mathrm{~mm}$, linear-lanceolate, with eglandular and sometimes glandular hairs on both surfaces and on the margin; pedicels $0.6-1.9 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $1.2-3.5 \mathrm{~mm}$ long and, sometimes, patent glandular hairs $0.3-1.1 \mathrm{~mm}$ long. Sepals $9-$ $13.3 \times 3.7-6.7 \mathrm{~mm}$, not accrescent, 5-7-nerved, with mucro $1.4-3.3 \mathrm{~mm}$ long, with scarious margins $0.1-0.5 \mathrm{~mm}$ wide, with patent eglandular hairs $1.6-3.8 \mathrm{~mm}$ long, and sometimes patent glandular hairs $0.5-1.6 \mathrm{~mm}$ long. Petals (15.4)19.5$24.9(28.4) \times 12.1-22.5 \mathrm{~mm}$ (ratio petal width/petal length $=0.62-0.79$ ), patent, emarginate (notch 1.13.5 mm deep), glabrous on both sides, ciliate on the basal margin, bluish. Staminal filaments 8.911.4 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $0.2-$ 3.2 mm long; anthers 2.2-3.3 $\times 0.7-1.9 \mathrm{~mm}$, blueblack; pollen bluish. Nectaries glabrous. Gynoecium 6.1-10.6 mm long, dark purplish. Fruit 29.739.4 mm long; mericarps 4.8-6.5 $\times 1.9-2.9 \mathrm{~mm}$, with $\pm$ patent, eglandular hairs $0.2-2.8 \mathrm{~mm}$ long, and sometimes patent, glandular hairs $0.3-0.9 \mathrm{~mm}$ long, brownish; rostrum $22.2-33 \mathrm{~mm}$ long, with a narrowed apex $2.6-6.7 \mathrm{~mm}$ long, with $\pm$ patent, eglandular hairs $0.8-2.3 \mathrm{~mm}$ long, and rarely patent, glandular hairs $0.3-0.4 \mathrm{~mm}$ long; stigmatic remains $2.4-4.4 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $3.3-4.2 \times 1.7-2.2 \mathrm{~mm}$, finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons entire.

Additional Illustrations. Sims (1811, tab. 1386); Sweet (1821, tab. 84); Yeo (2002, photograph 36).

Chromosome Number. $2 n=28$ (Van Loon 1984a: 266); $2 n=56$ (Gauger 1937: 529; Warburg 1938: 144).

Phenology. Flowering specimens from May to September.

Distribution and Habitat. Northeastern Turkey, Caucasus, and northern Iran (introduced in France, Great Britain, USA, and Canada); alpine meadows, rocky slopes, and among Rhododendron, on schistose or igneous rocks, between 1500 and 3100 m (Fig. 18). Additional map: Grossheim (1962, map 6).

Representative Specimens Examined. ARMENIA: Erevan, pr. Cahkadzor, $40^{\circ} 10^{\prime} \mathrm{N}, 44^{\circ} 30^{\prime} \mathrm{E}, 27 \mathrm{Jul}$ 1984, Cuba 212 (G); Kirovakaiskj rajon, s. Tamdzhagiran, $40^{\circ} 50^{\prime} \mathrm{N}, 44^{\circ} 35^{\prime} \mathrm{E}$, 8 Aug 1972, Avemus? s.n. (MA); pr. Zod, $40^{\circ} 12^{\prime} \mathrm{N}, 45^{\circ} 51^{\prime} \mathrm{E}$,


Fig. 17. Geranium ibericum Trautv. a. Habit; b. Bracteoles; c. Flower without petals and sepals; d-e. Indumentum of the pedicel; f. Sepal; g. Petal; h. Staminal filament; i. Fruit; j. Mericarp; k. Seed [a-d, f-h: Menishkiy \& al. s.n., 5 Aug 1986 (LE); b-c, e: Scheidweiler s.n., June 1861 (BR); i-k: without collector (BR-825853)].


Fig. 18. Area of distribution of Geranium ibericum.

26 Jul 1928, Schelkovnikov \& E. Kara-Murza s.n. (KRA, LE); Sevan, $40^{\circ} 35^{\prime}$ N, $44^{\circ} 55^{\prime}$ E, 12 Jul 1970, Avetisian $\mathcal{E}$ al. s.n. (G). AZERBAIJAN: Lenkoran, $38^{\circ} 45^{\prime} \mathrm{N}, 48^{\circ} 51^{\prime} \mathrm{E}, 21$ Jul 1931, Matveeva 695 (LE). CANADA: British Columbia, Victoria, 22 Jun 1896, Anderson \& al. 200 (V); Newfoundland, Beach Cove, $47^{\circ} 35^{\prime} \mathrm{N}, 53^{\circ} 15^{\prime} \mathrm{W}, 1928$, Ayre 605 (GH). GEORGIA: Bogdanovsky distr., between villages Bogdanovka and Dzhigrasheni, $41^{\circ} 19^{\prime} \mathrm{N}, 43^{\circ} 32^{\prime} \mathrm{E}, 12$ Jul 1960, Cvelev \& $S$. Yerepanov 1033 (LE); Kartli, Borjomi, $41^{\circ} 50^{\prime}$ N, $43^{\circ} 22^{\prime} \mathrm{E}, 1$ Sep 1951, Zamtaradze s.n. (MA); Mtiuleti, distr. Dusheti, r. Meketi, m. Meketi, $42^{\circ} 6^{\prime} \mathrm{N}, 44^{\circ} 40^{\prime} \mathrm{E}, 28$ Jul 1967, Zanitazadze s.n. (MA); South Osetia, the upper Big Liahva, the gorge of the river Middle Ermani-don, $42^{\circ} 31^{\prime} \mathrm{N}, 44^{\circ} 11^{\prime} \mathrm{E}, 17$ Aug 1956, Gochina s.n. (MA); Tiflis, Gori, mons Kochta pr. Bakuriani, $41^{\circ} 45^{\prime} \mathrm{N}, 43^{\circ} 28^{\prime} \mathrm{E}, 22 \mathrm{Jul} 1920$, Kochreidze s.n. (LE). GREAT BRITAIN: Abernant, Aberdare, $51^{\circ} 52^{\prime} \mathrm{N}, 4^{\circ} 24^{\prime}$ E, 13 Jun 1974, Pell s.n. (NMW); Pont Glanrafon, Cribyn, $52^{\circ}$ $7^{\prime}$ N, $4^{\circ} 9^{\prime} \mathrm{E}, 7$ Jun 1991, Chater s.n. (NMW). IRAN: Ghilan, $37^{\circ}$ $0^{\prime} \mathrm{N}, 49^{\circ} 50^{\prime} \mathrm{E}$, Aucher-Eloy 4303 (BM, FI, W); Mazandaran prov., Elburz mts., Kaladash valley N Elburz, $35^{\circ} 40^{\prime} \mathrm{N}, 52^{\circ} 3^{\prime}$ E, 2 Aug 1956, McDougall 44 (BM). TURKEY: Armenia turcica, Sipikordagh, $39^{\circ} 52^{\prime}$ N, $39^{\circ} 35^{\prime}$ E, 9 Aug 1890, Sintenis 3477 (E, BR, G, LD, PR, S, Z); Çoruh, Savval tepe, Murgul üstleri, $41^{\circ} 9^{\prime} \mathrm{N}, 41^{\circ} 27^{\prime} \mathrm{E}, 12$ Aug 1957, Davis \& Hedge 32285 (E, BM, ISTE); Giresun, Balabandaglari above Tamdere, above Avsar Yayla, $40^{\circ} 30^{\prime}$ N, $38^{\circ} 22^{\prime}$ E, 7 Aug 1952, Davis E al. 20570 (E, BM); Gümüshane, puerto de Kostandagi, vertiente $\mathrm{N}, 40^{\circ} 30^{\prime} \mathrm{N}, 39^{\circ} 46^{\prime} \mathrm{E}, 25$ Jun 2001, Herrero \& al. 1550 (MA); Rize, 4 km antes del Ovit dagi Gecidi, $40^{\circ} 37^{\prime}$ N, $40^{\circ} 46^{\prime}$ E, 28 Jun 2001, Nisa \& al. 886 (MA); Trabzon, N side of Soganli dag above Çaykara, $40^{\circ} 31^{\prime} \mathrm{N}, 40^{\circ} 13^{\prime} \mathrm{E}, 4$ Aug 1957, Davis \& Hedge 32137 (BM, E). USA: Colorado, Boulder Co., disturbed site along Boulder Creek, $37^{\circ} 48^{\prime} \mathrm{N}, 107^{\circ} 07^{\prime} \mathrm{W}, 16$ Jun 1993, EPOB 4520 (COLO); Maine, Bar Harbor, $44^{\circ} 23^{\prime}, 68^{\circ}$ 12', 2 Jun 1910, unknown collector (GH).
Discussion. Geranium ibericum has a characteristic dense indumentum of long, soft, patent eglandular hairs along the inflorescence. However, the presence and distribution of glandular hairs is variable. In some specimens, these hairs are lacking, while in others they are abundant and intermixed with eglandular ones, together with some intermediate forms. Collections with both extremes (Davis 32285, Sintenis 7053, Woronow $\mathcal{E}$

Schelkownikow, Herb. Fl. Cauc. 32) are not rare. Geranium montanum was accepted by Bobrov (1949), who also recognized G. ibericum. They were distinguished by the presence of glandular hairs on the inflorescence in the first and the absence in the second. Davis (1967) treated Turkish specimens with glandular hairs as G. ibericum subsp. jubatum. Both taxa are here considered as synonyms for the reasons above mentioned.

Geranium ibericum shares with G. platypetalum a general appearance as well as the indumentum of long, soft, patent eglandular hairs along the inflorescence. However, in G. platypetalum glandular hairs are always present, even on the basal part of the stem. G. ibericum has leaves with rhombic central segments, while G. platypetalum has obtriangular segments. Additionally, G. platypetalum has longer bracteoles, longer sepal mucros, and shorter petals than G. ibericum.

The first effective lectotypification of G. ibericum appears to be that of Novoselova (1998), who designated the Cavanilles plate as the "type." The proposal by Novoselova is technically correct, but it could be improved by designating an epitype for a more precise application of the name. However, during the review of the proposal to conserve the name G. ibericum (Aedo 2005), J. McNeill and J.H. Wiersema kindly suggested a simpler solution, and thus we have proposed a conserved type.
6. Geranium platypetalum Fisch. \& C.A. Mey., Index Sem. Hort. Petrop. [1]: 28. 1835. Geranium ibericum var. platypetalum (Fisch. \& C.A. Mey.) Boiss., Fl. Orient. 1: 876. 1867.-TYPE: AZERBAIJAN. In proclivibus saxosis altiorum regionum montis, Sarial im Elisabethpolytan. Provin. June-July 1834, Hohenacker s.n. (neotype: designated by Novoselova 1998: 157, LE!; isoneotypes: BM! BR! E! FI! GOET! HBG! JE! L! M! MA! WU!). Fig. 19.
Geranium platypetalum var. albipetalum Erik \& Demirkuş, Doga Bilim Derg, A 10(1): 101, fig. 2. 1986.-TYPE: TURKEY. Artvin, Kaçkal Daği, Cehennem Deresi, 13 Aug. 1984, Demirkuş 2635 (holotype: HUB).

Herbs perennial, $25-57 \mathrm{~cm}$ tall. Rootstock $6.2-$ 13.8 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, with patent eglandular hairs 0.24.9 mm long and, usually, patent glandular hairs $0.6-1.8 \mathrm{~mm}$ long. Basal leaves in a $\pm$ persistent rosette; lamina 3.6-11.2 $\times 4.6-12.8 \mathrm{~cm}$, palmatifid (ratio main-sinus length $/$ middle-segment length $=$ $0.43-0.58$ ), pilose, with appressed, eglandular (and sometimes glandular) hairs, nervation not reticulate, not projected; segments 5-7, obtriangular

-.L. Gastillo / O4
Fig. 19. Geranium platypetalum Trautv. a. Habit; b. Bracteoles; c. Flower without petals and sepals; d. Sepal; e. Petal; f. Staminal filament; g. Fruit; h. Mericarp; i. Seed [a-i: Marcowicz s.n., 4 June 1901 (MA)].
[ratio maximum width/middle-segment length $=$ (0.75)0.76-0.79(0.84)], $9.6-27.1 \mathrm{~mm}$ wide at the base, (9)17-25(29)-lobed in distal half (ratio sec-ond-sinus length $/$ middle-segment length $=0.15-$
0.26 ); cauline leaves opposite; petioles to 30 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $2.2-4.7 \mathrm{~mm}$ long and, usually, patent glandular hairs $0.3-1.8 \mathrm{~mm}$ long;
stipules $6.5-13 \times 2.2-4.6 \mathrm{~mm}$, broadly lanceolate, with eglandular and glandular hairs on both surfaces and on the margin. Inflorescence in dichasial cyme; cymules 2-flowered, solitary or in aggregates at the top of each branch; peduncles (0)2.2-13.4 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs (1.9)2.5$3.6(4.8) \mathrm{mm}$ long and, patent glandular hairs $0.7-$ 1.5 mm long; bracteoles (8.4)9.6-14.1(18.8) $\times 0.7-$ 1.6 mm , linear-lanceolate, with eglandular and glandular hairs on both surfaces and on the margin; pedicels $0.8-2.3 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $2.2-4.5 \mathrm{~mm}$ long and, patent glandular hairs $0.9-2 \mathrm{~mm}$ long. Sepals $8.2-12.5 \times 3-5.4 \mathrm{~mm}$, not accrescent, 5-7-nerved, with mucro $2-5.5 \mathrm{~mm}$ long, with scarious margins $0.1-0.5 \mathrm{~mm}$ wide, with patent eglandular hairs $0.2-5.4 \mathrm{~mm}$ long and patent glandular hairs $0.5-2.6 \mathrm{~mm}$ long. Petals (14.7)16.7-18.7(20.9) $\times 10.5-18.1 \mathrm{~mm}$ (ratio petal width/petal length $=0.59-0.86)$, patent, emarginate (notch $0.5-1.9 \mathrm{~mm}$ deep), glabrous on both sides, ciliate on the basal margin, bluish. Staminal filaments $8.4-12.5 \mathrm{~mm}$ long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $2.5-4.1 \mathrm{~mm}$ long; anthers $2.7-3.4 \times 0.8-$ 1.5 mm , blue-black. Nectaries glabrous. Gynoecium $7.8-11.2 \mathrm{~mm}$ long, dark purplish. Fruit 31.738.8 mm long; mericarps $4-5.5 \times 2-2.9 \mathrm{~mm}$, with $\pm$ patent, eglandular hairs $1-2.5 \mathrm{~mm}$ long, and patent glandular hairs $0.40-1 \mathrm{~mm}$ long, brownish; rostrum 22.3-30.9 mm long, with a narrowed apex $3.8-5.9 \mathrm{~mm}$ long, with $\pm$ patent, eglandular hairs $2.3-3.8 \mathrm{~mm}$ long, and patent, glandular hairs $0.7-$ 1 mm long; stigmatic remains $1.6-3.8 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $2.8-3.5 \times 1.8-2.4 \mathrm{~mm}$, finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons entire.
Additional Illustrations. Yeo (2002: 151).
Chromosome Number. $2 n=28$ (Warburg 1938: 144); $2 n=42$ ? (Gauger 1937: 529; Warburg 1938: 144).

Phenology. Flowering specimens from May to August.
Distribution and Habitat. Northeast Turkey, Caucasus, and northern Iran; forest of Betula, Picea or Abies, or alpine meadows, on igneous rocks, between 1200 and 2700 m (Fig. 20). Additional map: Grossheim (1962, map 7).

Representative Specimens Examined. ARMENIA: Megrinskiy, Zangezurskiy, Vardanad-zor, $38^{\circ} 58^{\prime} \mathrm{N}, 46^{\circ} 12^{\prime} \mathrm{E}, 4$ Jun 1956, Egorova $\mathcal{E}$ al. 1743 (LE); pr. Nor-Baiazet, in fuc. Grizör, $40^{\circ} 19^{\prime}$ N, $45^{\circ} 7^{\prime}$ E, 16 Aug 1928, Schelkovnikov \& KaraMurza s.n. (LE). AZERBAIJAN: Ahar, Kuh Kaleybar, $38^{\circ} 27^{\prime}$ N, $47^{\circ} 4^{\prime}$ E, 4 Aug 1968, Tremé 13185E (W); Baku, distr. Geokczai, in valle supra p. Dshuljan infer. ad m. Kupucz, $40^{\circ}$ $39^{\prime} \mathrm{N}, 47^{\circ} 44^{\prime} \mathrm{E}, 2$ Aug 1899, Alexeenko s.n. (LE); Karabach austr., m. Ziarat, $39^{\circ} 31^{\prime}$ N, $46^{\circ} 51^{\prime}$ E, 4 Jul 1932, Karjagin s.n.


FIg. 20. Area of distribution of Geranium platypetalum.
(S); Elisabethpol, distr. Adzikent, $40^{\circ} 40^{\prime}, 46^{\circ} 21^{\prime}$, 9 Jul 1912, Schelkovnikov s.n. (BM). GEORGIA: Kazbegi, $42^{\circ} 39^{\prime}, 44^{\circ} 38^{\prime}$, 16 Jul 1981, Fischer 346 (WU); Achalzich, $41^{\circ} 38^{\prime}$ N, $42^{\circ} 58^{\prime}$ E, 2 Jul 1926, Meffert 428 (LE); Edisi, $42^{\circ} 32^{\prime}$ N, $44^{\circ} 12^{\prime}$ E, 20 Aug 1923, Juzepczuk 534 (LE); Mestia, $43^{\circ} 2^{\prime}$ N, $42^{\circ} 43^{\prime}$ E, 28 Jul 1979, Vasak s.n. (G, W); Mingrelie, mt. Lekondelis, $42^{\circ} 48^{\prime} \mathrm{N}$, $42^{\circ} 25^{\prime}$ E, 28 Aug 1893, Alboff 507 (FI); Racha, between vil. Schon and glacier Buba, $42^{\circ} 30^{\prime} \mathrm{N}, 43^{\circ} 30^{\prime} \mathrm{E}, 2$ Aug 1928, Raoeller s.n. (MA); Utsera, $42^{\circ} 38^{\prime} \mathrm{N}, 43^{\circ} 32^{\prime} \mathrm{E}(\mathrm{H})$. IRAN: Alibulagh et Delhi, $38^{\circ} 52^{\prime}$ N, $46^{\circ} 41^{\prime}$ E, 20 Sep 1884, Knapp s.n. (WU). RUSSIA: Kabardino-Balkaria, in declivibus rivi Irik ad pedes montis Gubasanty, $43^{\circ} 41^{\prime} \mathrm{N}, 44^{\circ} 4^{\prime} \mathrm{E}, 17$ Aug 1978, Vasák s.n. (W); Dych-su, $43^{\circ} 3^{\prime}$ N, $43^{\circ} 7^{\prime}$ E, 12 Jul 1925, Bush E Bush s.n. (C); Karachayevo-Cherkasskaiya, Kubañ, vallis fl. Teberda, $43^{\circ} 32^{\prime} \mathrm{N}, 41^{\circ} 47^{\prime} \mathrm{E}, 11$ Jun 1908, Busch E Busch s.n. (LE, C, E, H, MPU, W, WA, WU). TURKEY: Artvin, 3 km E Karaköy, $41^{\circ} 13^{\prime}$ N, $42^{\circ} 27^{\prime}$ E, 4 Aug 1981, Sorger 81-73-10 (W); Erzurum, Dutlu Dagi nw Oltu, $40^{\circ} 43^{\prime}$ N, $41^{\circ} 59^{\prime} \mathrm{E}, 16$ Jul 1989, Nydegger 44462 (G); Rize, 4 km antes Ovit Dagi Geçidi, $40^{\circ} 37^{\prime}$ N, $40^{\circ} 46^{\prime}$ E, 28 Jun 2001, Nisa 891 (MA); Hemsin, Ortakoy-Cat, $41^{\circ} 3^{\prime} \mathrm{N}, 40^{\circ} 54^{\prime} \mathrm{E}, 2$ Sep 1952, Davis 21255 (E).

Discussion. Geranium platypetalum can be confused with glandular forms of G. ibericum (see discussion of G. ibericum, above). Basal leaves should be used to discriminate these species, because they show more clearly obtriangular segments than caulinar ones. Hohenacker (1833) published "G. platypetalum Fisch. \& Mey. in literis" based on a specimen collected in "montis Sarial," but with no description. This species was republished two years later by Fischer and Meyer (1835) with a full description, but without any reference to Hohenacker's publication. They indicated a general area, "Hab. in montibus et subalpinis Somchetiae, Iberiae, Talüsch," but did not list any particular specimens. Novoselova (1998) proposed the specimen collected in Sarial (and distributed by Hohenacker in the Unio Itineraria exsiccata) to be the lectotype. This specimen is not directly connected to the protologue. On the other hand, at LE there are no other
specimens clearly connected to the protologue that would be a better choice as lectotype. Thus, we have preferred to consider Hohenacker's specimen as neotype in order to avoid any nomenclatural disturbance and considering that it was collected in the area mentioned by Fischer and Meyer (1835), and perfectly fits the original description.
7. Geranium peloponnesiacum Boiss., Diagn. Pl. Orient. ser. 2, 1: 110. 1854.-TYPE: GREECE. Peloponneso, templum Phigaleae, May 1830, Fauchè s.n. (lectotype: here designated, GBoissier digital image!). Fig. 21.
Herbs perennial, $20-53 \mathrm{~cm}$ tall. Rootstock 5.313.3 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, with patent to retrorse eglandular hairs $0.2-2 \mathrm{~mm}$ long. Basal leaves in a $\pm$ persistent rosette; lamina 3-8.8 $\times 3.2-10 \mathrm{~cm}$, palmatifid (ratio main-sinus length $/$ middle-segment length $=0.54-$ 0.67 ), pilose, with appressed, eglandular hairs, nervation not reticulate, not projected; segments $5-7$, rhombic [ratio maximum width/middle-segment length $=(0.57) 0.59-0.66(0.70)], 4.1-10.8 \mathrm{~mm}$ wide at the base, (11)12-16(17)-lobed in distal half (ratio second-sinus length/middle-segment length $=0.20-0.29$ ); cauline leaves opposite; petioles to 18 cm long, with patent to retrorse eglandular hairs $0.2-2.9 \mathrm{~mm}$ long, and patent, glandular hairs $0.2-0.3 \mathrm{~mm}$ long at the apex; stipules $8.8-12.5 \times$ $1.2-2.4 \mathrm{~mm}$, lanceolate, with eglandular hairs on abaxial surface and on the margin, usually glabrous adaxially. Inflorescence in dichasial cyme; cymules 2-flowered, solitary or in aggregates at the top of each branch; peduncles (0)1.4-10.4 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $0.6-1(1.2) \mathrm{mm}$ long, and patent, glandular hairs $0.3-0.5 \mathrm{~mm}$ long; bracteoles (3.2)3.6-3.4(4.8) $\times 0.5-0.9 \mathrm{~mm}$, linear-lanceolate, with eglandular hairs on abaxial surface and on the margin, usually glabrous adaxially; pedicels $0.5-3.4 \mathrm{~cm}$ long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, patent eglandular hairs $0.6-1 \mathrm{~mm}$ long, and patent, glandular hairs $0.3-0.5 \mathrm{~mm}$ long. Sepals 7.2-10.8 $\times$ 2.2-3.9 mm, not accrescent, 3-5nerved, with mucro $1.2-3 \mathrm{~mm}$ long, with scarious margins $0.1-0.3 \mathrm{~mm}$ wide, with $\pm$ patent eglandular hairs $0.4-3.7 \mathrm{~mm}$ long, and patent, glandular hairs $0.2-0.5 \mathrm{~mm}$ long, usually at the base. Petals (15.4)16.9-18.3(18.9) $\times 9.5-12.8 \mathrm{~mm}$ (ratio petal width/petal length $=0.56-0.75), \pm$ patent, emarginate (notch $1.2-3.5 \mathrm{~mm}$ deep), hairy on the base of abaxial side, glabrous on the adaxial side, ciliate on the basal margin, purplish. Staminal filaments $6.5-8.4 \mathrm{~mm}$ long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs 1-

3 mm long; anthers $1.8-2.7 \times 0.7-1.4 \mathrm{~mm}$, cream with blue edges; pollen yellow. Nectaries glabrous. Gynoecium 4.4-8.6 mm long, greenish. Fruit 43.644.7 mm long; mericarps $6.3 \times 2.6 \mathrm{~mm}$, with $\pm$ patent, eglandular hairs $0.3-0.5 \mathrm{~mm}$ long, and patent glandular hairs $0.40-0.45 \mathrm{~mm}$ long, brownish; rostrum 33.7-35.1 mm long, with a narrowed apex $2.1-2.9 \mathrm{~mm}$ long, with $\pm$ patent eglandular hairs $0.5-0.6 \mathrm{~mm}$ long, and patent glandular hairs $0.4-0.5 \mathrm{~mm}$ long; stigmatic remains $2.3-3.2 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $3-3.1 \times 2-$ 2.2 mm , finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons entire.

Additional Illustrations. Rouy (1901, tab. 383); Yeo (2002, photograph 40).

Chromosome Number. Unknown.
Phenology. Flowering specimens from April to June.

Distribution and Habitat. Central and South Greece; forests of Abies, Castanea or Quercus, on limestone substrates, between 550 and 1500 m (Fig. 22). Qosja (1992: 205) recorded G. peloponnesiacum from Albania. Unfortunately, it has been impossible to examine the specimen supporting this record.

Representative Specimens Examined. GREECE: Achaia, mt. Olenos (Erymanthos vet.), $37^{\circ} 59^{\prime} \mathrm{N}, 21^{\circ} 50^{\prime} \mathrm{E}, 12$ Jun 1893, Halácsy s.n. (B, JE, LD, PR, W, WU); Attica, mt. Parnes pr. Limiko, $38^{\circ} 10^{\prime} \mathrm{N}, 23^{\circ} 40^{\prime} \mathrm{E}, 17$ Apr 1930, Guiol 1159 (BM, G); Etolia-Akarnania, 2,1 km SO Dhorvitsa, $38^{\circ} 32^{\prime} \mathrm{N}, 21^{\circ} 48^{\prime}$ E, 16 May 1991, Willing 12111 (B); Mesolongiou, 1 km S of Ano Kerasovon, $38^{\circ} 29^{\prime}$ N, $21^{\circ} 27^{\prime}$ E, 3 May 1996, Nielsen 11132 (B, UPA); Evrytania, 2,2 km NW Kokkalia-Gipfel, $38^{\circ}$ $51^{\prime}$ N, $21^{\circ} 52^{\prime}$ E, 3 Jun 1991, Willing 14175 (B); Evvia, ep. Karistias, Rouklia, ESE of the village, $38^{\circ} 4^{\prime} \mathrm{N}, 24^{\circ} 26^{\prime} \mathrm{E}, 8$ May 1996, Snogerup 12847 (LD); Grevena, 1,7 km SSW Dhasohori, $39^{\circ} 52^{\prime} \mathrm{N}, 21^{\circ} 48^{\prime} \mathrm{E}, 29$ May 1993, Willing 29044 (B); Kozanis, Kamvounia, $1,8 \mathrm{~km}$ SSO Elati, $39^{\circ} 57^{\prime} \mathrm{N}, 21^{\circ} 49^{\prime}$ E, 4 Jun 1992, Willing 16830 (B); Laconiae, in monte Malevo, pr. Hajos Petros, $37^{\circ} 10^{\prime} \mathrm{N}, 22^{\circ} 15^{\prime} \mathrm{E}, 26$ Apr 1857, Orphanides 624 (FI, S, UPS, W); Phthiotidos, mons Callichromon supra monasterium Damasta, $38^{\circ} 48^{\prime} \mathrm{N}, 22^{\circ} 30^{\prime} \mathrm{E}, 4$ May 1958, Pinatzi 14376 (G); mt. Iti, 3 km W of Pavliani, $38^{\circ} 44^{\prime} \mathrm{N}, 22^{\circ}$ 20' E, 4 Jun 1985, Gustavsson 9018 (C, G, LD).

Discussion. Geranium peloponnesiacum resembles G. ibericum and G. platypetalum by its long, soft, patent eglandular hairs along the inflorescence. However, in G. peloponnesiacum eglandular hairs are shorter, and petals are hairy on the base of the abaxial side (petals glabrous on both sides in G. ibericum and G. platypetalum). The leaf lamina is more similar to G. ibericum because it has a rhombic central segment (not obtriangular as in G. platypetalum). However, G. peloponnesiacum has fewer lobes per segment, and the bracteoles, anthers, staminal filaments and gynoecia are shorter than in both G. ibericum and G. platypetalum. Additionally, the sepal mucros of G. peloponnesiacum are relatively shorter (as in G. ibericum), while


Fig. 21. Geranium peloponnesiacum Boiss. a. Habit; b. Leaf; c. Bracteoles; d. Indumentum of the pedicel; e. Flower without petals and sepals; f. Sepal; g. Petal; h. Staminal filaments; i. Fruit; j. Mericarp; k. Seed [a: Guiol 1159 (BM); b-k: Snogerup 12847 (LD)].
the petals are more similar in size to G. platypetalum.

In dry specimens, the leaf abaxial side of $G$. peloponnesiacum may be a bit whitish, as may also
be found in G. libani. Nevertheless, the former species has always glandular hairs on the inflorescence, while in the latter they are only eglandular. Additionally, the notch at the apex of


Fig. 22. Area of distribution of Geranium peloponnesiacum (dots) and G. libani (triangles).
the petals is deeper in G. peloponnesiacum than in G. Libani. Geranium peloponnesiacum is usually proterandrous, but some specimens with shorter anthers suggest that this species may also show gynodioecy.
8. Geranium libani P.H. Davis, Notes Roy. Bot. Gard. Edinburgh 22: 25. 1955. Geranium peloponesiacum var. libanoticum Boiss. \& C.I. Blanche ex Boiss., Diagn. Pl. Orient. ser. 2, 5: 73. 1856 [syn. subst.]. Geranium libanoticum (Boiss. \& C.I. Blanche ex Boiss.) Boiss., Fl. Orient. 1: 877. 1867, nom. illeg., non Schenk (1840).-TYPE: LEBANON. Eden, 23 June 1854, Reygasse 1164 (lectotype: here designated, G-Boissier digital image!; isolectotype: JE!). Fig. 23.

Herbs perennial, $19-52 \mathrm{~cm}$ tall. Rootstock 612.7 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, with patent to retrorse eglandular hairs $0.3-0.9 \mathrm{~mm}$ long. Basal leaves in a $\pm$ persistent rosette; lamina $2.4-6.4 \times 3.2-8.8 \mathrm{~cm}$, palmatifid (ratio main-sinus length $/$ middle-segment length $=$ $0.49-0.66)$, pilose, with appressed, eglandular hairs, nervation not reticulate, not projected; segments 5-7, rhombic [ratio maximum width/ middle-segment length $=$ ( 0.59 )0.62-0.67(0.80)], $3.7-10.3 \mathrm{~mm}$ wide at the base, (8)9-13(16)-lobed in distal half (ratio second-sinus length/middlesegment length $=0.49-0.66$ ); cauline leaves opposite; petioles to 18 cm long, with patent to retrorse eglandular hairs $0.3-0.9 \mathrm{~mm}$ long; stipules 3.8-10.5 $\times 0.8-2 \mathrm{~mm}$, lanceolate, with eglandular hairs on abaxial surface and on the margin, usually glabrous adaxially. Inflorescence in dichasial cyme; cymules 2-flowered, solitary or in aggregates at the
top of each branch; peduncles (0)1.4-13.7 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long and patent eglandular hairs $0.4-0.7(0.8) \mathrm{mm}$ long; bracteoles (1.2)2-2.6(4.7) $\times 0.4-0.8 \mathrm{~mm}$, linearlanceolate, with eglandular hairs on abaxial surface and on the margin, usually glabrous adaxially; pedicels 1.3-2.7 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long and patent eglandular hairs $0.5-1.1 \mathrm{~mm}$ long. Sepals $6.4-9.5 \times 3-5.2 \mathrm{~mm}$, not accrescent, 3-5-nerved, with mucro $1.3-2.3 \mathrm{~mm}$ long, with scarious margins $0.1-0.4 \mathrm{~mm}$ wide, with $\pm$ patent, eglandular hairs $0.8-2.1 \mathrm{~mm}$ long. Petals (10.4)12.9-16.9(18.3) $\times 5.9-10.7 \mathrm{~mm}$ (ratio petal width/petal length $=0.45-0.71), \pm$ patent, emarginate (notch $0.2-1.3 \mathrm{~mm}$ deep), hairy on the base of abaxial side, glabrous on the adaxial side, ciliate on the basal margin, bluish. Staminal filaments 6.38.4 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $0.9-2.4 \mathrm{~mm}$ long; anthers $1.3-3 \times 0.7-1.4 \mathrm{~mm}$, bluish; pollen yellow. Nectaries glabrous. Gynoecium $4.6-8.6 \mathrm{~mm}$ long, purplish. Fruit $30.6-38 \mathrm{~mm}$ long; mericarps 5-6.1 $\times 1.9-2.5 \mathrm{~mm}$, with $\pm$ patent eglandular hairs $0.4-1.1 \mathrm{~mm}$ long, brownish; rostrum $23-$ 31.2 mm long, with a narrowed apex $1.7-4.6 \mathrm{~mm}$ long, with $\pm$ patent, eglandular hairs $0.2-0.6 \mathrm{~mm}$ long; stigmatic remains $1.4-2.2 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $2.6-4.4 \times 1.4-2.6 \mathrm{~mm}$, finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons entire.

Additional Illustrations. Zohary (1972, pl. 324). Chromosome Number. Unknown.
Phenology. Flowering specimens from April to June.

Distribution and Habitat. Southern Turkey, western Syria, Lebanon and northern Israel; forests of Cedrus, Ostrya or Quercus, scrublands with Quercus coccifera, on limestone substrates, between 500 and 2000 m (Fig. 22). Additional map: Meusel et al. (1978: 260).

Representative Specimens Examined. ISRAEL: Upper Galilea, Wadi Hish, $33^{\circ} 0^{\prime}$ N, $35^{\circ} 33^{\prime}$ E, 7 May 1926, Naftolsky s.n. (FI, H, MA). LEBANON: Ain Zahalta, $33^{\circ} 48^{\prime} \mathrm{N}, 35^{\circ} 54^{\prime} \mathrm{E}$, 19 Jun 1910, Bornmüller 11544 (BM, E, G, HBG, W); Dschbel Barûk, $33^{\circ} 42^{\prime}$ N, $35^{\circ} 43^{\prime}$ E, 15 Jun 1910, Bornmüller 11543 (BM, E, G, JE, LD, W, WU); E de Banias, route de Qsdmous, $35^{\circ} 9^{\prime} \mathrm{N}, 36^{\circ} 5^{\prime} \mathrm{E}, 7$ Apr 1956, Pabot s.n. (G); Hasroun, $34^{\circ} 15^{\prime}$ N, $36^{\circ} 1^{\prime}$ E, 14 May 1961, Mouterde 12421 (G); Jabal Kenissé, $33^{\circ} 32^{\prime} \mathrm{N}, 35^{\circ} 35^{\prime} \mathrm{E}, 15$ Jun 1938, Mouterde 6502 (G); Saidet el Hakle près Ghazir, $34^{\circ} 0^{\prime} \mathrm{N}, 35^{\circ} 39^{\prime} \mathrm{E}, 6$ May 1935, Bertschinger 1288 (MPU). SYRIA: col de Jaoubet Bourghal, Jebel Alaouite, $35^{\circ} 35^{\prime} \mathrm{N}, 36^{\circ} 12^{\prime} \mathrm{E}, 2$ Jun 1956, Pabot s.n. (G); Djebel Ansarieh, Slenfe, $35^{\circ} 32^{\prime}$ N, $36^{\circ} 12^{\prime}$ E, 18 May 1933, Samuelsson 5105 (S); Kessab, $35^{\circ} 55^{\prime}$ N, $35^{\circ} 58^{\prime}$ E, 9 May 1945 (BM); Slenfe, $35^{\circ} 35^{\prime}$ N, $36^{\circ} 12^{\prime}$ E, 6 May 1954, Pabot s.n. (G); Lattaquie, Aïn el Aramié, $35^{\circ} 56^{\prime}$ N, $35^{\circ} 59^{\prime}$ E, 19 Apr 1933, Gombault 2261 (P); Wei el Beida, $35^{\circ} 3^{\prime} \mathrm{N}, 36^{\circ} 21^{\prime} \mathrm{E}, 15$ May 1943, Davis 6010A (E). TURKEY: Hatay, Belen, Karlik tepe near Soguk Oluk, $36^{\circ} 30^{\prime}$ N, $36^{\circ} 5^{\prime}$ E, 23 Apr 1957, Davis $\mathcal{E}$


Fig. 23. Geranium libani P.H. Davis. a. Habit; b. Leaf; c. Bracteoles; d. Indumentum of the pedicel; e. Flower without petals and sepals; f. Sepal; g. Petal; h. Staminal filaments; i. Fruit; j. Mericarp; k. Seed [a-f: Samuelsson 5105 (S); g: Pabot s.n., 25 Apr. 1953 (G); h-k: Bornmüller 11544 (G)].

Hedge 27038 (E, BM); Iskenderun-Antakya, Belen, $36^{\circ} 30^{\prime} \mathrm{N}$, $36^{\circ} 5^{\prime}$ E, 27 Apr 1990, Nydegger 45264 (G).

Discussion. Differences between G. libani and G. peloponnesiacum are addressed in the discussion of that species. The leaf lamina of G. libani resembles that of G. ibericum, but it has fewer lobes per segment. Additionally, eglandular hairs are shorter than in G. ibericum, as are the petals and bracteoles. The petals of G. libani are hairy on the base of the abaxial side, while they are glabrous on both sides in G. ibericum.
9. Geranium gymnocaulon DC., Prodr. 1: 640. 1824. Geranium ibericum var. brachytrichum Boiss., Fl. Orient. 1: 876. 1867.-TYPE: GEORGIA. Iberia, 1819, Steven s.n. (lectotype: here designated, G-DC digital image!). Fig. 24.

Geranium amethystinum Ledeb., Bull. Sci. Acad. Imp. Sci. Saint-Pétersbourg 2: 314. 1837.TYPE: GEORGIA. Guriel and Kabuleti, Nordmann s.n. (lectotype: here designated, H!).
Geranium gymnocaulon f. grandiflorum Rupr., Mém. Acad. Imp. Sci. Saint Pétersbourg ser. 7, 15(2): 272. 1869.-TYPE: GEORGIA. Caucasus orientalis, Tuschetia, 8 Aug. 1861, Ruprechet s.n. (lectotype: here designated, LE!; isolectotype: W!).
Geranium gymnocaulon f. pumilum Rupr., Mém. Acad. Imp. Sci. Saint Pétersbourg ser. 7, 15(2): 272. 1869.-TYPE: GEORGIA. Caucasus orientalis, Tuschetia, inter Westomtha et Orizchale infra Samkuris zweri, 1500-1300, 8 Aug. 1861, Ruprechet s.n. (lectotype: here designated, LE!).
Herbs perennial, $11-38 \mathrm{~cm}$ tall. Rootstock $4.5-$ 12.2 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, with uncinate eglandular hairs 0.10.3 mm long. Basal leaves in a $\pm$ persistent rosette; lamina 2.6-5.3 $\times 2.5-6.1 \mathrm{~cm}$, palmatifid (ratio main-sinus length/middle-segment length $=$ $0.56-0.76)$, pilose, with appressed, eglandular hairs, nervation not reticulate, not projected; segments 5-7, rhombic [ratio maximum width/ middle-segment length $=$ ( 0.57 )0.63-0.70(0.75)], $2.8-6.6 \mathrm{~mm}$ wide at the base, (11)14-15(21)-lobed in distal half (ratio second-sinus length/middlesegment length $=0.32-0.55$ ); cauline leaves opposite; petioles to 18 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long; stipules 3.9-14.1 $\times 1.3-$ 2.8 mm , lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. Inflorescence in dichasial cyme; cymules 2-flowered, solitary or in aggregates at the top of each branch; peduncles ( 0 )0.13-9.1 cm long, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long; brac-
teoles (2.3)3.7-5.2(5.7) $\times 0.6-1.3 \mathrm{~mm}$, linear-lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels $0.4-$ 2.4 cm long, with uncinate eglandular hairs $0.1-$ 0.3 mm long, and patent eglandular hairs $0.4-$ 1 mm long. Sepals $7.2-10.9 \times 2.9-5.5 \mathrm{~mm}$, not accrescent, 5-7-nerved, with mucro $1.9-2.8 \mathrm{~mm}$ long, with scarious margins $0.15-0.45 \mathrm{~mm}$ wide, with uncinate eglandular hairs $0.1-0.3 \mathrm{~mm}$ long, and $\pm$ patent, eglandular hairs $0.4-2.1 \mathrm{~mm}$ long. Petals (12.1)15.4-16.7(20) $\times 8.4-14.2 \mathrm{~mm}$ (ratio petal width/petal length $=0.57-0.85$ ), patent, emarginate (notch 1.1-3.2 mm deep), glabrous on both sides, ciliate on the basal and, sometimes, on the apical margin, bluish. Staminal filaments 5.29.9 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $0.1-2.5 \mathrm{~mm}$ long; anthers 1.8-2.5 $\times 0.6-1.3 \mathrm{~mm}$, bluish. Nectaries glabrous. Gynoecium $4.3-9.1 \mathrm{~mm}$ long, dark purplish. Fruit $29.7-37.5 \mathrm{~mm}$ long; mericarps $5.2-$ $5.9 \times 2-2.8 \mathrm{~mm}$, with $\pm$ patent eglandular hairs $0.2-2.2 \mathrm{~mm}$ long, brownish; rostrum 20.8-29.2 mm long, with a narrowed apex $2.2-4.7 \mathrm{~mm}$ long, with $\pm$ patent, eglandular hairs $0.2-1.7 \mathrm{~mm}$ long; stigmatic remains $1.8-3.2 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $3.1-4.2 \times 1.7-2.4 \mathrm{~mm}$, finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons entire.
Additional Illustrations. Grossheim (1962: 17).
Chromosome Number. $2 n=28,56$ (Sokolovskaya and Strelova 1948).

Phenology. Flowering specimens from May to August.
Distribution and Habitat. Western and central Caucasus; alpine meadows, rocky slopes, and among Rhododendron or Empetrum, on schistose rocks, between 1700 and 3100 m (Fig. 25). Davis (1967: 474) mentioned G. gymnocaulon from "Turkish/Soviet border" based in the previous record of Grossheim (1962, map 9). Unfortunately, it has been impossible to examine the specimen supporting this record. Additional map: Grossheim (1962, map 9).

Representative Specimens Examined. GEORGIA: Abkhasie, inter montes Dzysra et Cipsira, $43^{\circ} 18^{\prime} \mathrm{N}, 40^{\circ} 54^{\prime} \mathrm{E}, 31$ Jul 1935, Kolakovsky s.n. (LE); Adjarie, mont Khino, $41^{\circ} 46^{\prime}$ N, $42^{\circ} 9^{\prime}$ E, 17 Jul 1893, Alboff 274 (FI, G); distr. Gulripshi, vicinitas pagi Sakeni latior, montis Guagua, $43^{\circ} 5^{\prime} \mathrm{N}, 41^{\circ} 53^{\prime}$ E, 15 Jul 1979, Mayasak s.n. (G); Georgian Military Road, Krestovyi Pass, $42^{\circ} 30^{\prime}$ N, $44^{\circ} 27^{\prime}$ E, 13 Jul 1975, Kukkonen 12092 (H); Guria, range Ajara-Imeretis, Bakhmaro, m. Sakornia, $42^{\circ} 22^{\prime} \mathrm{N}, 44^{\circ} 39^{\prime} \mathrm{E}, 23$ Aug 1950, Zanitaradze s.n. (MA); Ermani, $42^{\circ} 29^{\prime}$ N, $44^{\circ} 16^{\prime}$ E, 10 Jul 1939, Kutora s.n. (W); Mtiuleti, distr. Dusheti, Aragristavi, $42^{\circ} 21^{\prime} \mathrm{N}, 44^{\circ} 20^{\prime} \mathrm{E}$, 9 Aug 1967, Zamfaradze s.n. (MA); Svanetia in jugo Latpari inter flumina Hippum et Ingur, $42^{\circ} 52^{\prime} \mathrm{N}, 42^{\circ} 58^{\prime} \mathrm{E}, 5$ Aug 1890, Sommier $\mathcal{E}$ Levier s.n. (FI). RUSSIA: KabardinoBalkaria, Agashtan, $43^{\circ} 11^{\prime} \mathrm{N}, 43^{\circ} 10^{\prime} \mathrm{E}, 18 \mathrm{Jul}$ 1925, Busch \& Busch s.n. (LE, O); Ilkezi, Doguschja-su-aman, $43^{\circ} 18^{\prime} \mathrm{N}$,


Fig. 24. Geranium gymnocaulon P.H. Davis. a. Habit; b. Indumentum of the peduncle; c. Bracteoles; d. Flower; e. Flower without petals and sepals; f. Sepal; g. Petal; h. Staminal filament; i. Fruit; j. Mericarp; k. Seed [a-g: Ruprecht s.n., 8 Aug 1861 (LE); h-k: Sommier E Levier s.n., 1 Aug. 1890 (FI)].
$43^{\circ} 24^{\prime}$ E, 26 Jul 1925, Busch E Busch s.n. (S, WU); Baksan, montis Cheget, $43^{\circ} 8^{\prime}$ N, $43^{\circ} 17^{\prime}$ E, 15 Aug 1978, Vasák s.n. (G, W); Kabarda, Karasu, Ilkezi, Dogushja-su-algan, $43^{\circ} 18^{\prime}$ N, $43^{\circ} 24^{\prime}$ E, 24 Jul 1925, Busch \& Busch 2941 (C, G, H, K, KRA, LE, S, W, WA).

Discussion. Geranium gymnocaulon is sometimes mistaken for specimens of $G$. ibericum without glandular hairs. However, G. gymnocaulon has a characteristic indumentum on the peduncles


FIg. 25. Area of distribution of Geranium gymnocaulon (dots) and G. kurdicum (triangles).
and pedicels composed of short, uncinate hairs, lacking the long, soft, patent eglandular hairs of $G$. ibericum. From G. libani (which has an indumentum quite similar to G. ibericum), it can be further distinguished by its petal indumentum which are glabrous on both sides, as opposed to G. libani, where the petals are hairy on the base of the abaxial side, and by having a deeper notch at the petal apex. Some specimens of G. gymnocaulon have the basal part of the stem almost glabrous.
10. Geranium kurdicum Bornm., Repert. Spec. Nov. Regni Veg. 8: 82. 1910.-TYPE: IRAQ. Assyria, montis Helgurd ditionis oppidi Riwandus, Karduchiae austro-orientalis, $36^{\circ} 46^{\prime} \mathrm{N}$, $44^{\circ} 51^{\prime} \mathrm{E}, 26$ June 1893, Bornmuller 998 (lectotype: designated by Knuth 1912: 141, B $\dagger$; isolectotypes: BR! JE! K! LD! W! WU!). Fig. 26.

Herbs perennial, $10-43 \mathrm{~cm}$ tall. Rootstock 3.810.8 mm diam, $\pm$ horizontal. Stem erect, leafy, herbaceous, glabrous or with scattered patent to retrorse eglandular hairs $0.1-0.3 \mathrm{~mm}$ long. Basal leaves in a $\pm$ persistent rosette; lamina 2.4-5.5 $\times$ $3.2-6.9 \mathrm{~cm}$, deeply palmatifid [ratio main-sinus length/middle-segment length $=0.71-0.84(0.90)$ ], pilose, with scattered appressed, eglandular hairs, nervation not reticulate, not projected; segments 57, rhombic [ratio maximum width/middle-segment length $=(0.62) 0.68-0.73(0.77)], 0.7-5.6 \mathrm{~mm}$ wide at the base, (5)7-10(12)-lobed in distal half (ratio second-sinus length/middle-segment length $=0.28-0.68$ ); cauline leaves opposite; petioles to 19 cm long, glabrous or with scattered patent to retrorse eglandular hairs $0.1-0.2 \mathrm{~mm}$ long; stipules $3.5-7.6 \times 1.2-1.7 \mathrm{~mm}$, lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. Inflorescence in dichasial cyme;
cymules 2-flowered, solitary or in aggregates at the top of each branch; peduncles (0) $1.8-10.1 \mathrm{~cm}$ long, with scattered patent to retrorse eglandular hairs $0.1-0.7 \mathrm{~mm}$ long; bracteoles (1.9)2.4-3.1(4.6) $\times 0.5-$ 0.8 mm , linear-lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels $0.9-3.4 \mathrm{~cm}$ long, with scattered patent to retrorse eglandular hairs $0.2-0.7 \mathrm{~mm}$ long. Sepals $6.7-9.2 \times 3-4.5 \mathrm{~mm}$, not accrescent, $3-5$-nerved, with mucro $0.7-2.7 \mathrm{~mm}$ long, with scarious margins $0.2-0.4 \mathrm{~mm}$ wide, with $\pm$ patent, eglandular hairs $0.8-1.5 \mathrm{~mm}$ long. Petals (9.8)12.8$14.1(15.2) \times 7.9-11.1 \mathrm{~mm}$ (ratio petal width/petal length $=0.52-0.87$ ), erect-patent, emarginate (notch $0.9-2.5 \mathrm{~mm}$ deep), hairy on the base of adaxial side, glabrous on the abaxial side, ciliate on the basal margin, purplish. Staminal filaments 5.37.6 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half, with hairs $0.5-1.2 \mathrm{~mm}$ long; anthers 1.7-2.5 $\times 0.6-1.2 \mathrm{~mm}$, yellow; pollen yellow. Nectaries glabrous. Gynoecium $5-7.4 \mathrm{~mm}$ long, dark purplish. Fruit $23.4-30.2 \mathrm{~mm}$ long; mericarps 4.2-4.9 $\times 1.7-2.2 \mathrm{~mm}$, with $\pm$ patent eglandular hairs $0.4-1.5 \mathrm{~mm}$ long, brownish; rostrum 16.2-23.3 mm long, with a narrowed apex 12.9 mm long, with $\pm$ patent, eglandular hairs $0.2-$ 0.6 mm long; stigmatic remains $1.2-1.5 \mathrm{~mm}$ long, with 5 glabrous lobes. Seeds $3.1 \times 1.6 \mathrm{~mm}$, finely reticulate, reddish; hilum $1 / 4$ as long as the perimeter. Cotyledons unknown.

Chromosome Number. Unknown.
Phenology. Flowering specimens from June to September.

Distribution and Habitat. Southeastern Turkey and northern Iraq; in moist areas of alpine meadows, between 2300 and 3500 m (Fig. 25). Additional map: Meusel et al. (1978: 260).

Representative Specimens Examined. IRAQ: Arl Gird Dagh, $36^{\circ} 45^{\prime}$ N, $44^{\circ} 51^{\prime}$ E, 24 Jul 1932, Guest 2905 (K); N \& W slopes in Helgord, $36^{\circ} 45^{\prime}$ N, $44^{\circ} 51^{\prime}$ E, 15 Aug 1956, Haley 136 (BM, K; N of Helgord Range near Berma Sand Lake, $36^{\circ} 46^{\prime} \mathrm{N}$, $44^{\circ}$ 51' E, 3 Sep 1957, Rawi 24776 (K). TURKEY: Bitlis, Kambos Dag above Hurmuz, $38^{\circ} 17^{\prime} \mathrm{N}, 41^{\circ} 58^{\prime} \mathrm{E}, 31$ Jun 1954, Davis 23386 (BM, K); Hakkari, Cilo Tepe, $37^{\circ} 30^{\prime} \mathrm{N}, 44^{\circ} 0^{\prime} \mathrm{E}, 8$ Aug 1954, Davis 24034 (BM, K); Kara Dag, $37^{\circ} 42^{\prime}$ N, $43^{\circ} 42^{\prime}$ E, 15 Aug 1954, Davis 24403 (K, BM); Van, Satak, Kavussahap Dag, $38^{\circ} 15^{\prime} \mathrm{N}, 42^{\circ} 15^{\prime} \mathrm{E}, 23 \mathrm{Jul}$ 1954, Davis 23217 (BM).

Discussion. Geranium kurdicum can be easily distinguished from other species of subsect. Mediterranea by its deeply palmatifid leaves with deep and narrow secondary divisions. This species is glabrous or with scattered eglandular hairs on stem and petioles, and shows a more dense indumentum on peduncles and pedicels. In $G$. kurdicum, petal indumentum is similar to G. gracile, with hairs on the base of adaxial side, although in the latter species petals are relatively longer and narrower.


Fig. 26. Geranium kurdicum Bornm. a. Habit; b. Leaf; c. Bracteoles; d. Indumentum of the pedicel; e. Flower; f. Flower without petals and sepals; g. Sepal; h. Petal; i. Staminal filaments; j. Fruit; k. Mericarp; 1. Seed [a-h: Bornmüller 998 (BR); i-l: Bornmüller $998(\mathrm{~K})]$.

## Excluded NAmes

Geranium brotherusianum Trautv. ex R. Knuth in Engl., Pflanzenr. IV. 129 (Heft 53): 109 (1912), nom. nud., pro syn., in sched.
Geranium grandiflorum Gueldenst., Reis. Russland 1: 426 (1787), nom. nud.
Geranium gypsum Bobrov in Kom. \& al., Fl. URSS 14: 60 (1949), nom. nud.
Geranium ibericum var. talyshense E.F. Warb., New Phytol. 38: 144. 1938, nom. nud.
Geranium sect. Perennia Boiss., Diagn. Pl. Orient. ser. 2, 1: 111. 1854, nom. nud.
Geranium platypetalum Fisch. \& C.A. Mey. ex Hohen., Bull. Soc. Imp. Naturalistes Moscou 6: 246. 1833, nom. nud.

Acknowledgements. The authors wish to thank C. Jarvis, M. Novoselova, P. Perret, and Cl. Roux for help in locating some type or critical material, M. Amadio and D. Victor for sending some cuttings of living material, V. Valcárcel for her cooperation to develop the Euro+Med PlantBase project, M. Jerez and A. Martín for their technical support, María P. Martín for her lab assistance, and S. Castroviejo for uncompromising support. M. Á. Moreno and O. Fiz kindly provided us the ITS sequences of G. robertianum and G. tuberosum. We are also grateful to the curators of the cited herbaria for kind assistance during our visits and for loan of specimens. We also thank to the editor and two anonymous reviewers who greatly improved the manuscript. This work was partly financed by the Spanish Government through the research projects REN2003-00982/GLO, and CGL2004-00172/BOS, and by the European Union through the COLPARSYS program.

## Literature Cited

Aedo, C. 1996. Revision of Geranium subgenus Erodioidea (Geraniaceae). Systematic Botany Monographs 49: 1-104.

- 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.
—_. 2005. (1680) Proposal to conserve the name Geranium ibericum against G. montanum (Geraniaceae) with a conserved type. Taxon 54: 207-208.
-, F. Muñoz Garmendia, and F. Pando. 1998a. World checklist of Geranium L. (Geraniaceae). Anales del Jardin 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). Bluтеа 47: 205-297.
L. Sáez, and C. Navarro. 2003. Taxonomic revision of Geranium sect. Gracilia (Geraniaceae). Brittonia 55: 93-126.
-, C. Navarro, and M. L. Alarcón. 2005. Taxonomic revision of Geranium sections Andina and Chilensia (Geraniaceae). Botanical Journal of the Linnean Society 149: 1-68.
Armbruster, W. S. 1993. Evolution of plant pollination
systems: hypotheses and tests with the neotropical vine Dalechampia. Evolution 47: 1480-1505.
BaKer, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347-349. - 1967. Support for Baker's law as a rule. Evolution 21: 85-56.
Bell, G. 1985. On the function of flowers. Proceedings of the Royal Society of London. Series B. Biological Sciences 224: 223-265.
Bobrov, E. G. 1949. Geranium L. Pp. 2-62 (pags. 3-49 in the English ed.) in Flora of the U.R.S.S., vol. 14, eds. B. K. Shishkin and E. G. Bobrov. Koenigstein: Koelzt Scientific Books.
Boesewinkel, F. D. 1988. The seed structure and taxonomic relationships of Hypseocharis Remy. Acta Botanica Neerlandica 37: 111-120. - and W. Been. 1979. Development of ovule and testa of Geranium pratense L. and some other representatives of the Geraniaceae. Acta Botanica Neerlandica 28: 335-348.
Cavanilles, A. J. 1787. Monadelphiae classis dissertationes decem. Quarta dissertatio botanica. Paris: F. A. Didot.
Corner, E. J. H. 1976. The seeds of dicotyledons. Cambridge: Cambridge University Press.
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.
DAhLGREN, K. V. O. 1952. Chromosomes in Geranium bohemicum and G. lanuginosum with some notes on the hybrid. Hereditas (Lund) 38: 314-320.
Davis, P. H. 1967. Geranium L. Pp. 451-474 in Flora of Turkey, vol. 2, eds. P. H. Davis, J. Cullen, and J. E. Coode. Edinburgh: Edinburgh University Press.
Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783-791.
Fiori, A. and G. Paoletti. 1899-1904. Iconographia Florae Italicae. Padova: Tipografia Antoniana.
Fischer, F. E. L. and C. A. Meyer. 1835. Index seminum, quae Hortus Botanicus Imperialis Petropolitanus pro mutua commutatione offert. Accedunt animadversiones botanicae nonnullae. Petropoli.
Gams, H. 1924. Geranium L. Pp. 1668-1716 in Illustrierte Flora von Mittel-Europa vol. 4(3), ed. G. Hegi. Munich: J. F. Lehmann.
Gauger, W. 1937. Ergebnisse einer zytologischen Untersuchung der Familie der Geraniaceae. Planta 26: 529-531.
GILbert, D. G. 1993. SEQAPP, version 1.9a157. Bloomington, Indiana, USA: Biocomputing Office, Biology Department, Indiana University.
Godron, D. A. 1847. Geranium L. Pp. 297-306 in Flore de France, vol. 1, eds. J. Ch. M. Grenier and D. A. Godron. Paris: J. B. Baillière.
Grossheim, A. A. 1962. Flora Kavkaza, vol. 6, 2 ed. Baku, Moscova \& Leningrad: Akademia Nauk SSSP.
Heslop-Harrison, Y. and K. R. Shivanna. 1977. The receptive surface of the angiosperm stigma. Annals of Botany 41: 1233-1258.
Hohenacker, R. F. 1833. Enumeratio Plantarum in territorio Elisabethopolensi et in provincia Karabach sponte nascentium, quas collegit R. Fr. Hohenacker. Bulletin de la Société Impériale des Naturalistes de Moscou 6: 210-261.
Hultén, E. and M. Fries. 1986. Atlas of north European vascular plants, vol. 2. Königstein: Koeltz Scientific Books.
Hylander, N. 1961. Kungsnävan, våra trädgårdars praktfullaste Geranium. Lustgården 42: 109-114.

Janchen, E. 1959. Catalogus Florae Austriae. Wien: SpringerVerlag.
Knuth, R. 1912. Geranium L. Pp. 43-221575-583 in Das Pflanzenreich IV. 129 (Heft 53), ed. A. Engler. Leipzig: Engelmann.
Meusel, H., E. JÄger, S. Rauschert, and E. Weinert. 1978. Vergleichende Chorologie der zentraleuropäischen Flora Karten, vol. 2. Jena: G. Fischer.
Milberg, P. 1994. Germination of up to 129 -year old, dry stored seeds of Geranium bohemicum (Geraniaceae). Nordic Journal of Botany 14: 27-29.
Mobayen, S. 1996. Flora of Iran, vol. 4. Tehran: Tehran University Publications.
Netolitzky, F. 1926. Anatomie der Angiospermen-Samen. Handbuch der Pflanzenanatomie band X. Berlin: Borntraeger.
Nickrent, D. L., M. A. García, M. P. Martín, and R. L. MATHiASEN. 2004. A phylogeny of all species of Arceuthobium (Viscaeae) using nuclear and chloroplast DNA sequences. American Journal of Botany 91: 124-138.
Novoselova, M. S. 1998. Vidy roda Geranium L. (Geraniaceae) podroda Geranium flory Kavkaza [Generis Geranium L. (Geraniaceae) subgeneris Geranium species florae Caucasi]. Novosti Sistematiki Vyssih Rastenij 31: 143-158.
Payne, W. W. 1978. A glossary of plant hair terminology. Brittonia 30: 239-255.
Philipp, M. 1985. Reproductive biology of Geranium sessiliflorum, 1. Flower and flowering biology. New Zealand Journal of Botany 23: 567-589.

- 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.
Posada, D. and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14: 917-818.
Qosja, X. (ed.). 1992. Flore de l'Albanie, vol. 2. Tirane: Academie des Sciences.
Reichenbach, L. 1841. Icones florae germanicae et helveticae, vol. 5. Leizpig: Sumptibus Ambrosii Abel.
RONQUIST, F. 1997. DIVA, version 1.1. Computer program and manual available by anonymous FTP from Uppsala University (http:/ /ftp.uu.se).
- and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572-1574.
Roux, H. 1880. Catalogue des Plantes de Provence spontanées ou généralement cultivées (suite). Bulletin, Société Botanique et Horticole de Provence 2: 117-148.
Rouy, G. 1901. Illustrationes plantarum Europae rariorum, vol. 16. Paris: Chez les fils d'Émile Deyrolle.
Schönbeck-Temesy, E. 1970. Geraniaceae. Pp. 1-67 in Flora Iranica, vol. 69, ed. K. H. Rechinger. Graz: Akademische Druck.
Sims, J. 1811. Geranium ibericum. Botanical Magazine 34, tab. 1386.

Sokolovskaya, A. P. and O. S. Strelova. 1948. Geografičeskoe raspredelenie poliploidov II. Issledovanie Flory Altaja. Uchenye Zapiski Leningradskii Gosudarstvennyi Pedagogicheskii Instituta imeni A. I. Gertsena 66: 179-193. [n.v.].
Soó, R. 1966. A Magyar Flóra és Vegetáció RendszertaniNövényföldrajzi Kézikönyve II. Budapest: Akadémiai Kiadó.
Stafford, P. J. and S. Blackmore. 1991. Geraniaceae. Pp. 4978 in The northwest European pollen flora, VI, eds. W. Punt and S. Blackmore. Amsterdam, London, New York \& Tokyo: Elsevier.
Stebbins, G. L. 1957. Self fertilization and population
variability in the higher plants. American Naturalist 91: 337-354.
-. 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. Annual Review of Ecology and Systematics 1: 307-326.
Sweet, R. 1820-22. Geraniaceae, vol. 1. London: J. Ridgway. SWOFFORD, D. L. 2002. PAUP*: phylogenetic analysis using parsimony ( ${ }^{*}$ and other methods). Sunderland: Sinauer.
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.
Theobald, W. L., J. L. Krahulik, and R. C. Rollins. 1979. Trichome description and classification. Pp. 40-53 in Anatomy of the Dicotyledons, vol. 1, ed. 2, eds. C. R. Metcalfe and L. Chalk. Oxford: Claredon Press.
Van Loon, J. C. 1984a. Chromosome numbers in Geranium from Europe, I. The perennial species. Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen. Series C. Biological and Medical Sciences 87: 263-277.
. 1984b. Chromosome numbers in Geranium from Europe, II. The annual species. Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen. Series C. Biological and Medical Sciences 87: 279-296.
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. D. Bruns, S. B. Lee, and J. W. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315-322 in PCR protocols and applications - a laboratory manual, eds. N. Innis, D. Gelfand, J. Sninsky, and T. White. New York: Academic Press.
Yeo, P. F. 1984. Fruit-discharge-type in Geranium (Geraniaceae): its use in classification and its evolutionary implications. Botanical Journal of the Linnean Society 89: 1-36.
二. 2002. Hardy geraniums, ed. 2. Portland, Oregon: Timber Press.
Zohary, M. 1972. Flora Palaestina part two, text $\mathcal{E}$ plates. Jerusalem: Israel Academy of Sciences.

APPENDIX 1. Vouchers or source, country of origin, accession numbers and databank numbers for the taxa used in the phylogenetic analyses of Geranium subsect. Mediterranea. GenBank numbers are for ITS followed by $\operatorname{trnL}-\operatorname{trnF}$. "-" indicates no sequence for that region.
G. gracile (1), Merello E al. 2792 (MA 630225), Georgia, AJ884924, -; G. gracile (2), Valcárcel \& al. 370VV01 (MA 689760), Turkey, AJ884925, -; G. gymnocaulon, Cuba s.n. (G), Georgia, AJ884926, AJ884717; G. ibericum (1), Sorger 81-64-6 (W), Turkey, AJ884927, -; G. ibericum (2), Herrero \& al. 1550 (MA 687418), Turkey, AJ884928, AJ884718; G. ibericum (3), Chater s.n. (NMW), Great Britain, AJ884929, -; G. ibericum (4), Nisa \& al. 893 (MA 688785), Turkey, AJ884936, -; G. kurdicum (1), Davis 23386 (BM), Turkey, AJ884930, AJ884719; G. kurdicum (2), Davis 23217 (BM), Turkey, AJ884931, -; G. libani, Nydegger 45264 (G), Turkey, AJ884932, AJ884720; G. peloponnesiacum (1), Nielsen 11132 (UPS), Greece, AJ884933, AJ884721; G. peloponnesiacum (2), Snogerup 12847 (LD), Greece, AJ884934, -; G. platypetalum (1), Menishki s.n. (LE), Russia, AJ884935, -; G. platypetalum (2), Nisa \& al. 891 (MA 688786), Turkey, AJ884938, -; G. platypetalum (3), Eggli 396 (Z), Georgia, AJ884937, -; G. renardii (1), Arnold s.n. (JE), Russia,

AJ884939, -; G. renardii (2), Konechnaya \& Khaare s.n. (LE), Georgia, AJ884940, AJ884722; G. lanuginosum (1), Lindén s.n. (H), Sweden, AJ884941, -; G. lanuginosum(2), Simon s.n. (LD), France, AJ884943, -; G. lanuginosum (3), Gutiérrez s.n. (MA 611351), Spain, AJ884942, ; G. bohemicum (1), Karis \& Wanntorp s.n. (S), Sweden, AJ884944, -; G. bohemicum (2), Engelskjon $\mathcal{E}$ Steilness s.n. (C), Norway, AJ884945, -; G. bohemicum (3), Herranz s.n. (MA 646238), Spain, -, AJ884716; G. tuberosum, Aldasoro \& al. 2475 (MA 690231), Turkey, AJ884946, -; G.
robertianum, Catalán s.n. (MAF 144413), Great Britain, AJ884947, -; G. robertianum, GenBank, Pankhurst 2 (RNG), Great Britain, -, AF167152; G. pusillum, GenBank, Pankhurst 1 (RNG), Great Britain, -, AF167151; G. retrorsum, GenBank, Gardner \& al. AK285249, New Zealand, AY752473, -; G. solanderi, GenBank, Gardner E al. AK285206, New Zealand, AY752467, -; G. homeanum, GenBank, Gardner \& al. AK285216, New Zealand, AY752471, -; G. brevicaule (sub G. sessiliflorum ), GenBank, Gardner \& al. AK286142, New Zealand, AY752474, -.

