# TAXONOMIC REVISION OF *GERANIUM* SECTIONS *BATRACHIOIDEA* AND *DIVARICATA* (GERANIACEAE)[1]

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## Abstract

*Geranium* subg. *Robertium* (Geraniaceae) comprises eight sections, of which section *Batrachioidea* and section *Divaricata* are revised here. *Geranium* sect. *Batrachioidea* consists of four species centered in Eurasia, between the Mediterranean region and the Himalaya Mountains, although they have also expanded to many temperate areas in America, South Africa, and Australia. In contrast to the current literature, we consider *G. brutium* to be a synonym of *G. molle*. We also accept *G. aequale* to include plants similar to *G. molle* but with smooth mericarps. *Geranium* sect. *Divaricata* comprises two species, one widespread between the Mediterranean region and the Himalaya Mountains and the other endemic to the Caucasus. A cladistic analysis using a data set of 15 characters showed that both sections are well supported by synapomorphic features. Conversely, no new character (other than pollen color) was found to support a relationship between them. Brief accounts are also given of chromosome number, hybrids, and diagnostic aspects of morphology. Nomenclature for all species is reviewed, 32 lectotypes are designated, and descriptions, distribution maps, and illustrations are provided.

The genus *Geranium* L. (Geraniaceae) is distributed throughout most of the world. A brief history of generic delimitation and infrageneric classification, as well as a description of the genus, can be found in Aedo (1996). *Geranium* comprises about 430 species and is divided, according to the currently accepted classification (Yeo, 1984), into three subgenera: subg. *Geranium*, subg. *Erodioidea* (Picard) Yeo, and subg. *Robertium* (Picard) Rouy. Only subgenus *Erodioidea* has been monographed recently (Aedo, 1996). *Geranium* subg. *Geranium* comprises over 380 species, grouped in at least 10 sections. Some of these sections have been revised (Davis, 1970; Carlquist & Bissing, 1976), but much more work is necessary to attain a satisfactory knowledge of subgenus *Geranium*.

*Geranium* sects. *Batrachioidea* W. D. J. Koch and *Divaricata* Rouy, the taxa studied here, belong to subgenus *Robertium*, which is firmly supported by both morphological and chloroplast-DNA data (Yeo, 1984; Price & Palmer, 1993). According to Yeo's (1984) sectional classification, subgenus *Robertium* comprises eight sections and 30 species. Section *Polyantha* Reiche (8 species) is endemic to the eastern Himalayas and southern China. Section *Anemonifolia* R. Knuth (2 species) also has a limited distribution, being endemic to Madeira Island. Section *Trilopha* Yeo (5 species) is restricted to mountains in tropical Africa, western Asia, and the eastern Himalayas. The distribution of the remaining five sections, *Lucida* R. Knuth, *Ruberta* Dumort., *Divaricata*, *Batrachioidea*, and *Unguiculata* (Boiss.) Reiche, is centered in the Mediterranean region and western Asia, though section *Ruberta* extends in the east to Japan, and in the south to mountains of tropical Africa.

Sections *Anemonifolia* and *Ruberta* were revised by Yeo (1973). The same author also studied most of the species of section *Polyantha* (Yeo, 1992: 192). Following upon the recent revision of *Geranium* subg. *Erodioidea* (Aedo, 1996), and in pursuit of our aim to prepare a comprehensive monograph of the genus, we here present a revision of two sections of subgenus *Robertium:* sect. *Batrachioidea* and sect. *Divaricata*.

The taxonomic problems of section *Batrachioidea* were confined to two species, *G. pyrenaicum* and *G. molle*. The variability of *G. pyrenaicum* had

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not been well studied except for Ortiz's (1989) work, which included mainly Iberian material. *Geranium molle* is a highly variable species from which the most robust forms had been segregated and named *G. brutium*. Another problem to address in this revision was the taxonomic status of some plants similar to *G. molle* but with smooth mericarps. Section *Divaricata*, comprising two nonproblematic species, had not been revised since Knuth's (1912: 57, 154) monograph. Both sections could constitute a monophyletic group, as suggested by the presence of a derived character state (blue pollen). However, at present, there are no other data to confirm this hypothesis.

This revision of sections *Batrachioidea* and *Divaricata* is a first attempt to explore the phylogenetic relationships within *Geranium* subg. *Robertium*. Future work may be focused only on sections *Trilopha* and *Unguiculata*, because section *Lucida* is monotypic and non-problematic.

## Materials and Methods

This revision is based on more than 2000 herbarium specimens from the following herbaria: AK, B, BAF, BC, BISH, BM, BR, C, CAN, CAS, CHR, G, JE, H, K, L, LE, LISI, LOU, LY, M, MA, MAF, MO, MPU, MUB, NY, OXF, PAL, PH, PO, RO, and W. Furthermore, microfiche, photographs, and other data have been examined from the following additional herbaria: BREG, DS, E, GB, GFW, HAL, LD, LINN, LISU, MANCH, NAP, S, SGO, SZU, TBI, U, UPS, US, and WRSL. Unfortunately, we have had difficulties in obtaining some types on loan. The most relevant cases are those of F. Schur, A. Terracciano, and N. Terracciano. Schur's original material is spread through several herbaria. B, C, E, L, PH, and W have none of Schur's original material, while BP, BRNU, GOET, LW, MW, NA, P, and WU did not respond to our requests. Terracciano's herbarium constitutes a separate collection in NAP. However, this collection has not been available for study since World War II (fide A. Santangelo, in litt.). The dispositions of names for which no type material could be located or obtained are based on the opinions of previous authors (as indicated). Where no reliable opinion was found, these names are included in a "Dubious Names" section.

Cladistic analyses were carried out using the PAUP software package (Swofford, 1993). All characters were unweighted and unordered. Data were analyzed using the exhaustive option. Polarization of characters into plesiomorphic and apomorphic states was assessed using the standard procedure of outgroup comparison (Watrous & Wheeler, 1981). MacClade version 3.04 was used to edit the data set analyzed with PAUP (Maddison & Maddison, 1992). It was also used to map the distribution of particular character-state changes. A bootstrap analysis (Felsenstein, 1985) with 1000 replicates was conducted.

Descriptions of leaf venation in this work follow the terminology of Hickey (1973). Seeds were cut with a razor blade both longitudinally and transversely in order to reveal their internal structure. Thin hand-cut sections were taken in the micropylar third and photographed under optical microscopy. Other sections were made with a SLEE-MAINZ-MTC microtome and stained with Fasga mixture (Tolivia & Tolivia, 1987) or with Sudan red and Malachite green. For scanning electron microscopy (SEM), samples were glued to aluminum stubs, coated with 40–50 nm gold, and examined with a JEOL-TSM T330A scanning electron microscope at 20 kV.

Species-distribution maps were based primarily on exsiccatae, though for *G. albanum* literature records were also used.

## Results

### Morphological Characters

*Duration and habit.* Most *Geranium* species are herbaceous perennial plants with horizontal rhizomes; however, some species in subgenera *Robertium* and *Geranium* are annuals. The different annual species in the genus do not resemble one another, and they share characters with different groups of perennials. Consequently, we consider that annual species have probably been derived from perennials several times in the genus. One species of section *Divaricata* is perennial and the other is annual, while section *Batrachioidea* has one perennial and three annual species. *Geranium albanum* (sect. *Divaricata*) has a horizontal rhizome that has been codified, according to the outgroup, as plesiomorphic. *Geranium pyrenaicum* (sect. *Batrachioidea*) is also perennial, but it has a vertical, napiform rhizome. All remaining species from both sections are annuals. We consider that this could be interpreted as a linear transformation series, with horizontal to vertical rhizomes leading to annuals without rhizomes. Among the perennials, a vertical rhizome should arise from a horizontal one, and thus ought to be considered as derived. Finally, in *Geranium* annuals are usually considered derived while perennials are primitive (Yeo, 1984). Moreover, Sanderson (1991) proposed a similar multistate series for *Astragalus* (Fabaceae: Papilionoideae): 0 = perennials with well-developed

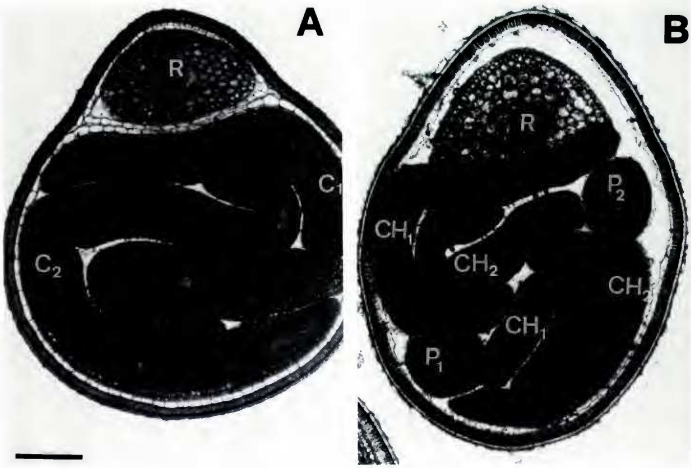


Figure 1. Optical photomicrographs of transverse sections of *Geranium* seeds showing different patterns of cotyledon folding. —A. Seeds of *Geranium pyrenaicum* subsp. *lusitanicum* (*Carreira s.n.* (MA-473325)), section *Batrachioidea*, with conduplicate cotyledons, each lying in the primary fold of the other. —B. Seeds of *G. divaricatum* (*Sánchez Mata s.n.* (MAF-118241)), section *Divaricata*, with the proximal part of cotyledons deeply cordate and cotyledon petioles longer than in section *Batrachioidea*; thus, transverse sections at the micropylar third of the seed show the cotyledons in two parts (the basal auricles of the cotyledons) and their petioles. $C_1$, $C_2$ = cotyledons; $CH_1$ = half of cotyledon $C_1$; $CH_2$ = half of cotyledon $C_2$; $P_1$ = petiole of cotyledon $C_1$; $P_2$ = petiole of cotyledon $C_2$; R = radicle. Scale bar = 300 μm.

rhizomes, 1 = short-lived perennials with poorly developed rhizomes, and 2 = annuals without rhizomes.

The aerial portion of the stem is usually erect in all species of sections *Batrachioidea* and *Divaricata*; however, the annual species of section *Batrachioidea* can also have decumbent stems.

*Cotyledons.* The cotyledons usually have entire margins in *Geranium*, but those of a few species are incised. *Geranium aculeolatum* Oliv., with cotyledons having two notches on each side, is the only species in subgenus *Erodioidea* without entire cotyledons (Yeo, 1990: 13). In subgenus *Geranium*, only *G. bohemicum* L. has cotyledons with a single incision on each side (Dahlgren, 1943: 137 fig. 5). Finally, in subgenus *Robertium*, the two species included in section *Divaricata* have cotyledons with a single incision on each margin. According to the outgroup, in all these cases incised cotyledons are considered as a derived condition.

The cotyledons in *Geranium* are always conduplicate, one half of each cotyledon lying in the primary fold of the opposite cotyledon (Yeo, 1990: 14). Moreover, seeds of section *Batrachioidea* show some differences from those of section *Divaricata*. In section *Divaricata*, the proximal part of the cotyledons is deeply cordate and the cotyledon petioles are longer than in section *Batrachioidea*. Consequently, transverse sections at the micropylar third of seeds of section *Divaricata* showed both the petiole and the cotyledons, the latter divided into two parts (the basal auricles). Conversely, in section *Batrachioidea*, as in most of *Geranium*, the cotyledon base is truncate and the petioles are very short (Fig. 1). These differences were not considered by Tokarski (1972), who showed a similar pattern of simply conduplicate cotyledons in these sections.

*Leaves.* All species in sections *Divaricata* and *Batrachioidea* have more or less deeply palmatifid leaves. Leaf outline is pentagonal in section *Divaricata*, whereas it is usually orbicular to reniform in section *Batrachioidea*. The segments can be rhombic, as in section *Divaricata*, or obdeltate, as in

section *Batrachioidea*. Obdeltate segments seem to be derived, according to the outgroup (Nieto Feliner & Aedo, 1995). The number of lobes per segment varies between 7 and 15 in section *Divaricata*, and between 3 and 12 in section *Batrachioidea*. The lower cauline leaves can be either opposite or alternate in both sections. According to Davis (1970), alternate leaves should be the primitive state in *Geranium*, as well as the outgroup.

*Inflorescence and branching.* The inflorescence in both sections is cymose, composed of axillary, two-flowered cymules. All cymules arise along aerial stems. The most significant inflorescence feature taxonomically is the indumentum of the peduncles and pedicels. Almost all species have two types of hairs. One type comprises patent, eglandular hairs 0.7–1.8 mm long, as in *G. albanum*, *G. divaricatum*, *G. pyrenaicum* subsp. *lusitanicum*, *G. molle*, and *G. aequale*. This type of hair is lacking in *G. pusillum*, and usually also in *G. pyrenaicum* subsp. *pyrenaicum*. The other type of indumentum, composed of glandular or eglandular patent hairs less than 0.5 mm long, is present in all species.

*Sepals.* The mucro of the sepals is very short (less than 0.6 mm) in all species of both sections, except for *G. divaricatum*, in which it is ca. 1 mm long. The last-mentioned species seems to be unusual in this regard, in subgenus *Robertium*, according to Yeo's (1992) description. Long, eglandular sepal hairs are common in most species, but lacking in *G. divaricatum* and *G. pyrenaicum*.

*Petals.* Petals in both sections have emarginate apices, with the notch usually ca. 1 mm deep. *Geranium pyrenaicum* has more deeply emarginate (2–3 mm) petals, while its closest relative, *G. pusillum*, has shallowly emarginate petals (0.2–0.5 mm). The longest are those of the perennial species, *G. albanum* and *G. pyrenaicum*. However, the annual *G. molle* occasionally also has long petals, as discussed under that species. In section *Divaricata*, as in most other *Geranium* taxa, the petals are tapered uniformly toward the base, without any claw; however, in section *Batrachioidea*, a very short claw is evident.

*Stamens and pollen.* In both sections, as in the entire genus, the ten stamens are arranged in two whorls. In *G. pusillum*, the anthers of the external whorl are missing. The filaments are usually hairy on the abaxial side, as in many species of the genus. However, those of *G. molle* and *G. aequale* are glabrous abaxially, which should be interpreted as a derived character state, according to the outgroup. Another character is the presence or absence of cilia along the filament margins. All species studied have ciliate filament margins, except for *G. albanum*.

According to Stafford and Blackmore (1991: 51), pollen of *Geranium divaricatum*, *G. pyrenaicum*, *G. pusillum*, and *G. molle* belongs to the *G. molle* type, which includes most of the *Geranium* species studied by them. This type is characterized by reticulate exine ornamentation with distinctly baculate, clavate, or gemmate supratectal elements. Four groups were recognized by these authors on the basis of secondary variation in exine ornamentation. These groups showed no concordance with subgeneric or sectional classifications. Thus, *G. pusillum* and *G. pyrenaicum* were placed in the *G. robertianum* group, and *G. molle* and *G. divaricatum* in the *G. molle* group.

Blue pollen is the only feature known to be shared by sections *Divaricata* and *Batrachioidea*. The other sections of subgenus *Robertium* have yellow (sects. *Anemonifolia*, *Lucida*, *Polyantha*, *Ruberta*, and *Unguiculata*) or white pollen (sect. *Trilopha*) (Yeo, 1984: 13–17). All species of subgenus *Erodioidea* and most of subgenus *Geranium* have yellow pollen, though in the latter subgenus at least three species (*G. dissectum* L., *G. pratense* L., and *G. richardsonii* Fisch. & Trautv.) have blue pollen. Consequently, blue pollen is viewed most parsimoniously as derived.

*Fruit.* *Geranium* sects. *Divaricata* and *Batrachioidea* belong to subgenus *Robertium*, which exhibits the "carpel-projection-type" of fruit discharge (Yeo 1984). Here, the whole mericarp is actively discharged by the explosive recoiling of the awn, which remains attached to the columella. According to Yeo (1984), this discharge type is presumably derived, the *Erodium*-type discharge being the primitive condition. In section *Divaricata*, decrease in rostrum length reduces the effectiveness of the discharge mechanism. According to the outgroup, this decrease is also viewed as derived. A rostrum that tapers gradually to the remains of the stigmas is the most frequent condition in those Geraniaceae exhibiting the *Erodium*-type discharge (see discussion following the generic description). The alternative condition, a columnar rostrum abruptly narrowed at the apex, as in *G. molle* and *G. aequale*, is probably derived (Nieto Feliner & Aedo, 1995: 203).

The mericarp surface is smooth in all species of section *Batrachioidea* except *G. molle*, which has transversely wrinkled mericarps, as do the two spe-

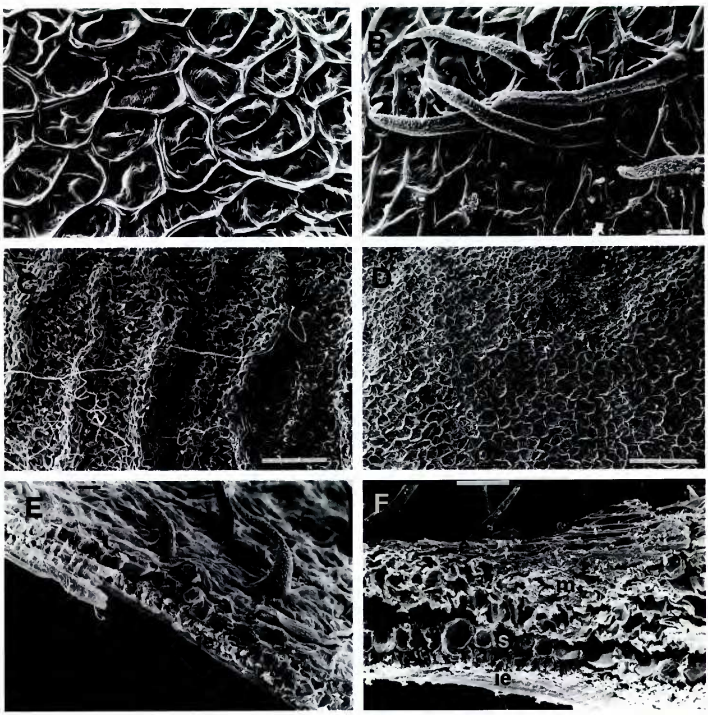


Figure 2. SEM photomicrographs of *Geranium* mericarp. A–D. Surface ornamentation in sect. *Batrachioidea*. —A. *G. pyrenaicum* subsp. *lusitanicum* (*Luceño & Vargas s.n.* (MA-407065)). —B. *G. pyrenaicum* subsp. *pyrenaicum* (*Granzow & Zaballos 365* (MA)). —C. *G. molle* (*López 590* (MA)). —D. *G. aequale* (*Airy Shaw & Nelmes s.n.* (MA-71231)). E, F. Transverse cuts of the mericarp in section *Divaricata*. —E. *G. divaricatum* (*Bernouilli s.n.* (MA-71169)). —F. *G. albanum* (*Aedo 3864* (MA)). e = exocarp, m = mesocarp, s = sclerenchyma region, ie = endocarp. Scale A, B, bar = 10 μm; C, D, bar = 100 μm; E, bar = 10 μm; F, bar = 50 μm.

cies of section *Divaricata*. According to the outgroup, transversely rugose mericarps are here interpreted as the derived condition. In both sections, the mericarps are usually covered by short hairs, but *G. pyrenaicum* exhibits two conditions: subsp. *pyrenaicum* (Fig. 2B) has hairy mericarps, while subsp. *lusitanicum* (Fig. 2A) has glabrous mericarps. The mericarp surface is also virtually glabrous in *G. molle* and *G. aequale* (Fig. 2C, 2D), with only a few cilia along the margins. According to the outgroup, glabrous mericarps are here interpreted as the derived condition.

The mericarp wall in *G. albanum* is wider and has a more well-developed mesocarp than that of the other species studied here. *Geranium divaricatum* and species in section *Batrachioidea* have relatively thin mericarps due to no or limited development of the mesocarp, with at most a single layer of cells. The mericarps of all the studied species had well-developed sclerenchyma regions with crystals (Fig. 2E, 2F). The thicker mericarp of *G. albanum* could be related to a different germination strategy in this perennial species. Several authors have reported a relationship between dormancy and

the permeability of seed testas and fruit walls (Aldasoro et al., 1981; Rangaswamy & Nandakumar, 1985; Bewley & Black, 1994).

*Seeds.* Seeds are more or less elliptical in outline in section *Batrachioidea*, and obovate in section *Divaricata*. The seed-coat in both sections appears smooth at a magnification of 30×, but SEM shows a reticulate surface due to the prominence of the outer and the middle layer of the outer integument. The outer layer has cells with thickened walls and collapsed lumina, forming a polygonal structure. The seed-coat is usually brownish and bears scattered stomata. The cells of the inner part of the outer integument are strongly lignified and contain tannin and crystals. The next layer (the outer layer of the inner integument) is also sclerified, but the cells are not so compacted, being prismatic with undulate anticlinal walls.

In *G. albanum*, a species with thick mericarp, the testa is weaker because the cells of the outer layer of the inner integument are wider (ca. 24 μm), almost cubic, and the lignified walls are more widely separated (8–15 μm) than in the other species here studied. Conversely, *G. aequale*, with seeds only partially covered by the mericarp, has the thickest testa (Fig. 3) in sections *Batrachioidea* and *Divaricata* (ca. 41 μm, vs. 25–30 μm in the other taxa).

### CHROMOSOME NUMBER

The chromosome number of all species in *Geranium* sect. *Batrachioidea* is $2n = 26$ (see Appendix 1). There has been some controversy in the case of *G. pyrenaicum* and *G. pusillum*, but Van Loon's (1984a, b) work has clarified the situation.

All chromosome counts carried out to date for *G. divaricatum* are $2n = 28$. However, for *G. albanum*, Warburg (1938: 145) reported $n = 14$ and Van Loon (1984a: 276) $2n = 20$ (see Appendix 1). Material of both species was unvouchered and collected in botanical gardens. Thus, the chromosome number in section *Divaricata* is probably $2n = 28$, but more counts should be done for *G. albanum*.

According to Van Loon (1984b: 286), the basic chromosome number in *Geranium* is $x = 14$, as in most of the perennial species of the genus. The annual taxa, with various other base numbers, probably evolved independently. In this context, the number $2n = 26$ in section *Batrachioidea* could be seen as a derived character state.

### HYBRIDS

Hybridization experiments in *Geranium* subg. *Robertium* have involved species of sections *Anemonifolia*, *Batrachioidea*, *Lucida*, *Ruberta*, and *Unguiculata* (Van Loon, 1984c; Widler-Kiefer & Yeo, 1987). No data are available for sections *Divaricata*, *Polyantha*, and *Trilopha*.

In section *Batrachioidea*, three hybrids have been described: *G.* ×*oenense* (said to be *G. molle* × *G. pusillum*); *G.* ×*luganense* (said to be *G. molle* × *G. pyrenaicum*); and *G.* ×*hybridum* (said to be *G. pusillum* × *G. pyrenaicum*). According to Van Loon (1984c), intraspecific crosses were usually highly successful in this section, but the only successful interspecific cross was that involving *G. molle* and *G. brutium*. Other crosses (*G. pyrenaicum* × *G. brutium*, *G. pyrenaicum* × *G. molle*) also produced seeds, but the seedlings succumbed at an early stage. Thus, according to Van Loon's data, species of this section seem reproductively isolated.

Having thoroughly studied original material and/or original descriptions, we consider that *G. luganense*, *G. oenense*, and *G. hybridum* are probably not hybrids but synonyms of *G. molle* (the first two) or *G. pusillum*. Considering the difficulty in obtaining interspecific hybrids (Van Loon, 1984c), the only successful cross, involving *G. brutium* and *G. molle*, supports our interpretation of *G. brutium* as a synonym of *G. molle*.

### DISTRIBUTION

*Geranium* subg. *Robertium* is distributed widely in temperate regions from Macaronesia to Japan, and sections *Trilopha* and *Ruberta* reach tropical areas of central and east Africa.

Section *Divaricata* comprises two species, with very different patterns of distribution. *Geranium albanum* is endemic to the Caucasus and northern Iran, whereas *G. divaricatum* is distributed in a wide longitudinal range between Spain and the central Himalayas. At present, neither species has been reported as introduced in other areas of the world.

The four species of *Geranium* sect. *Batrachioidea* are centered in Eurasia, between Macaronesia and the Himalayas, though all but *G. aequale* reach north Africa. They are spreading rapidly in temperate areas of North and South America, southern Africa, Australia, and Japan, where representatives of subgenus *Geranium* mainly grow. This process of colonization predominantly involves the three annual species, which occur in perturbed habitats, but also *G. pyrenaicum*.

### PHYLOGENETIC RELATIONSHIPS

A cladistic analysis of *Geranium* sects. *Divaricata* and *Batrachioidea* was carried out using a data

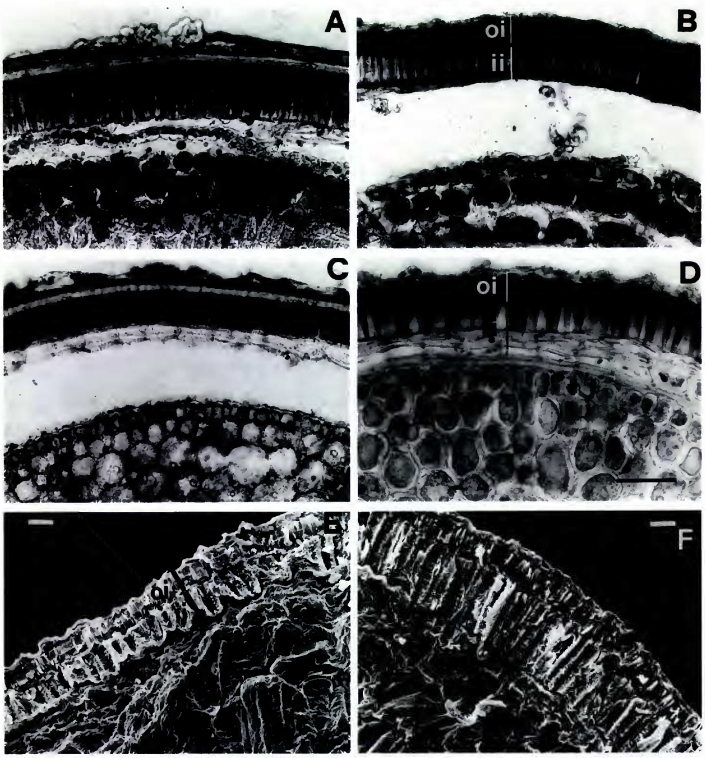


Figure 3. Optical (A–D) and SEM (E, F) photomicrographs of *Geranium* seed sections, showing the testa with the outer part of the inner integument more developed in *G. aequale* (ca. 41 μm) than the other species (25–30 μm). However, the testa cells are wider in *G. albanum* (ca. 24 μm) than in the other species (8–15 μm). —A, F. *G. aequale* (*Airy Shaw & Nelmes s.n.* (MA-71231)). —B. *G. pusillum* (*Navarro et al. 792* (MA)). —C. *G. divaricatum* (*Sánchez Mata s.n.* (MAF-118241)). —D, E. *G. albanum* (*Aedo 3864* (MA)). oi = outer integument; ii = inner integument. Scale A–D, bar = 50 μm; E, F, bar = 10 μm.

set of 15 characters (Tables 1 and 2). The species used as outgroup was *G. sylvaticum* L. This decision is supported by the results of an *rbc*L-sequence data analysis, which places the clade composed of subgenus *Erodioidea* and subgenus *Geranium* as sister to subgenus *Robertium* (Price & Palmer, 1993). We have selected *G. sylvaticum*, a member of subgenus *Geranium*, since in this species many characters of the in-group are applicable. Species of subgenus *Erodioidea* have quite different fruits, and many of the codified characters (characters 10, 11, and 12) are inapplicable (Nieto Feliner & Aedo, 1995). One most-parsimonious cladogram was obtained, with length 20, consistency index (C.I.) 80, and retention index (R.I.) 81 (Fig. 4).

Two well-supported clades were obtained in the cladogram, corresponding with sections *Divaricata* and *Batrachioidea*. In section *Divaricata*, mono-

Table 1. Data matrix used in the cladistic analysis of *Geranium* sects. *Batrachioidea* and *Divaricata* (subg. *Robertium*). Polymorphic, inapplicable, or missing data are coded as '?.' Characters 1–15 are in Table 2.

| | Acronym | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 1 0 | 1 1 | 1 2 | 1 3 | 1 4 | 1 5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *G. sylvaticum* | SYL | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 |
| *G. aequale* | AEQ | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| *G. molle* | MOL | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| *G. pusillum* | PUS | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *G. pyrenaicum* subsp. *pyrenaicum* | PYR | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| *G. pyrenaicum* subsp. *lusitanicum* | LUS | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| *G. albanum* | ALB | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 0 | ? | 0 | 1 | ? |
| *G. divaricatum* | DIV | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | 0 | 0 | 0 | 1 | 0 |

phyly is supported by three synapomorphies: (a) the incised margins of the cotyledons (character 2, see Table 2); (b) the inoperative fruit-discharge mechanism (character 9); and (c) the obovate outline of the seeds (character 14). As previously described, this clade is also upheld by seedling structure. In section *Batrachioidea*, monophyly is also supported by three synapomorphies: (a) the obdeltate leaf segments (character 4); (b) the presence of a petal claw (character 5); and (c) the chromosome number $2n = 26$ (character 15).

*Geranium molle* and *G. aequale* constitute a

Table 2. Characters and character states used for cladistic analysis of *Geranium* sects. *Batrachioidea* and *Divaricata* (subg. *Robertium*).

| Characters | Character states |
|---|---|
| 1. Habit | 0 = perennial with well-developed horizontal rhizome |
| | 1 = perennial with poorly developed vertical rhizome |
| | 2 = annual, without rhizome |
| 2. Cotyledon margins | 0 = entire |
| | 1 = incised |
| 3. Basal cauline leaves | 0 = alternate |
| | 1 = opposite |
| 4. Shape of leaf segments | 0 = rhombic |
| | 1 = obdeltate |
| 5. Petal claw | 0 = absent |
| | 1 = present |
| 6. Stamen pubescence on abaxial side | 0 = hairy |
| | 1 = glabrous |
| 7. Pollen color | 0 = yellow |
| | 1 = blue |
| 8. Fruit discharge type | 0 = seed-ejection-type |
| | 1 = carpel-protection-type |
| 9. Fruit discharge mechanism | 0 = operative |
| | 1 = inoperative |
| 10. Fruit rostrum | 0 = tapering gradually |
| | 1 = narrowed abruptly |
| 11. Mericarp surface | 0 = smooth |
| | 1 = transversely wrinkled |
| 12. Mericarp with longitudinal rib | 0 = absent |
| | 1 = present |
| 13. Mericarp indument | 0 = hairy |
| | 1 = glabrous |
| 14. Seed shape | 0 = elliptical |
| | 1 = obovate |
| 15. Chromosome number | 0 = $2n = 28$ |
| | 1 = $2n = 26$ |

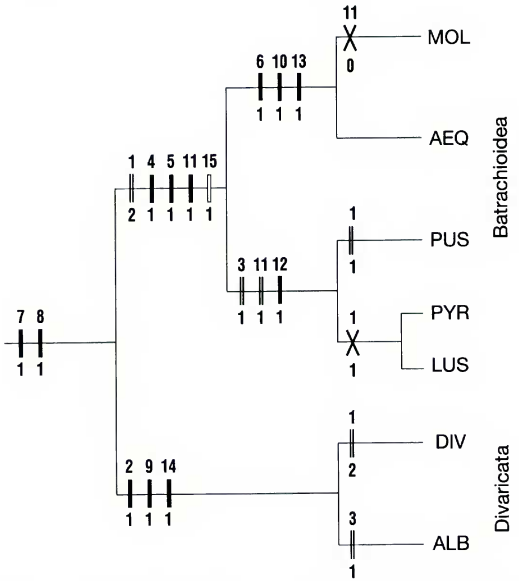


Figure 4. The most-parsimonious cladogram of *Geranium* sects. *Divaricata* and *Batrachioidea*. Solid bars are synapomorphies, open bars are synapomorphies that reverse elsewhere in the cladogram, double bars are parallelisms, and crosses are reversals (length 20, C.I. = 80, R.I. = 81). See Table 1 for acronyms.

clade within section *Batrachioidea* supported by two synapomorphies (characters 6 and 10). The clade comprising *G. pyrenaicum* subsp. *pyrenaicum*, *G. pyrenaicum* subsp. *lusitanicum*, and *G. pusillum* is supported by one synapomorphy (character 12). In this clade, *G. pusillum* appears as sister to the other two taxa.

Monophyly of a group composed of sections *Divaricata* and *Batrachioidea* is supported by only one character, pollen color. In the previously mentioned tree, character 8 (fruit-discharge type) is actually irrelevant, because it is shared by all sections in the subgenus. However, in this study it was used to support the in-group. The emarginate petal apices also seem to support monophyly of this group, but we lack sufficient data to preclude their existence in the other sections. In contrast, blue pollen seems to be a derived feature useful at this level of analysis. No other evidence was obtained about the relationships between the two sections. A comprehensive study of subgenus *Robertium* could be expected to provide more information on this matter.

## Taxonomic Treatment

**Geranium** L., Sp. Pl. 1: 676. 1753. TYPE: *Geranium sylvaticum* L. (lectotype, designated by Hanks & Small, 1907: 4).

Annual, biennial, or perennial herbs, rarely shrubs. Leaves simple, usually palmately divided, sometimes entire or pinnately lobed, stipulate, petiolate; basal leaves usually forming a rosette; cauline leaves opposite or alternate. Inflorescence terminal or axillary, cymose, bracteate. Flowers usually paired, actinomorphic, rarely somewhat zygomorphic. Sepals 5, imbricate, obtuse to caudate at apex. Petals 5, free, frequently emarginate at apex, sometimes clawed. Stamens 10, in two whorls, the outer one opposite to and the inner one alternating with the petals, all bearing anthers or, very rarely, 5 with staminodes; filaments broad, free

or united at the base. Nectaries 5, alternating with the petals. Ovary 5-locular, with 2 superposed ovules per locule, the style distinctly 5-fid. Fruit a schizocarp, long-beaked, splitting into five 1-seeded mericarps. Seed without or with very little endosperm; embryo with massive induplicate or convoluted cotydelons.

*Geranium* is divided into three subgenera, distinguished by their fruit-discharge mechanisms (Yeo, 1984). The "seed-ejection-type," which characterizes subgenus *Geranium*, involves a single seed actively discharged by the explosive recoiling of the awn, which remains attached to the columella together with the mericarp. A second type of discharge, the "carpel-projection-type," characterizes subgenus *Robertium*. Here, the explosive recurvature of the awn also acts as the propelling force, but in this case the whole mericarp, containing the seed, is dispersed, whereas the awn remains with the columella. Subgenus *Erodioidea* is identified by the "*Erodium*-type" of fruit discharge, in which the mericarp, including the coiled awn, is propelled over a short distance.

**Geranium** subg. **Robertium** (Picard) Rouy, in Rouy & Foucaud., Fl. France 4: 94. 1897. *Robertium* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 134. 1837. TYPE: *Geranium robertianum* (Greuter et al., 1994, Art. 22.5).

Annual, biennial, or perennial herbs. Leaves palmately divided to the base or more shallowly divided; cauline leaves opposite or alternate. Flowers usually actinomorphic, rarely somewhat zygomorphic. Sepals erect or patent, sometimes longitudinally carinate. Petals rounded or emarginate at apex, ± unguiculate; claw ecarinate or carinate. Stamens exserted or not; filaments glabrous to pilose; pollen yellow, blue, or white. Fruit discharge by carpel projection, each mericarp thrown off explosively with the seed in it and the awn dropping away at the moment of explosion (discharge mechanism sometimes inoperative); mericarps acute or obtuse, smooth, reticulate, ribbed or cristate. Cotyledons entire or laterally incised.

KEY TO THE SECTIONS OF *GERANIUM* subg. *ROBERTIUM*

1a. Leaves divided to the base.
  2a. Glandular hairs of the inflorescence purple; more than half the length of the stamens exserted from throat of flower ..... *Geranium* sect. *Anemonifolia*
  2b. Glandular hairs of the inflorescence with colorless stalks and red heads; less than half the length of the stamens exserted from throat of flower ..... *Geranium* sect. *Ruberta*
1b. Leaves shallowly divided.
  3a. Fruit discharge mechanism inoperative ..... *Geranium* sect. *Divaricata*
  3b. Fruit discharge mechanism operative.
    4a. Pollen blue ..... *Geranium* sect. *Batrachioidea*
    4b. Pollen yellow, sometimes white.
      5a. Calyx longitudinally carinate ..... *Geranium* sect. *Lucida*
      5b. Calyx not carinate.
        6a. Mericarp apex obtuse; stamens exserted ..... *Geranium* sect. *Unguiculata*
        6b. Mericarp apex acute; stamens not exserted.
          7a. Plants perennial ..... *Geranium* sect. *Polyantha*
          7b. Plants annual ..... *Geranium* sect. *Trilopha*

**Geranium** sect. **Batrachioidea** W. D. J. Koch ["Batrachioides"], Syn. Fl. Germ. Helv. Ed. 1 139. 1835. *Geranium* sect. *Pyrenaica* R. Knuth, in Engl., Pflanzenr. IV.129 (Heft 53): 46, 152. 1912, nom. illeg. TYPE: *Geranium pyrenaicum* Burm. f. (designated by Yeo, 1984: 15; see Aedo & Muñoz Garmendia, 1996: 104).

Perennial or annual herbs; stems to 110 cm long, with simple or bifurcate monopodial branching, leafy, erect, decumbent or ascending, with patent eglandular and glandular hairs. Basal leaves in persistent rosettes; venation actinodromous, basal, perfect, marginal; lamina orbicular or reniform in outline, palmatifid, concolorous, hairy; segments 5–9, obdeltate, 3–12-lobed at apex; lower cauline leaves alternate or opposite; stipules lanceolate to ovate, papery, brown, pilose. Cymules solitary, arising from aerial stems; bracts lanceolate, sometimes lobed, papery, brown; peduncles present, with patent eglandular and glandular hairs; bracteoles linear to lanceolate, papery, brown; pedicels 2 per cymule, ± ascending and often curved upward after anthesis, subequal, with patent glandular or eglandular hairs; peduncle and pedicel together very often exceeding the subtending leaf. Sepals ovate, erect-patent at anthesis and erect in fruit, briefly mucronulate, marginally scarious; abaxial surface with eglandular or glandular hairs; adaxial surface glabrous, with a subapical tuft of hairs. Petals erect-patent, ± obovate, emarginate, with a very short claw, without nectar passages, ciliate at base, with sessile glands on the adaxial surface, ± purple, without a dark basal spot. Stamens 10, both whorls bearing anthers or the inner one without anthers; filaments lanceolate, expanded at base, persistent in fruit, with a conspicuous midvein, ± ciliate, usually pilose on abaxial surface, yellow with pink apex; pollen blue. Nectaries hemispherical,

glabrous. Stigmas purple. Fruit of the carpel-projection-type, with discharge mechanism operative; mericarps smooth or transversely wrinkled, sometimes with a longitudinal dorsal rib but never cristate, usually covering the seed completely, without a basal beak and without a callus, glabrous or hairy; rostrum not reduced, narrowed apically or not; stigmatic remains with 5 pilose lobes. Seeds ellipsoidal, smooth, brownish or reddish, the hilum ⅕–⅙ as long as the perimeter. Cotyledons entire. Chromosome number: $n = 13$, $2n = 26$.

*Distribution.* Africa and Macaronesia, Europe to central Asia and the Indian subcontinent, Australia, North America, southern South America, subantarctic and north-central Pacific Islands.

The three most distinctive character states for *Geranium* sect. *Batrachioidea* are its obdeltate leaf segments, short petal claws, and chromosome number of $2n = 26$. The chromosome number is especially relevant as a derived character, as it has not been found in any other section of subgenus *Robertium*.

KEY TO THE SPECIES OF *GERANIUM* sect. *BATRACHIOIDEA*

1a. Stamens 10, the external whorl without anthers ..... 3. *G. pusillum*

1b. Stamens 10, both whorls bearing anthers.

2a. Mericarps rugose ..... 2. *G. molle*

2b. Mericarps smooth.

3a. Plants annual; petals 3.5–4.5 mm long ..... 1. *G. aequale*

3b. Plants perennial; petals 7–11 mm long ..... 4. *G. pyrenaicum*

**1. Geranium aequale** (Bab.) Aedo, Anales Jard. Bot. Madrid 55: 466. 1997. *Geranium molle* var. *aequale* Bab., Man. Brit. Bot. Ed. 2: 65. 1847. TYPE: United Kingdom. England: near Leamington [52°15′N, 1°29′W], *J. J. Murcott s.n.* (lectotype, designated by Carolin (1965), CGE not seen).

*Geranium molle* f. *preuschoffii* Abrom., Fl. Ost- & Westpreussen 156. 1898. TYPE: Germany. "Westpreussen, Magdebug, Pfarrgarten in Tannsee," [51°43′N, 10°43′E], *Abromeit s.n.* (no authentic material located; synonymy according to Yeo, 1984).

Annual herb to 40 cm tall; stem erect or decumbent, usually branched from the base, pilose, with long eglandular hairs 1–1.2 mm long and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a persistent rosette; lamina 1.5–3 (–5) × 1.5–3.7(–5.8) cm, divided for 0.6–0.75 of its length, pilose, with eglandular, appressed hairs; segments 7–9, 2–4 mm wide at the base, 3(–5)-lobed at apex; lower cauline leaves alternate; petioles to 14 cm long, with patent, long eglandular hairs ca. 1 mm long and short glandular and eglandular hairs < 0.5 mm long; stipules 6–7 × 3–4 mm, ovate-lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 2–4 × 1.5–2 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 1–7 cm long, pilose, with eglandular patent hairs 1–1.7 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 1.5–3 × 1–1.5 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–2.2 cm long, pilose, with eglandular, patent hairs 1–1.8 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals 3–5 × 1.5–2 mm, mucronulate (with mucro 0.1–0.2 mm long), with scarious margins 0.1 mm wide, with eglandular hairs 1–2 mm long and some shorter (< 0.5 mm) eglandular and glandular ones on the abaxial side, glabrous on the adaxial side. Petals 3.5–4.5 × 2–3 mm, emarginate (with notch 1 mm deep), with short claw, bright purple. Stamens 10, both whorls bearing anthers; filaments 3–4.5 mm long, lanceolate, glabrous except for a few ciliae on the proximal half; anthers 0.4–0.6 × 0.2–0.3 mm, purple. Gynoecium ca. 5 mm long; stigma purple. Fruit 9–12 mm long; mericarps 1.4–1.5 × 1–1.1 mm, smooth, without longitudinal rib, not covering the seed completely, glabrous on most of the surface, densely ciliate at the base; rostrum 7–10.5 mm long, with a narrowed apex 1–1.5 mm, pilose (with erect-patent eglandular hairs 0.1–0.3 mm long); stigmatic remains ca. 1–2 mm long, with 5 hairy lobes. Seeds 1.6–1.7 × 0.9–1 mm, brownish, the hilum ⅕–⅙ as long as the perimeter. Chromosome number: $2n = 26$. Figure 5.

*Distribution* (Fig. 6). Northern, middle, and southwestern Europe; introduced in the northeastern United States and New Zealand (North I.); cultivated fields and dry places near villages, between 0 and 200 m.

*Phenology.* Flowering May–August.

*Representative specimens examined.* NEW ZEALAND. North I., Colenso, 39°44′S, 17°4′E, 1821, *Anonymous s.n.* (K). BELGIUM. Liège, Rocherath, vallée du Tröglichtenbach, 560 m, 50°26′N, 6°18′E, *Fabri 857* (BR); Semois, 49°53′N, 4°45′E, *Vinck 422* (BR); pr. Tintomoje, route Tintomoje-Rome[?]ohomoje, 50°51′N, 5°28′E, *Wilezek 1127* (K). DENMARK. Fu[?]termglatte, 1938, *Marsen s.n.* (C). GERMANY. SW of Saxony, 51°20′N, 12°25′E, Aug. 1882, *Anonymous s.n.* (K); Samensammlung des Hamburgischen Staatsinstituts für angewandte Botanik, 53°33′N, 10°0′E, *Bredemann & Nieser 50* (K). UNITED KINGDOM. **England:** Little Sark, Channel Islands, 49°26′N,

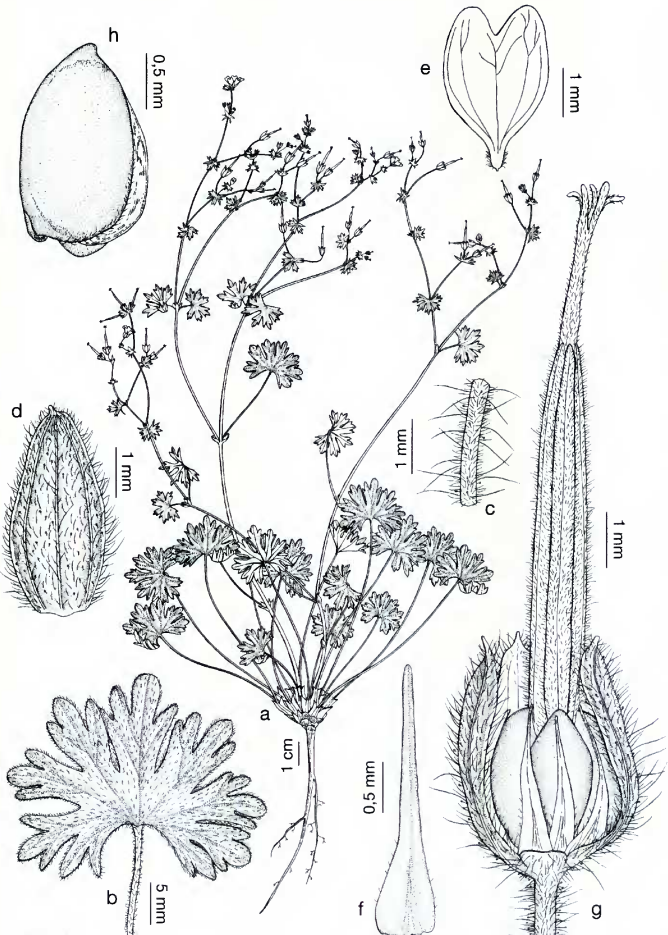


Figure 5. *Geranium aequale*. —a. Habit. —b. Leaf. —c. Peduncle. —d. Sepal. —e. Petal. —f. Stamen. —g. Fruit and sepals. —h. Mericarp. (Based on *Airy Shaw & Nelmes s.n.* (MA-71231).)

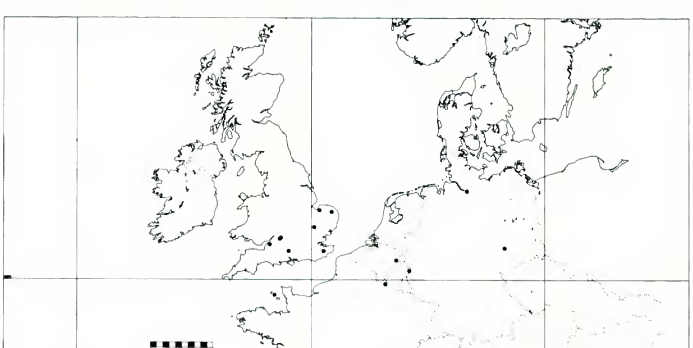


Figure 6. Natural distribution of *Geranium aequale*, based on herbarium records (also introduced in northeastern U.S.A. and New Zealand).

2°22′W, *Ballard & Gollon 228* (K); Andover, Hampshire, *Clarke 46129* (K); Norfolk, Buxton, 52°45′N, 1°18′E, 1847, *Mann s.n.* (K); W Gloucester, 34, Tarlton, Coates, m. Cirencester, 100 m, *Airy Shaw & Nelmes 45* (K, MA); W Gloucester, 34, Avonmounth Docks, 51°29′N, 2°41′W, 20 May 1933, *Sandwith s.n.* (K); West Norfolk, Appleton, 52°49′N, 0°31′W, *Hubbard 9243* (K).

U.S.A. **Massachusetts**: Wellesley, 27 May 1[?]48, *Cummings s.n.* (NY). **New Jersey**: Tom's River, 3 July 1916, *Wilson s.n.* (NY); Morris Co., above Sterlington, *Mackenzie 1261* (NY). **New York**: Long Island, Hewlett, *Bicknell 5377* (NY); Tompkins Co., lawn of East Roberts Hall, *Burnham 16985* (MO); Monroe Co., Sweden, Brockport, *Hammond 8256c* (NY). **Pennsylvania**: Lancaster, July 1894, *Bitner s.n.* (NY); Philadelphia, *Williamson s.n.* (NY); Delaware River, N of Easton, Lancaster, 4 July 1890, *Small s.n.* (NY).

*Geranium aequale* is close to *G. molle*, from which it is easily distinguished by its smooth, densely ciliate mericarps (those in *G. molle* are transversely wrinkled and sparsely ciliate at the base). Moreover, the mericarps of *G. aequale* do not cover the seed completely, as in *G. molle*. The seeds of *G. aequale* have a thick testa, which may compensate for the slight protection provided by the mericarp. We were not able to find any intermediates between *G. aequale* and *G. molle*.

*Geranium* subg. *Robertium* exhibits several different patterns of mericarp ornamentation, which are useful to differentiate the species. Thus, the absence of such ornamentation should also be of relevance. Consequently, we have decided to recognize *G. aequale* as specifically distinct from *G. molle*. *Geranium aequale* cannot be considered a variation included within the geographic range of *G. molle*, because it has a very different and smaller distribution area.

**2. Geranium molle** L., Sp. Pl. 682. 1753. TYPE: tab. 15 fig. 3–3a in Vaill., Bot. Paris. 1727 (lectotype, designated by Carolin, 1965: 332–333).

*Geranium villosum* Ten., Fl. Napol. 1: LXI. 1811–1815, nom. illeg., non Mill. (1768). *Geranium pyrenaicum* subsp. *villosum* (Ten.) Nyman, Consp. Fl. Eur. 138. 1878. *Geranium molle* subsp. *villosum* (Ten.) A. Terracc., Malpighia 4: 202. 1890. *Geranium molle* var. *villosum* (Ten.) Cout., Fl. Portugal Ed. 1: 371. 1913. TYPE: Italy. Pollino, *Tenore s.n.* (lectotype, here designated, NAP, the right-hand specimen; photocopy!).

*Geranium molle* var. *parvulum* Ten., Syll. Pl. Fl. Neapol. 334. 1831. *Geranium molle* [c] *parvulum* (Ten.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Calabria: Monteleone," *Tenore s.n.* (lectotype, here designated, NAP, the upper right specimen; photocopy!).

*Geranium villosum* var. *villosissimum* Ten., Syll. Pl. Fl. Neapol. 334. 1831. *Geranium molle* var. *arenarium* A. Terracc., Malpighia 4: 202. 1890, nom. illeg. TYPE: Italy. Monteleone, *Tenore s.n.* (lectotype, here designated, NAP, the middle specimen; photocopy!).

*Geranium molle* var. *album* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 129. 1837. *Geranium molle* [1] *album* (Picard) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: France. "Manchecourt, etc." (no authentic material located; synonymy according to Knuth, 1912).

*Geranium abortivum* De Not. ex Ces., Bibliot. Ital. Giorn. Lett. 91: 349. 1838. *Geranium molle* var. *abortivum* (De Not. ex Ces.) Nyman, Consp. Fl. Eur. 138. 1878.

TYPE: Italy. Prope Terranova in Sicilia, 1832, *Balsamo s.n.* (lectotype, here designated, RO!).

*Geranium brutium* Gasp., Rendiconto Accad. Sci. Soc. Borbon. Napoli 1: 49. 1842. *Geranium molle* var. *brutium* (Gasp.) K. Malý, Verh. K.K. Zool.-Bot. Ges. Wien 54: 229. 1904. *Geranium molle* subsp. *brutium* (Gasp.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 53. 1913. TYPE: Italy. Calabriae, *Gasparrini s.n.* (lectotype, here designated, BM!).

*Geranium leiocaulon* Ledeb., Fl. Ross. 1: 470. 1842. *Geranium molle* [b] *leiocaulon* (Ledeb.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Azerbaijan. Lenkoran, *Hansen s.n.* (lectotype, here designated, H!).

*Geranium stipulare* Kunze, Flora 29: 698. 1846. *Geranium molle* var. *grandiflorum* Lange, in Willk. & Lange, Prodr. Fl. Hispan. 3: 528. 1878, nom. illeg., non Viv. (1824). *Geranium molle* var. *stipulare* (Kunze) Nyman, Consp. Fl. Eur. 138. 1878. *Geranium molle* f. *stipulare* (Kunze) K. Malý, Verh. K.K. Zool.-Bot. Ges. Wien 54: 229. 1904. *Geranium molle* [B] *stipulare* (Kunze) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. *Geranium molle* subsp. *stipulare* (Kunze) Holmboe, Bergens Mus. Årbok 13: [6]. 1907. TYPE: Spain. In arenosis isthmi Gaditani copiose, *Kunze 537* (lectotype, here designated, K!; isolectotypes, BM!, W!).

*Geranium molle* var. *macropetalum* Boiss., Fl. Orient. 1: 882. 1867. *Geranium macropetalum* (Boiss.) Posp., Fl. Oesterr. Küstenl. 2: 30. 1898. *Geranium molle* subvar. *macropetalum* (Boiss.) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1703. 1924. TYPE: Greece. Prope Mazeïca, Arcadia, *Heldreich 3404* (lectotype, here designated, G!).

*Geranium molle* var. *annuum* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1877. *Geranium molle* f. *annuum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1702. 1924. *Geranium molle* [I] *annuum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Austria. "Auf Rasenplätzen im Augarten, Oktober, November 1872," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium molle* var. *subperenne* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1877. *Geranium molle* [II] *subperenne* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. *Geranium molle* f. *subperenne* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1702. 1924. TYPE: Czech Republic. "Bei Brünn die gewöhnliche Form, Mai–Juni," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium oenense* Borbás ex Hallier, in W. D. J. Koch, Syn. Deut. Schweiz. Fl. Ed. 3, 1: 454. 1891. TYPE: Austria. Innsbruck, Hall, 1890, *Murr s.n.* (lectotype, here designated, W!, the left-hand flowering specimen; isolectotypes, K!, W!).

*Geranium molle* var. *caespitosum* N. Terracc., Nuov. Giorn. Bot. Ital. n.s., 14: 138. 1907. *Geranium molle* [b] *caespitosum* (N. Terracc.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Pisterola," *N. Terracciano s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium molle* subsp. *sinjaricum* Al-Shehbaz & Al-Khakani, Candollea 38: 353. 1983. TYPE: Iraq. Sinjar Mt., Gulley of Dair Aasy, *Al-Shehbaz, Al-Mayah & Sharifi s.n.* (holotype, BUH-30568 not seen).

Annual herb to 45 cm tall; stem erect or decumbent, usually branched from the base, pilose, with long eglandular hairs 1–1.7 mm long and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a persistent rosette; lamina 0.9–4 × 0.9–5.2 cm, divided for 0.5–0.75 of its length, pilose, with eglandular appressed hairs; segments 7–9, 1.5–5 mm wide at the base, usually 3(–4)-lobed at apex; lower cauline leaves alternate; petioles to 14 cm long, with patent, long eglandular hairs 1–1.5 mm long and short glandular and eglandular hairs < 0.5 mm long; stipules 6–9 × 1.5–4 mm, ovate-lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 2–3 × 1.3–1.5 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 0.5–8 cm long, pilose, with eglandular patent hairs 1–1.8 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 1–2 × 0.5–1.2 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 0.5–1.5 cm long, pilose, with eglandular patent hairs 1–1.8 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals (1–)2.5–5.5(–6) × (0.9–)1.2–2.1(–2.5) mm, mucronulate (with mucro 0.1–0.2 mm long), with scarious margins 0.1–0.2 mm wide, with eglandular hairs 1–1.5 mm long and some shorter (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals (3–)4.5–8.5 (–10.5) × (1.5–)2–5(–7) mm, emarginate (with notch 1–2.5 mm deep), with short claw, bright purple. Stamens 10, both whorls bearing anthers; filaments 4–5 mm long, lanceolate, glabrous except for few cilia on the proximal half; anthers 0.7–1.5 × 0.3–0.5 mm, purple. Gynoecium 5–6 mm long; stigma purple. Fruit 8–14 mm long; mericarps 1.8–2.1 × 1.2–1.4 mm, transversely wrinkled, without longitudinal rib, covering the seed completely, glabrous on the surface, with a few ciliae at the base; rostrum 6–11 mm long, with a narrowed apex 1–3 mm, pilose (with erect-patent eglandular hairs ca. 0.3 mm long); stigmatic remains ca. 1–2 mm long, with 5 pilose lobes. Seeds 1.4–1.8 × 1–1.2 mm, brownish, the hilum 1/6 as long as the perimeter. Chromosome number: $n = 13$; $2n = 26$. Figure 7. *Additional illustrations.* Cavanilles (1787: tab. 83 fig. 3); Reichenbach (1841–1842: tab. 191); Ross-Craig (1952: pl. 34); Tokarski (1972: 66, pl. 22).

*Distribution* (Fig. 8). Africa and Macaronesia, Australia, New Zealand, Europe; to western Asia and to the Indian subcontinent, North America, South America, subantarctic and north-central Pa-

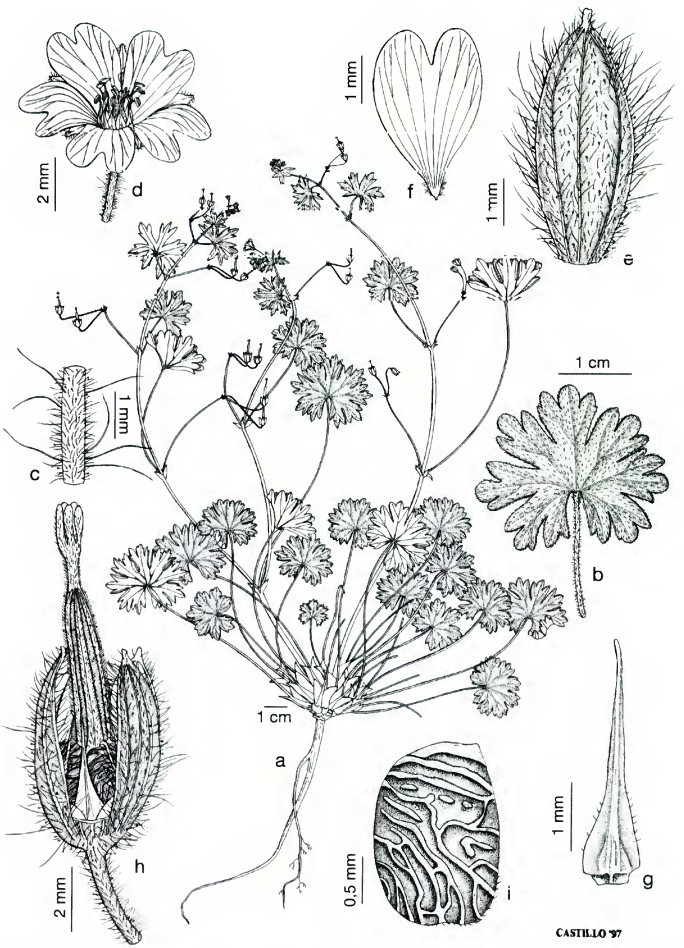


Figure 7. *Geranium molle*. —a. Habit. —b. Leaf. —c. Peduncle. —d. Flower. —e. Sepal. —f. Petal. —g. Stamen. —h. Fruit and sepals. —i. Mericarp. (Based on *Rigual s.n.* (MA-371877).)

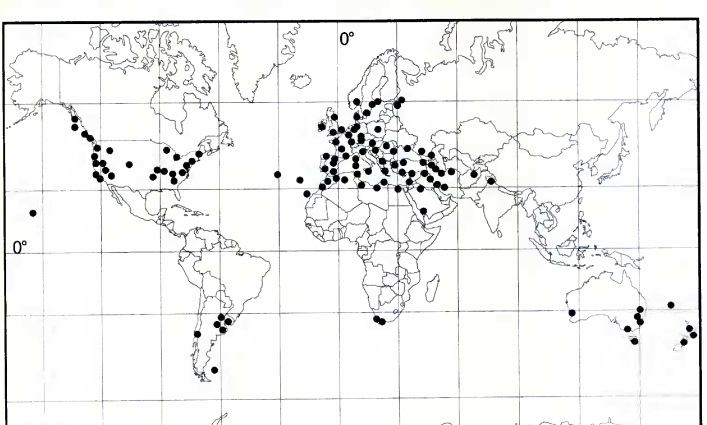


Figure 8. Distribution of *Geranium molle*, based on herbarium records.

cific Islands; also reported from Japan (Knuth, 1912: 58); cultivated and waste places, open habitats, dunes, dry grassland, or roadsides, between 0 and 1400 m. *Additional maps.* Meusel et al. (1978: 263); Hultén & Fries (1986: 635, map 1269).

*Phenology.* Flowering February–August (October–January in Southern Hemisphere).

*Representative specimens examined.* ALGERIA. Arrew, *Munby s.n.* (K); Cherchell, 36°36′N, 2°12′E, 8 Mar. 1962, *Charpin s.n.* (G). EGYPT. Quarry Bourg el Arab, *Simpson 3277* (K); Gedeirat, East Sinai, Mar. 1950, *Meinertzhagen s.n.* (BM). LIBYA. Bughailan, *Guichard 317* (BM). MOROCCO. 2 km SW of El Jadida, roadside by coast, 10 m, *Lambert 47A* (BM). SOUTH AFRICA. Cape Peninsula, *Salter 6855* (K). TUNISIA. Ain Sebaa to Jebbara beach, E of Tabarka, *Davis 57759* (BM).

AUSTRALIA. Lord Howe I., 0.4 km N of Pine Trees, 10 m, *Johnson & Rodd 1210* (K). **New South Wales:** 6.5 mi. E of Scone towards Moonan Flat, 150 m, *Coveny 2384* (K). **Queensland:** Ballandean, from property of F. W. Coll, Darling Downs district, 19 Oct. 1956, *Clark s.n.* (K). **Tasmania:** embankment of R. Mersey, Devonport, 28 Oct. 1943, *Curtis s.n.* (K). **Victoria:** Port Lonsdale, *Jones 18* (K). **Western Australia:** Perth, *Howard 324* (K); Subiaco, *Morrison 19095* (K). NEW ZEALAND. North I., Mypres Bush, 1861, *Lindsay s.n.* (K); South I., Christchurch, 43°3′S, 172°3′E, *Healy 71/300* (AK).

AFGHANISTAN. "Afghanistan," 20 Apr. 1915, *Anonymous s.n.* (K). ALBANIA. Bertiscus, Alpes boreales albanicae, in monte Lumbardska Planina, pr. Pec, 700 m, *Rechinger f. & Scheffer 624* (K). AUSTRIA. Tyrol sept., Innsbruck, *Kerner s.n.* (K). BELGIUM. Alleur, 50°41′N, 5°30′E, 20 June 1895, *Polchet s.n.* (BR). CYPRUS. Agios Philon, nr. Rizohanpzo, *Davis 2209* (K). CZECH REPUBLIC. Doksy, Bohemia bor., 270 m, 5 July 1980, *Hadinec et al. s.n.* (G). DENMARK. Brabrand W of Aarhus, 22 May 1968, *Nielsen s.n.* (MA-204309). FINLAND. Alandia, Lemland, in insula Slätholm, 9 June 1907, *Florström s.n.* (K). FRANCE. Corcega, Aitony valley, near Evisa, 21 Apr. 1928, *Edwards s.n.* (BM); Andresselles, Pas de Calais, *Coutrez 3816* (MA). GEORGIA. Abchasia, Suchumi, *Markovicz 2942* (G). GERMANY. Bad.-Württ., Mindelsee, Unterberger am See, 6 May 1980, *Anonymous s.n.* (B). GREECE. Cholomondos mountains, Chalchidiki peninsula, 5 May 1931, *Chick 29a* (K); Corfu, Feb. 1862, *Mill s.n.* (K). INDIA. Chamba, 32°N, 76°E, *Clarke 23581* (K). IRAN. 15 km from Masiri to Basht, 700 m, *Davis & Bokhari 55856* (K). ISRAEL. Ghor, 4 km S Dair Alla, Al-Masri Triangular, *Al-Eisawi 1724* (BM). ITALY. Calabria, Reggio, supra Bagnara, 1000 m, 29 Apr. 1920, *Anonymous s.n.* (K); Sardinia, Lido San Giovanni, along the coastal road from Alghero to Fertillia, *Dunford 22* (BM); Sicilia, Palermo, *Todaro 1122* (K). LEBANON. Beirout, *Post s.n.* (K). NETHERLANDS. Friescheveen, *Bloemberger 1391* (L). NORWAY. Tisler, en af Slvolöerne, 25 May 1865, *Collet s.n.* (K). POLAND. Varsoviae, *Fuckel s.n.* (BM). PORTUGAL. Matosinhos, Esposade, 13 Mar. 1977, *Alexandre & Serra s.n.* (MA-484473); Madeira, S. Seb. up the valley, *Lowe 139* (K); Azores, Fayal, 1865, *Godman s.n.* (K). ROMANIA. Dobrogea, N von Costinesti, am Bahndamm, 30 m, 14 May 1976, *Krendl s.n.* (BM). RUSSIA. North Caucasus, Dagestan, Tarkitan u Machackaln, 42°53′N, 47°33′E, *Kuvaev 1–7* (LE); Russia Northwest: Lublinskoj gub., 60°19′N, 29°55′E, 18 May 1907, *Ganesin s.n.* (W). SAUDI ARABIA. Jabal Aja nr. Hail off the

Jaharah road, *Collenette 8585* (K). SPAIN. Mon, San Martín de Oscos, 570 m, 29TPH6993, *Aedo et al. A226* (MA); Baleares, Alcudia, 1899, *Gandoger s.n.* (W); Canary Is., Canaria, San Matheo, Apr. 1846, *Bourgeau s.n.* (K). SWEDEN. Smolandia, 57°0′N, 15°0′E, *N. J. Andersson s.n.* (MA-99920). SWITZERLAND. Lausanne, Aug. 1879, *Favrat & Barbey s.n.* (K). TURKEY. A1 Edirne, 8 km W of Edirne, 100 m, *Davis 41972* (K). UKRAINE. Krym, Gornaja Grjada mezdu m. Aija S. Rezerv, Sevastopolja, 44°28′N, 34°8′E, *Crelev et al. 366* (LE). UNITED KINGDOM. **Scotland:** Braemar, *Croall 411* (K). YUGOSLAVIA. **Serbia:** Jablanica, 29 Apr. 1914, *Malý s.n.* (K).

CANADA. **British Columbia**: Cadborough Bay, Vancouver Island, *Whiting & Stewart 431* (K). U.S.A. **Arkansas**: Marion Co., Buffalo State Park, ca. 15 mi. SE Yellville, *D'Arcy & Porter 4426* (MO). **California**: Mendocino Co., 2 mi. N Point Arena between Coast Highway and beach, 15 m, *True 4222* (CAS). **Georgia**: Oconee Co., 3 mi. ESE of Farmington, *Duncan 29037* (NY). **Hawaii**: Hamakua, Upper Paauhau, 1500 m, *Hosaka 2203* (BISH). **Idaho**: Idaho Co., Clearwater River Canyon between Syringa and Orofino, ca. 5 mi. downstream of Syringa, *Henderson & Cholewa 6486* (NY). **Maryland**: Prince George Co., Beltsville, *Hill 16730* (NY). **Massachusetts**: Nantucket Island, Siasconset, *Mackeever 991* (BM). **Missouri**: McDonald Co., 1.5 mi. S of Goodam, T23N, R32W S 19, roadside park on W side of Hwy. 71, *Summers 2944* (MO). **New Jersey**: Camden, 11 June 1876, *Parker s.n.* (NY). **New York**: Long Island, Hunter's Point, 19 May 1880, *Brown s.n.* (NY). **North Carolina**: Avery Co., entrance to Grandfather Mountain on US 221, 1400 m, *Boufford & Wood 23898* (MO). **Ohio**: Painesville, 4 June 1886, *Werner s.n.* (NY). **Oklahoma**: 4.3 mi. SE of Eagletown, *Goodman 8336* (G). **Oregon**: Baker Co., old campground along Pine Creek, below North Pine Creek, between Halfway and Homestead, *Cronquist 6543* (NY). **Pennsylvania**: Chester Co., Brookfield, July 1817, *Canby s.n.* (NY). **Tennessee**: Blount Co., Mt. Nebo, Walland, *Thomas 71177* (NY). **Utah**: Utah Co., Provo Bench near Pleasant View, Utah Ditchbank, 1500 m, *Harrison 7543* (MO). **Virginia**: Isle of Wight Co., Fort Boykin, 5 May 1991, *Grimm s.n.* (BM). **Washington**: King Co., 1 mi. N Snoqualmie Falls on the road between Falls City and Snoqualmie, Cascade Mountains, 250 m, *Anderson 2138* (MO). **West Virginia**: Pendleton Co., Pike Gap rd., 0.5 mi. SE jct. of St. Rt. 28 at Circleville, *Cusick 28120* (NY). **Wisconsin**: Olga, 10 June 1905, *Engberg s.n.* (NY).

ARGENTINA. **Entre Ríos**: Gualeguay, Estancia San Ambrosio, 33°10′S, 59°14′W, *Burkart 18088* (NY). CHILE. **Concepción**: región de Biobio, La Posada, 17 km S Concepción, 36°51′S, 73°3′W, *Rechinger 63095* (W). FALKLAND IS. Byron Sound, West Falkland I., 7 Feb. 1912, *Vallentin s.n.* (K). URUGUAY. **Montevideo**: Cerro, 50 m, *Herter 1312b* (MO).

*Geranium molle* is a very distinctive species, easily identified by its transversely wrinkled mericarp, glabrous on the surface and sparsely ciliate at the base. It grows naturally almost throughout Europe, in the circum-Mediterranean area, Macaronesia, and central and western Asia. The eastern limit in Europe is not well known, because of the scarcity of herbarium material. In Asia, this species reaches the western Himalayas to 76°E in India. It has been introduced in many temperate areas of North America, South America, southern Africa, and Australia.

*Geranium molle* shares some derived character states with *G. aequale*, such as glabrous stamen filaments, an abruptly tapered fruit rostrum, and glabrous mericarp surface, supporting their close phylogenetic relationship.

A number of minor morphological variants of *G. molle* have been recognized in the literature, of which the most notable seems to be *G. brutium*. According to Webb and Ferguson (1968: 198), this is an eastern Mediterranean species similar to *G. molle* but frequently perennial (*G. molle* was considered annual by these authors), with the lowermost inflorescence leaves shorter than the peduncle or slightly exceeding it (as opposed to considerably longer in *G. molle*) and with petals 6–11 mm long (3–7 mm long in *G. molle*). Davis (1967: 460) and Persson (1987: 547) considered *G. brutium* as a subspecies of *G. molle*, whereas Pignatti (1982: 10) preferred specific rank. All of these authors used the above-mentioned characters to recognize *G. brutium*.

All the studied material identified (by several authors) as *G. brutium* is clearly annual, though variable in stature and robustness. This was already pointed out by Boissier (1867: 880, 882). *Geranium molle* subsp. *sinjaricum*, described by Al-Shehbaz et al. (1983: 353) from Iraq, was said to be perennial. Unfortunately, we were not able to examine any original material on which this name was based, but all specimens studied from Iraq were annuals. The ratio between the length of the lowest inflorescence leaf and the peduncle varies considerably in *G. molle*, but independently of plant robustness and petal length. This suggests that *G. brutium* has been distinguished from *G. molle* only because of its longer petals. However, some plants with long petals can be found throughout the geographic range of *G. molle*, even in populations with mainly short petals. According to Yeo (pers. comm.) and our own observations, the earliest flowers usually exhibit the longest petals, with petal length diminishing as the season progresses. Moreover, the type specimen of *G. brutium* has petals 7.8 mm long, not far from the *G. molle* values. Consequently, the forms with long petals are here not accorded taxonomic recognition.

Sometimes it is possible to find depauperate plants of *G. molle* (up to 5 cm high), fertile but with the leaves not fully developed. Some such specimens [e.g., *Florström s.n.* (K) from Finland, or *Davis & Bokhari 55856* (K) from Iran] have leaves with undivided lobes. However, no other character state is associated with this size reduction, which sug-

gests that this form also does not deserve taxonomic recognition.

**3. Geranium pusillum** L., Syst. Nat. Ed. 10: 1144. 1759 [May–June]. *Geranium parviflorum* Curtis, Fl. Londin. 4(43): tab. 46. 1782, nom. illeg. *Geranium parviflorum* Chevall., Fl. Gén. Env. Paris Ed. 1, 2: 802. 1828, nom. illeg. TYPE: "Habitat in Anglia, Galia" [according to L., Sp. Pl. Ed. 2: 957. 1763] (lectotype, here designated, LINN-858.86; microfiche!).

*Geranium humile* Cav., Diss. 4: 202, tab. 83 fig. 2. 1787. *Geranium pusillum* var. *humile* (Cav.) Steud., Nomencl. Bot. 1: 365. 1821. *Geranium parviflorum* var. *humile* (Cav.) Chevall., Fl. Gén. Env. Paris Ed. 1, 2: 803. 1828. TYPE: locality and collector unknown, specimen annotated in Cavanilles's hand as "*humile*" (lectotype, here designated, MA-475736!).

*Geranium dubium* Chaix, Pl. Vap. 23. 1785. TYPE: France. "Circà pagos frequens" [in agro vapincense, Gap], *Chaix s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium delicatulum* Ten. & Guss., in Ten., Fl. Napol. 5: XII, 84. 1835–1836. *Geranium pusillum* subsp. *delicatulum* (Ten. & Guss.) A. Terracc., Malphigia 4: 212. 1890. TYPE: Italy. Majella, *Tenore s.n.* (lectotype, here designated, NAP; photocopy!).

*Geranium pusillum* var. *elatum* Picard, in Mém. Soc. Agric. Boulogne-sur-Mer 1: 133. 1837. TYPE: France. "Dans les terres fortes et les endroits herbeux," *Picard s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium circinatum* Kanitz ["*circinatnm*"], Linnaea 32: 570. 1863. *Geranium pusillum* [β] *circinatum* (Kanitz) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Hungary. "Habitat ad Varasdinum et in valle Vilena draga monte Croatiae," *Kanitz s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pusillum* var. *axilliflorum* Schur, Enum. Pl. Transsilv. 137. 1866. *Geranium pusillum* f. *axilliflorum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1704. 1924. *Geranium pusillum* [β] *axilliflorum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 41. 1913. TYPE: Romania. "Auf Sandboden am Zibinfluss bei Neppendorf. Jul.," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pseudopusillum* Schur, Oesterr. Bot. Z. 18: 317. 1868. *Geranium pusillum* [II] *pseudopusillum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Austria. "Auf unbehauten steinigsandigen Aeckern und Plätzen, unweit des Landgutes vor der Favoriten-Linie. Anfang Mai 1867," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pusillum* var. *albiflorum* Schur, Verh. Naturf. Vereins Brünn 15: 163. 1876. *Geranium pusillum* [1] *albiflorum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 41. 1913. TYPE: Austria. "In Obstgärten bei Hermannstadt, eine Schattenform, Mai 1850," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pusillum* var. *gracillimum* Schur, Verh. Naturf. Vereins Brünn 15: 162. 1876. *Geranium pusillum* f. *gracillimum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1704. 1924. *Geranium pusillum* [1] *gracillimum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Czech Republic. "Auf der Spitalswiese bei Brünn truppweise, Juni 1872," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pusillum* var. *majus-grandifolium* Schur, Verh. Naturf. Vereins Brünn 15: 162. 1876. *Geranium pusillum* [2] *majus-grandifolium* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Austria. "In der Au an der Schwarzawa bei Komein nächst Brünn, July 1870," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pusillum* var. *rigidum* Schur, Verh. Naturf. Vereins Brünn 15: 163. 1876. *Geranium pusillum* f. *rigidum* (Schur) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1704. 1924. *Geranium pusillum* [2] *rigidum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Austria. "Auf steinig-sandigem Boden vor der Favoritenlinie in der Nähe des Landgntes bei Wien, Mai 1867," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium* ×*hybridum* Hausskn., Mitt. Geogr. Ges. (Thüringen) Jena 3: 278. 1884, nom illeg., non L. (1767). TYPE: Germany. Ilmviaduktes bei Weimar, *Hausknecht s.n.* (lectotype, here designated, JE!).

*Geranium pusillum* var. *condensatum* Druce, Bot. Soc. Exch. Club Brit. Isles 5: 17. 1917. TYPE: United Kingdom. England: The Haven, Mudditord, Hants., 27 July 1916, *Green s.n.* (lectotype, here designated, OXF!).

*Geranium pusillum* var. *tenuilobum* Sennen, Pl. Espagne 1927, no. 6058. 1928, in sched. TYPE: France. Cerdagne: Angoustrine [42°29'N, 1°56'E], 7 July 1927, *Sennen s.n.* (lectotype, here designated, BC-825290!; isolectotypes, BM!, MA-71059!, MA-71060!, MA-470864!, W!).

Annual herb to 50 cm tall; stem erect or decumbent, usually branched from the base, pilose, with short glandular and eglandular patent hairs (< 0.3 mm long). Basal leaves in a persistent rosette; lamina 1.5–3.8 × 1.5–4.8 cm, divided for 0.3–0.75 of its length, pilose, with eglandular, appressed hairs; segments 7, 2–4 mm wide at the base, 3–5-lobed at apex; lower cauline leaves opposite; petioles to 12 cm long, with short (< 0.3 mm) eglandular and glandular patent hairs; stipules 2–4 × 1–1.5 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 2–4 × 1–1.5 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 0.5–3.2 cm long, pilose, with short (< 0.3 mm) glandular and eglandular patent hairs; bracteoles 1.5–2 × 0.5 mm, linear-lanceolate; pedicels 0.6–1.6 cm long, pilose, with short (< 0.3 mm) glandular and eglandular patent hairs. Sepals 3–4.5 × 1.5–2 mm, mucronulate (with mucro 0.1 mm long), with scarious margins ca. 0.1 mm wide,

with eglandular hairs ca. 1 mm long and some shorter (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 2–3 × 1–1.5 mm, emarginate (with notch 0.2–0.5 mm deep), with short claw, pale purple. Stamens 10, the inner whorl with filaments 1.2–1.5 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half; anthers 0.3 × 0.2 mm, purple; external whorl with filaments 1 mm long, almost glabrous, lacking anthers. Gynoecium ca. 3 mm long; stigma light purple. Fruit 9–11 mm long; mericarps 1.7–1.9 × 1–1.1 mm, smooth, with a longitudinal rib, covering the seed completely, pilose, with appressed-eglandular hairs to 0.2 mm long, with a few ciliae at the base; rostrum 7–9 mm long, obtuse at apex, pilose (with erect-patent, eglandular and glandular hairs ca. 0.2 mm long); stigmatic remains 0.5–0.7 mm long, with 5 pilose lobes. Seeds 1.7–1.8 × 1–1.1 mm, reddish; hilum ⅓ as long as the perimeter. Chromosome number: $2n = 26$. Figure 9. *Additional illustrations.* Curtis (1782: tab. 46) [sub *G. parviflorum*]; Reichenbach (1841–1842: tab. 190 fig. 4877); Gams (1924: 1703 fig. 1641); Ross-Craig (1952: pl. 35); Tokarski (1972: 68, pl. 28).

*Distribution* (Fig. 10). Europe to central Asia and the Indian subcontinent, North Africa, and North America; also reported from Bermuda (Britton & Brown, 1913: 429) and Uruguay (Hetter, 1954); cultivated and waste places, open habitats, rocky slopes, and dry grassland, between 0 and 1900(–2500) m. *Additional maps.* Meusel et al. (1978: 263); Hultén & Fries (1986: 635, map 1270).

*Phenology.* Flowering March–September (December–January in Southern Hemisphere).

*Representative specimens examined.* MOROCCO. Refugio de Taffert, Atlas Medio, 33°38′N, 4°09′W, 1950 m, *Aedo 4144* (MA).

NEW ZEALAND. Wellington Harbour, 41°18′S, 174°47′E, 2 Apr. 1941, *Healy s.n.* (CHR); Burwood Hospital, Christchurch, 43°30′S, 172°42′E, *Healy 70.188* (CHR).

AFGHANISTAN. Mazari-I Sharif, N Afghanistan, faucibus fluvii Balkh supra Aq Kupruk, 700 m, 36°5′N, 66°52′E, *Rechinger 16298* (W). ARMENIA. Gdzi[?]rakaia, Such[?]ch, 9 July 1966, *Anonymous s.n.* (G). AUSTRIA. Austria superior, pr. Wildberg ad Lentiam urbem, 6 Sep. 1884, *Topiz s.n.* (BC-12605). BELARUS. Prov. Minsk, S Khojn Mozyr., 52°4′N, 29°12′E, 1905, *Bordzilowski s.n.* (LE). BELGIUM. Aarschot, 50°59′N, 4°50′E, 5 Sep. 1940, *Michelis s.n.* (BR). BOSNIA AND HERZEGOVINA. Sarajevo, *Gilliat-Smith 3321* (K). BULGARIA. Planities Thraciae, pr. Karlovo, 28 May 1975, *Petrova s.n.* (MA-209947). CYPRUS. Pagum Prodromo, *Kotschy 704* (K). CZECH REPUBLIC. Moravia australis, Uhersky Ostroh, 6 June 1949, *Podpera s.n.* (K). DENMARK. Saltholm, 55°38′N, 12°46′E, *Hansen 46* (C). ESTONIA. Wormsö, Hullo, 6 Aug. 1924, *Grontved s.n.* (C). FINLAND. Kyrkbackecc, Nagu, 18 June 1912, *Dahl s.n.* (MA-71056). FRANCE. Alençon, Orne, 48°26′N, 0°05′E, 25 June 1889, *Beaudouin s.n.* (MA-71055). GERMANY. Bayern, Oberbayern, Gräfelfing bei München, auf Brachäckern, 28 June 1902, *Dihm s.n.* (MA-360452). GREECE. Pisoderion, 1000 m, *Alston & Sandwith 684* (K). HUNGARY. Evdely, 12 June 1912, *Bark s.n.* (K). IRAN. Ardebil-Astara, 1300 m, *Bowles Schol. Bot. Exp. 2313* (K). IRAQ. Pught Ashan, 15 km NE of Rania, 36°15′N, 44°53′E, 1150 m, *Rawi 23906* (K). IRELAND. Dublin, July 1903, *Meade s.n.* (K). ITALY. Aprutium, montis Magellae, valle Orfenta, 41°38′N, 14°00′E, 200 m, July 1908, *Guadagno s.n.* (K). JAMMU-KASHMIR. Kashmir, *East India Company 323* (W). KAZAKSTAN. Almatinsk u., pr. Almati, 43°3′N, 76°56′E, *Pavlova 32* (LE). NETHERLANDS. Friesland, Harich, 52°54′N, 5°34′E, 4 July 1972, *Slim s.n.* (L). NORWAY. Holmsbo, 59°54′N, 12°06′E, 29 June 1869, *Collet s.n.* (K). PAKISTAN. Chitral, Drosh, 35°52′N, 71°58′E, *Toppin 91* (K). POLAND. Cracovia, pr. Zabierzów, ad vicum Modlniczka Mala versus, 27 Apr. 1974, *Sztyler & Tacik s.n.* (MA-252530). PORTUGAL. Francoso, *Sampaio 1909* (MA). ROMANIA. Oltenia, distr. Dolj, 120 m, 9 May 1931, *D. Cîrtu & M. Cîrtu s.n.* (MA-252531). RUSSIA. North Caucasus, ad fl. Terek, Ossetia, Balta, *Brotherus 216* (BM); Russia Central, Briansk, Pogar, in valle fluv. sudest prope Markovsk, 52°35′N, 33°15′E, 8 June 1980, *Skvortsov s.n.* (M); Russia North, Pskovsk gub., Opochetskij, st. Novgorodki, 57°3′N, 28°35′E, *Kuznetsova 461* (LE); Russia Northwest, prope urb. Pskow, 57°50′N, 28°20′E, *Andrejew 1608* (G). SPAIN. Lérida, Alto Arán, Bagergue, 1465 m, 31TCH2736, *Aedo 2273* (MA). SWEDEN. Gästrikland, Gävle, 60°40′N, 17°10′W, *Nannfeldt 17173* (K). SWITZERLAND. Disentis beim Kloster, 1160 m, 46°43′N, 8°51′E, 19 May 1920, *Bühler s.n.* (BC-12603). SYRIA. Kessab, 35°56′N, 35°59′E, *Pabot 194* (G). TURKEY. Elmoli, 1200 m, *Tengevall 364* (K). TURKMENISTAN. Ashabad, 37°58′N, 58°24′E, *Litwinow 1144* (G). UKRAINE. Kiew, Belaja Tserkov, 20 Aug. 1966, *Skvortsov s.n.* (M); Krym, Severnoe Chernomovskoe poberezhe, 45°34′N, 32°52′E, *Pobedimora 189* (LE). UNITED KINGDOM. **England:** Aylesford, Kent, Aug. 1902, *Gregor s.n.* (MA-170873). UZBEKISTAN. Tian-shan, montes Keksuiski khrebet, in vicinitati pagi Brichmulla, 1900 m, 41°37′N, 70°5′E, 11 July 1973, *Vasak s.n.* (G).

CANADA. **Alberta**: Banff, 51°10′N, 115°34′W, *Sanson 1028* (NY). **British Columbia**: Agarriz, 20 May 1889, *Macoun s.n.* (NY). **Manitoba**: Brandon, 49°50′N, 99°57′W, *Stevenson 788* (CAN). **Ontario**: Bruce Co., Crane Lake, 45°10′N, 81°24′W, *Soper et al. 13637* (CAN). U.S.A. **Arkansas**: Carroll Co., Elk Ranch, *Palmer 39459* (NY). **California**: Santa Cruz Co., Boulder Creek, 200 m, *Hesse 1118* (CAS). **Colorado**: St. Lupton, *Johnston 555* (MO). **Delaware**: Brandywine, Aug. 1863, *Canby s.n.* (NY). **Hawaii**: Maunakea, 2000 m, *Faurie 856* (BISH). **Idaho**: Moscow, 46°43′N, 116°59′W, *Werner 13599* (NY). **Illinois**: Alton, along the track of the Illinois Terminal Railroad, E of Piasa Street, 38°53′N, 90°11′W, 100 m, *Muehlenbach 4336* (MO), **Indiana**: St. Joseph Co., E side of Wolverton bog, along Road 23, 7 mi. SW of South end, *Friesner 20440* (MO). **Kansas**: Ellsworth Co., Kanopolis Reservoir, N Shore St. Park, *Brooks 17145* (NY). **Kentucky**: Boyle Co., Bellevue Cemetery, N Danville, *Cusick 30297* (NY). **Maryland**: Bladensburg, 38°56′N, 76°56′W, June 1879, *Chickering s.n.* (NY). **Massachusetts**: Martha's Vineyard, Edgartown, *MacKeever 445* (NY). **Michi-**

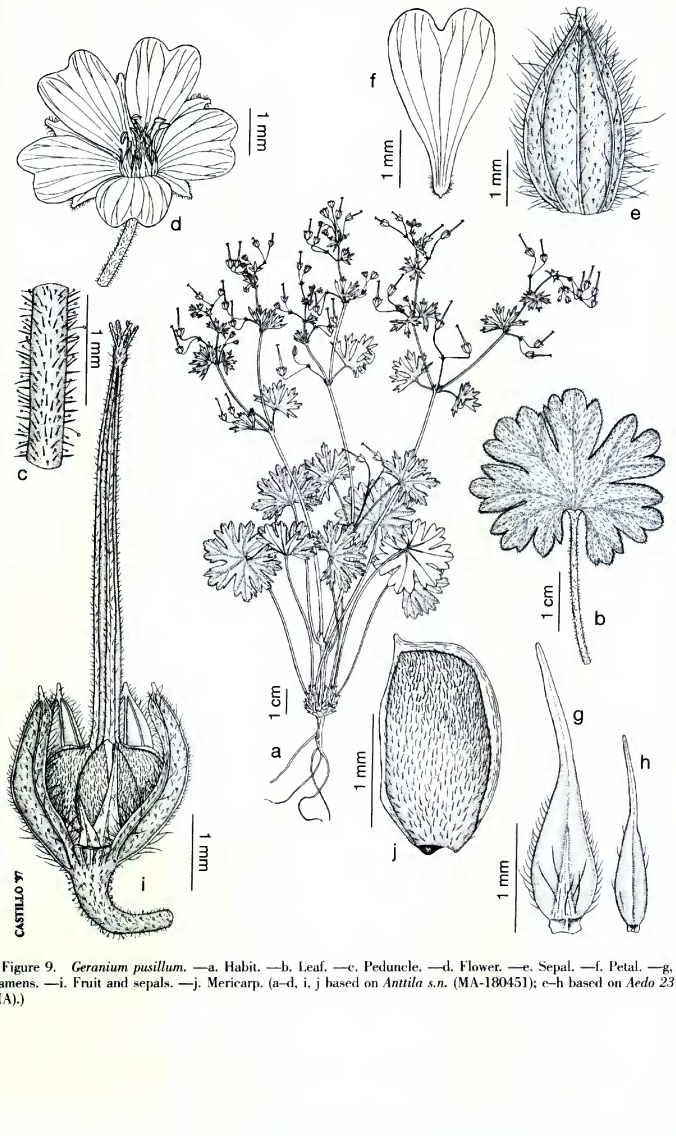


Figure 9. *Geranium pusillum*. —a. Habit. —b. Leaf. —c. Peduncle. —d. Flower. —e. Sepal. —f. Petal. —g, h. Stamens. —i. Fruit and sepals. —j. Mericarp. (a–d, i, j based on *Anttila s.n.* (MA-180451); e–h based on *Aedo 2371* (MA).)

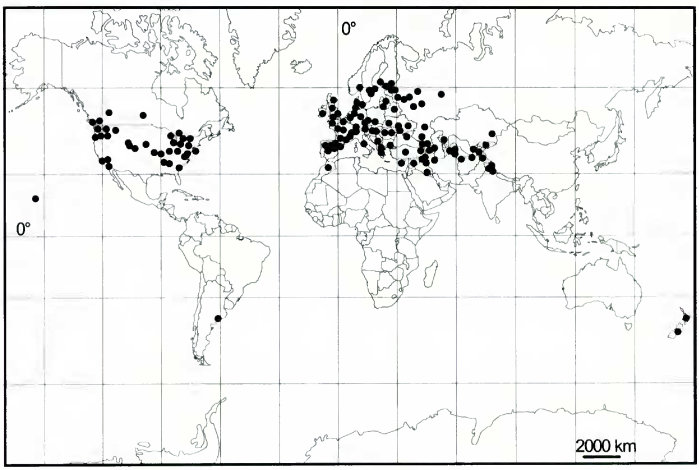


Figure 10. Distribution of *Geranium pusillum*, based on herbarium records.

**gan**: Flint, *Clarke s.n.* (NY). **Missouri**: Noel, *Bush 5727* (NY). **Montana**: Flathead Mission, 47°55′N, 114°5′W, Sep. 1899, *Blankinship s.n.* (NY). **Nebraska**: Minden, 10 June 1931, *Hapeman s.n.* (MO). **New Jersey**: Camden, *Parker s.n.* (NY). **New York**: Albany, 16 June 1882, *Dudley s.n.* (CAS). **Ohio**: Euclid, 41°34′N, 81°33′W, *Scair s.n.* (NY). **Oregon**: Wallowa Co., Imnaha canyon, *Peck 17528* (NY). **Pennsylvania**: Allegheny Co., 1869, *Porter s.n.* (NY). **South Dakota**: pr. Brookings, 44°18′N, 96°47′W, 26 July 1893, *Willians s.n.* (CAS). **Tennessee**: Davison Co., Belle Meade area, *Kral 50321* (MO). **Utah**: Bidolph's garden on road to Green Canyon, *Shaw 36* (NY). **Virginia**: Smyth Co., Laurel Creek, North Fork of the Holston River Valley, 700 m, 22 June 1892, *Britton et al. s.n.* (NY). **Washington**: Asotin Co., 10 mi. S of Asotin, on bluffs along W side of Snake R., *Hitchcock & Muhlick 21801* (NY). **West Virginia**: Smyth Co., Fork Holston river, near Broad Ford, 750 m, 20 June 1892, *Small s.n.* (MO). **Wyoming**: Laramie Expt. Farm, 41°18′N, 105°35′W, *Nelson 2038* (CAS).

ARGENTINA. Campo La Susana, 10 km de Peralta, 38°03′N, 61°40′W, 320 m, *Huidobro 1160* (NY).

*Geranium pusillum* has only five anther-bearing stamens, which is the best character to identify this species. It has been frequently confused with *G. pyrenaicum*, a closely related perennial species with ten anther-bearing stamens. It is also often confused with *G. rotundifolium*, another widespread annual species. However, *G. rotundifolium*, a member of subgenus *Geranium*, has typical seed-ejection fruits, reticulate seeds, and ten anther-bearing stamens.

*Geranium pusillum* is indigenous in the Eurasian portion of its range. The eastern limit of *G. pusillum* in Europe is not well known, because of the scarcity of herbarium material. In Asia, this species reaches the western Himalayas to 75°E in Jammu-Kashmir. *Geranium pusillum* has been introduced to many temperate areas of North America, South America, and Australia.

A search of the Linnaean Herbaria has yielded three sheets potentially related to the protologue of *G. pusillum*: LINN-858.85, LINN-858.86, and S-282.19. LINN-858.85 is not a suitable choice, because it represents *Geranium molle*. S-282.19 was annotated only by Linnaeus's son, hence is not relevant. Consequently, we prefer to select LINN-858.86, annotated by Linnaeus himself, as lectotype.

The name *G. pusillum* has often been attributed to "Burm. f., Spec. Bot. Geran. 1759"; however, that work was published on 17 August, about two months after the Linnaean protologue.

**4. Geranium pyrenaicum** Burm. f., Spec. Bot. Geran. 27. 1759. TYPE: "Habitat in Pyrenaeis" (authentic specimens in G, lectotype not designated; see discussion below).

Perennial herb with short vertical napiform rhizome; stem 15–70(–110) cm tall, erect, usually

branched from the base, pilose, with long eglandular hairs 1–1.4 mm long and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a persistent rosette; lamina 2.8–6.2 × 2.5–7.5 cm, divided for 0.5–0.6 of its length, pilose, with eglandular, appressed hairs; segments 5–7, 4–8 mm wide at the base, (3–)7–10(–12)-lobed at apex; lower cauline leaves opposite; petioles to 25 cm long, with patent, long eglandular hairs 1–1.5 mm long and short glandular and eglandular hairs < 0.5 mm long; stipules 3–9 × 1–3.5 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 4–7 × 1.5–2.5 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 1–3.8 cm long, pilose, with eglandular, patent hairs 1–1.3 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 2.5–5 × 0.5–0.8 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–3 cm long, pilose, with short (< 0.5 mm) glandular and eglandular hairs and sometimes with eglandular patent hairs 0.7–1.3 mm long. Sepals 3.5–5 × 1.6–2.5 mm, ovate, mucronulate (with mucro 0.2–0.3 mm long), with scarious margins ca. 0.1 mm wide, with short (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 7–11 × 5–6.5 mm, emarginate (with notch 2–3 mm deep), with short claw, bright purple. Stamens 10, both whorls bearing anthers; filaments 4–5 mm long, lanceolate, pilose on the abaxial side, ciliate on the proximal half; anthers 1–1.2 × 0.5–0.7 mm, purple. Gynoecium 4–4.5 mm long; stigma purple. Fruit 18–20 mm long; mericarps 2.4–3.1 × 1.1–1.4 mm, smooth, with a longitudinal rib, covering the seed completely, pilose, with appressed-eglandular hairs ca. 0.1 mm long or glabrous, not ciliate at the base; rostrum 10–15 mm long, obtuse at apex, pilose (with erect-patent, eglandular and glandular hairs ca. 0.1 mm long); stigmatic remains 1.5–1.8 mm long, with 5 pilose lobes. Seeds 2.2–2.7 × 1.2–1.4 mm, brownish; hilum 1/5–1/6 long.

*Geranium pyrenaicum* is the only perennial species in section *Batrachioidea*. *Geranium pusillum* seems to be the closest relative of *G. pyrenaicum*. The mericarps of *G. pyrenaicum* are quite similar to those of *G. pusillum*: smooth, with appressed-eglandular hairs (except for subsp. *lusitanicum*), but slightly smaller. Moreover, *G. pyrenaicum* and *G. pusillum* share one derived character state: the presence of a dorsal, longitudinal rib on the mericarp.

*Geranium pyrenaicum* grows naturally in almost all of Europe, the Caucasus, Asia Minor, northern Iran, and northwest Africa. It has been introduced in some temperate areas of northeastern North America, and probably in northern Europe.

Among the great number of morphological variants formally described under *Geranium pyrenaicum*, only that here segregated as subspecies *lusitanicum* seems of some importance.

According to F. Jacquemoud (in litt.), two sheets of *G. pyrenaicum* are kept in the Burman herbarium at G. However, neither can be related unequivocally to the protologue because of the lack of dates, locality, and other relevant information.

KEY TO THE SUBSPECIES OF *GERANIUM PYRENAICUM*

1a. Mericarps pilose; pedicels with hairs shorter than 0.1 mm ..... 4a. *G. pyrenaicum* subsp. *pyrenaicum*

1b. Mericarps glabrous; pedicels usually with hairs (0.5–)0.7–1.3 mm long ..... 4b *G. pyrenaicum* subsp. *lusitanicum*

### 4a. Geranium pyrenaicum subsp. pyrenaicum

*Geranium perenne* Huds., Fl. Angl. Ed. 1: 265. 1762. TYPE: England. "Habitat in pratis montanis. Ad ripam fluvii inter Bingley et Kighley in agro Eboracensis; prope Enfield, et inter Hyde-Park et Little-Chelsea," collector unknown (lectotype, here designated, LINN-858.80; microfiche!).

*Geranium umbrosum* Waldst. & Kit., Descr. Icon. Pl. Hung. 2: 131, tab. 124. 1803–1805. *Geranium pyrenaicum* var. *umbrosum* (Waldst. & Kit.) DC., Prodr. 1: 643. 1824. *Geranium pyrenaicum* subvar. *umbrosum* (Waldst. & Kit.) Nyman, Consp. Fl. Eur. 137. 1878. *Geranium pyrenaicum* [b] *umbrosum* (Waldst. & Kit.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Hungary. *Kitaibel s.n.* (lectotype, here designated, BM!).

*Geranium pyrenaicum* var. *pumilum* Picard, Mém. Soc. Agric. Boulogne-sur-Mer 1: 131. 1837. TYPE: France. "à Abbeville, sur le versant du rempart, du côté du champs de Foire, et à la porte St.-Gilles, dans les fortifications; à Amiens, sur le rempart, auprès du Jardin des Plantes, et dans le jardin même, sur le petit rideau qui se trouve au-devant de la salle des Démonstrations," *Picard s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium minae* Tineo, Pl. Rar. Sicil. 25. 1846. *Geranium pyrenaicum* var. *minae* (Tineo) Nyman ["Minaae"], Consp. Fl. Eur. 138. 1878. TYPE: Italy. Minà, *Tineo 514* (lectotype, here designated, PAL!, the left-hand specimen).

*Geranium pyrenaicum* var. *subvillosum* Schur, Enum. Pl. Transsilv. 137. 1866. TYPE: Romania. "In den Weinbergen bei Hammersdorf. Jun," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pyrenaicum* var. *albiflorum* Schur, Oesterr. Bot. Z. 18: 316. 1868. *Geranium pyrenaicum* [1] *albiflorum* (Schur) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Austria. "Wächst auf schattigen Rasenplätzen in Wäldern und Obstgär-

den, häufig ist sie im Garten des k.k. Theresianums, wo ich nur diese beobachtet habe," *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pyrenaicum* var. [β] *pilosum* Rupr., Mém. Acad. Imp. Sci. Saint Pétersbourg, sér. 7, 15: 275. 1869. TYPE: Georgia. "15–22 Sept. . . . in m. Bai Gora alt. 1140–900 hex.," *Owerin s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium rhaeticum* Brügger, Jahresber. Naturf. Ges. Graubündens 39: 56. 1885. TYPE: Switzerland. Chur, Lürlibad, *Brügger s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pyrenaicum* subsp. *australe* A. Terracc., Malpighia 4: 209. 1890. TYPE: Italy. Palermo alla Pizzuta, *Todaro 638* (lectotype, here designated, K!).

*Geranium pyrenaicum* var. *gracilescens* A. Terracc., Malpighia 4: 211. 1890. *Geranium pyrenaicum* [*b*] *gracilescens* (A. Terracc.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Italy. "D'Abruzzo e degli alti monti romani, e qui e là sino in Basilicata," *Terracciano s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pyrenaicum* var. *patulivillosum* Hausskn. & Bornm. ex Bornm., Mitth. Thüring. Bot. Vereins 20: 10. 1904–1905. TYPE: Turkey. Pontus australis, Amasia, mte. Lokman, 9 May 1890, *Bornmüller 1974* (lectotype, here designated, JE!).

*Geranium crinitum* N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 122. 1913. TYPE: Italy. Pisterola, *N. Terracciano s.n.* (lectotype, here designated, NAP; photocopy!).

*Geranium pyrenaicum* [2] *grandiflorum* Schur ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Romania. *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pyrenaicum* [3] *parviflorum* Schur ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Romania. *Schur s.n.* (no authentic material located; synonymy according to Knuth, 1912).

*Geranium pyrenaicum* var. *malvaceum* Beauverd, Bull. Murith. Soc. Valais. Sci. Nat. 42: 183. 1925. TYPE: Switzerland. Bourg-St-Pierre, *Beauverd s.n.* (lectotype, here designated, G!, the specimen on the lower part).

*Geranium pyrenaicum* var. *longepedicellatum* Sennen, Pl. Espagne 1926, no. 5083. 1927, in sched. TYPE: Spain. Cerdagne: Llivia, Estavar, les Escaldes, *Sennen s.n.* (lectotype, here designated, BC-12495!; isolectotypes, BM!, MA-71633!, MA-471335!, W!).

*Geranium pyrenaicum* f. *pallidum* Gilmour & Stearn, J. Bot. 70, Suppl.: 6. 1932. TYPE: England. Hab. Hills Road, near Strangeways Research Hospital, Cambridge, *Gilmour & Stearn s.n.* (lectotype, here designated, K!; isolectotype, W!).

*Geranium pyrenaicum* var. *turolense* Sennen, Diagn. Nouv. 262. 1936. TYPE: Spain. Teruel, *León s.n.*, Pl. Espagne no. 9773 (lectotype, here designated, BC-88765!).

*Geranium elbursense* Gilli, Repert. Spec. Nov. Regni Veg. 46: 44. 1939. TYPE: Iran. Demawend, alm ober Rehne, 2640 m, 22 July 1930, *Gilli s.n.* (lectotype, here designated, W!).

Stem (15–)25–50(–70) cm tall. Pedicels 1–3 cm long, pilose, with glandular and eglandular hairs shorter than 0.1 mm, usually without long eglandular hairs. Mericarps 2.4–3.1 mm long, pilose. Chromosome number: $n = 13$; $2n = 26$. Figure 11a–g. *Additional illustrations.* Cavanilles (1787: tab. 79 fig. 2); Reichenbach (1841–1842: tab. 192); Ross-Craig (1952: pl. 33); Tokarski (1972: 69, pl. 30).

*Distribution* (Fig. 12). Europe, North Africa, the Caucasus, western Asia, and North America; also reported from Chile (Marticorena & Quezada, 1985: 47); waste places, field margins, and forest margins, between 0 and 2650 m. *Additional maps.* Meusel et al. (1978: 263); Hultén & Fries (1986: 634, map 1268).

*Phenology.* Flowering May–September.

*Representative specimens examined.* MOROCCO. 71 km S Marrakech, 2 km below Oukaimeden, 2520 m, 31°12′N, 7°50′W, *Jury et al. 9004* (BM).

ALBANIA. M. Parmu, Alpes alb. sept., distr. Scutari, *Baldaci 257* (BM). ARMENIA. Pr. oz. Sevan, 40°33′N, 44°57′E, *Aretisian et al. s.n.* (MA-252462). AUSTRIA. In pratis agri Vindobonensis, *Kerner s.n.* (K). BELGIUM. Caestert, 23 May 1950, *Bakhuizen s.n.* (K). BULGARIA. Rila pr. Samokov, 42°8′N, 23°33′E, *Petrova & Kozuharov 838* (MA). CZECH REPUBLIC. Moravia SW, Dacice, pago Police haud procul ab opp. Jemnice, 450 m, *Unar 1537* (MA). DENMARK. Stautrup near Aarhus, 56°10′N, 10°13′E, *Nielsen & Pedersen 429* (MA). FINLAND. Aloa, 1878, *Hollmén s.n.* (MA-71628). FRANCE. Aveyron, St. Paul des-Fonts, cultivé de gr. orig. d'Igny (Seine-et-O.), May 1905, *Coste s.n.* (BC-825302). GERMANY. Bavaria, pr. Bamberg, 380 m, May 1907, *Harz s.n.* (BM). GREECE. Bordag, 20 km NW Drama, Macedonia, 1000 m, *Stainton 7704* (K). HUNGARY. Erdely, Brafsó, 18 May 1898, *Kuel s.n.* (BC-12504). IRAN. Fao project Camp, 1520 m, 36°0′N, 53°0′E, *Fishwick 8* (K). IRELAND. Dublin, *Gamble 20055* (K). ITALY. Lucania, M. Sacro, 1700 m, July 1907, *Guadagno s.n.* (MA-71635); Sicilia, Madonie, *Citarda 331* (LY); Madonie mts., well above Isnello towards Piano Battaglia on slopes Pzo Antenna Grande, 1000 m, 26 May 1972, *Stace & Cotton s.n.* (BM); Messina, Nebrodie Mountains, mt. Soro, 1710 m, 37°56′N, 14°41′E, *Akeroyd et al. 3744* (BM); Palermo, ca. 45 km S of Cefalù, SE of Rifugia Marini, 1600 m, *Davis & Sutton 63866* (BM); in silvaticis montosis Madonie, 1882, *Citarda s.n.* (K); m. Pizzuta, 1300 m, 7 June 1907, *Lacaita s.n.* (BM). NETHERLANDS. Culemborg, 51°57′N, 5°14′E, 5 June 1938, *Van Soest s.n.* (L). NORWAY. Akershus amt, *Werenskiold 15298* (C). POLAND. Dittmannsdorf, pr. Waldenburg in Silesia, 50°46′N, 16°17′E, 400 m, 17 June 1884, *Felsmann s.n.* (BC-12492). ROMANIA. Transylvania, *Schur 756* (K). RUSSIA. North Caucasus, Terek prov., 43°28′N, 44°11′E, 8 June 1911, *Busch s.n.* (W). SPAIN. Potes, bajada hacia Sotres, *Castroviejo et al. 4131EV* (MA). SWEDEN. Uppsala, 59°55′N, 17°38′E, *N. J. Andersson s.n.* (MA-99906). SWITZERLAND. Bern, *Thring H965.34* (K). SYRIA. Gifi el Hajar, June 1822, *Ehrenberg s.n.* (K). TURKEY. A4 Ilgaz Daglari, Karasu Valley, Gulmezler, S of Kastamonu, 1780 m, *Cheese 1751* (K). UKRAINE. Krym, Bisetka Vetrov, 15 km NNE of Yalta, 1250 m, *Chater 140* (BM). UNITED KINGDOM. **England:** Bakewell, NW Derbyshire, *Bailey 277* (K). YUGOSLAVIA. **Montenegro:** Crna Gora, Zablzak, lower

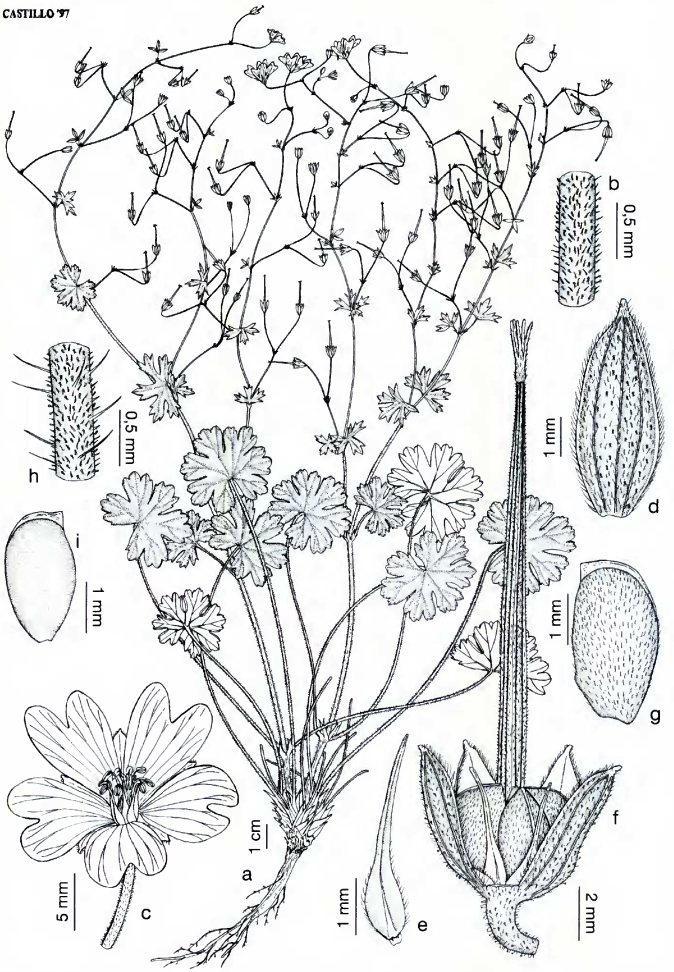


Figure 11. a–g. *Geranium pyrenaicum* subsp. *pyrenaicum*. —a. Habit. —b. Pedicel. —c. Flower. —d. Sepal. —e. Stamen. —f. Fruit and sepals. —g. Mericarp. h, i. *Geranium pyrenaicum* subsp. *lusitanicum*. —h. Pedicel. —i. Mericarp. (a, b, d–g based on *Aedo 2084* (MA); c based on *Aedo et al. CN340* (MA); h, i based on *Losa s.n.* (MA-71620).)

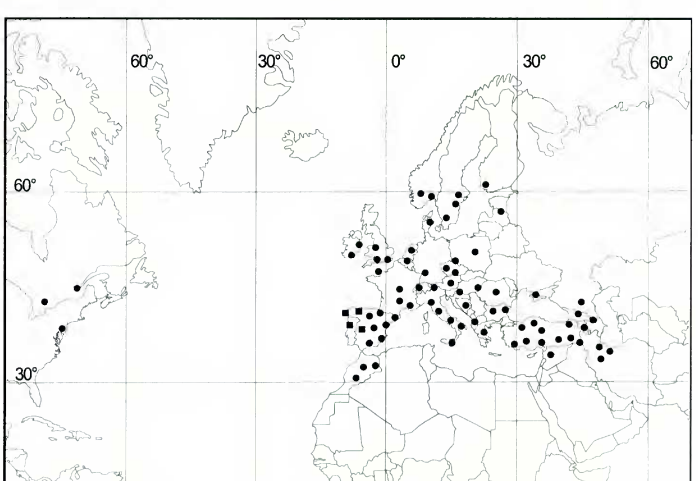


Figure 12. Distribution of *Geranium pyrenaicum* subsp. *pyrenaicum* (dots) and subsp. *lusitanicum* (squares), based on herbarium records.

slopes of Savin Kuk, above Crno Jezero, 1750 m, *Gardner 2441* (BM).

CANADA. **Ontario:** Grey Co., W of Beaverdale, 44°24′N, 80°38′W, *Whiting 1666* (CAN). **Québec:** Sillery, cimetière St-Patrice, 46°46′N, 71°15′W, *Bernard B84–53* (CAN). U.S.A. **New York:** Bronx Co., New York Botanical Garden, Bronx Park, *Gilly 426* (NY).

**4b. Geranium pyrenaicum** subsp. **lusitanicum** (Samp.) S. Ortiz, Anales Jard. Bot. Madrid 47: 244. 1990. *Geranium pyrenaicum* raça *lusitanicum* Samp., Man. Fl. Port. 273. 1911. *Geranium lusitanicum* (Samp.) Samp. ex J. M. M. Lopes, Bol. Soc. Brot. ser. 2, 5: 245. 1928. *Geranium pyrenaicum* var. *lusitanicum* (Samp.) Samp., Fl. Port. Ed. 2: 331. 1947. TYPE: Portugal. Castro Laboreiro, July 1903, *Sampaio s.n.* (lectotype, here designated, PO-4606!).

*Geranium pyrenaicum* var. *majus* Pau ex Merino, Fl. Galicia 1: 283. 1905. TYPE: Spain. ad Rivas Pequeñas, *Merino 305* (lectotype, here designated, LOU!).

Stem (23–)40–75(–110) cm tall. Pedicels 1–2.5 mm long, pilose, with glandular and eglandular hairs shorter than 0.1 mm and usually also with long eglandular hairs (0.5–)0.7–1.3 mm. Mericarps 2.4–2.6 mm long, glabrous. Chromosome number: $2n = 26$. Figure 11h, i. *Additional illustration.* Ortiz (1989: 242 fig. 1).

*Distribution* (Fig. 12). Spain and Portugal; waste places, field margins, and forest margins between 0 and 2000 m. *Additional map.* Ortiz (1989: 244 fig. 3).

*Phenology.* Flowering June–July.

*Representative specimens examined.* PORTUGAL. Bragança, Paramio, Zeibe, 28 July 1971, *Dias Pereira s.n.* (LISI); Caldas do Gerez, June 1887, *Murray s.n.* (K); Campea, 3 Aug. 1961, *Rozeira et al. s.n.* (PO-15435); Castelo de Vide, June 1908, *Sampaio s.n.* (PO-4609); Fafe, Armil, 8 May 1943, *Barros s.n.* (PO-30979); Macedo de Cavaleiros, 23 Apr. 1943, *Rozeira & Castro s.n.* (MA-191371); Mata do Fundao, June 1906, *Tavares s.n.* (PO-4607); Meda, dentro do Castelo, 5 Oct. 1976, *Costa s.n.* (PO-45102); Mogadouro a Azinhoso, Qta. da Nogueira, *Barbosa & García 6754* (LISI); Moimenta da Beira, Vila da Rua, beira da Ribeira, 26 June 1977, *Costa s.n.* (PO-28436); Póvoa de Lanhoso, Quintal de S. Geus, May 1908, *Sampaio s.n.* (PO-4608); Sabugal, Quadrazais, junto ao rio Côa na reserva, 2 June 1988, *Ladero & Lousa s.n.* (LISI); Serra da Estrela, Fonte Paulo Martius, *Rozeira s.n.* (PO-15434);

Tabuaço, Vale da Figueira, *Barbosa & García 8083* (LISI); Vinhais, Tuizelo, 28 May 1972, *Marcos & Almeida s.n.* (LISI); Castro Laboreiro, Povoaçao, June 1903, *Sampaio s.n.* (PO-4606). SPAIN. Ávila, El Arenal, 1300 m, 12 Aug. 1986, *Luceño & Vargas s.n.* (MA-407065); Vizcaya, Gorbea, *Guinea 4020* (MA); Burgos, La Revilla, Carazo, 1400 m, 30TVM6949, 6 July 1979, *Pons & Susana s.n.* (MA-414207); Cáceres, Baños de Montemayor, 17 May 1944, *Caballero s.n.* (MA-71194); León, Los Apóstoles, La Guiana, 42°30′N, 6°36′W, 26 June 1984, *Fernández Alonso et al. s.n.* (MA-518975); La Rioja, Arnedillo, Peñalmonte, 1100 m, 14 Oct. 1972, *Segura Zubizarreta s.n.* (MA-359912); Lugo, 13 June 1979, *Carreira s.n.* (MA-493007); Madrid, El Escorial, 16 June 1907, *Rodríguez s.n.* (MA-341882); Asturias, Belmonte, Faedo, 685 m, *Aedo 3700* (MA); Palencia, Dehesa de Montejo, valle de Tosande, 1350 m, *Monasterio 1341* (MA); Salamanca, Castañar de las Honfrías, Linares del Río Frío, 15 June 1974, *Castroviejo s.n.* (MA-324277); Segovia, Altos del puerto de la Quesera, 1340 m, 24 June 1973, *Gómez et al. s.n.* (MA-323972); Soria, Cañón del río Lobos, 7 June 1980, *Buades s.n.* (MA-571625); Álava, Ichine, mt. Gorbea, *Guinea 4019* (MA); Zamora, Rivadelago, barranco del Fornillo, June 1945, *Losa s.n.* (MA-71620).

*Geranium pyrenaicum* subsp. *lusitanicum* comprises plants from northwestern Spain and Portugal with glabrous mericarps and long, patent, eglandular hairs on the peduncles and pedicels. In this area, all specimens examined exhibit these features. However, eastward, in the eastern portion of the Cantabrian range and in the Iberian range, where the two subspecies occur sympatrically, the indumentum of the peduncles and pedicels is variable. This was pointed out by Ortiz (1989: 243), who proposed subspecific rank for these entities. The rank of subspecies is here used according to Du Rietz (1930), for allopatric taxa merging morphologically where they come into contact. Lidén (1986) described subspecies as "taxa believed to be allopatrically evolved from a common ancestor, not sufficiently different to be recognized as species, i.e. resulting from primary speciation at an early stage." This could be the case in *G. pyrenaicum*, considering its geographical distribution and weak morphological divergence.

We consider occasional specimens with glabrous mericarps from within the geographic range of *G. pyrenaicum* subsp. *pyrenaicum* to be discordant elements representing minor variation of no taxonomic relevance. However, if such individuals were confirmed as more common, the status of subsp. *lusitanicum* would have to be reconsidered.

**Geranium** sect. **Divaricata** Rouy, in Rouy & Foucaud, Fl. France 4: 88. 1897. TYPE: *G. divaricatum* Ehrh.

Perennial or annual herbs; stems to 60 cm long, with simple or bifurcate monopodial branching, leafy, erect, with patent eglandular and glandular hairs. Basal leaves in persistent or deciduous rosettes; venation actinodromous, basal, perfect, marginal; lamina pentagonal in outline, palmatifid, concolorous, hairy; segments 5–7, rhombic, 7–15-lobed at apex. Cauline leaves opposite or alternate; stipules lanceolate, sometimes lobed, papery, brown, pilose. Cymules solitary, arising from aerial stems; bracts lanceolate, papery, brown; peduncles present, with patent glandular and eglandular hairs; bracteoles linear-lanceolate, sometimes lobed, papery, brown; pedicels 2 per cymule, ± ascending and often curved upward after anthesis, subequal, with patent glandular and eglandular hairs; peduncle and pedicel together very often exceeding the subtending leaf. Sepals ovate, erect-patent at anthesis and erect in fruit, briefly mucronulate, marginally scarious; abaxial surface with eglandular or glandular hairs; adaxial surface glabrous, with a subapical tuft of hairs. Petals erect-patent, ± obovate, emarginate, without claw, without nectar passages, ciliate at base, with sessile glands on the adaxial surface, ± purple, without a dark basal spot. Stamens 10, both whorls bearing anthers; filaments lanceolate, expanded at base, persistent in fruit, with a conspicuous midvein, sometimes ciliate, pilose on abaxial surface, pale pink; pollen blue. Nectaries hemispherical, glabrous. Stigmas pink-purple. Fruit of the carpel-projection-type, with discharge mechanism inoperative; mericarps transversely wrinkled, sometimes cristate, covering the seed completely, without a basal beak and without a callus, hairy; rostrum reduced, obtuse at apex; stigmatic remains with 5 pilose lobes. Seeds obovoid, smooth, brownish, the hilum 1/6 as long as the perimeter. Cotyledons laterally incised. Chromosome number: $2n = 20?, 28$.

*Distribution.* Southwestern Europe to central Asia and China.

The most distinctive feature of *Geranium* sect. *Divaricata* is the inoperative fruit-discharge mechanism. Other characters states, such as the incised margin of the cotyledons and the obovate seed outline, also support this section as a natural entity.

KEY TO THE SPECIES OF *GERANIUM* sect. *DIVARICATA*

1a. Plants perennial; mericarps with a longitudinal crest ..... 5. *G. albanum*

1b. Plants annual; mericarps without a longitudinal crest ..... 6. *G. divaricatum*

**5. Geranium albanum** M. Bieb., Fl. Taur.-Caucas. 2: 137. 1808. TYPE: Georgia. "Ex Albaniâ iberică, Wakiri" [Bakir district, pr. Signakh, 41°37′N, 45°54′E], *Steven s.n.* (lectotype, here designated, LE, photo!).

*Geranium cristatum* Steven, Mém. Soc. Imp. Naturalistes Moscou 4: 50, tab. 5. 1813. TYPE: Georgia. Jucharibasch [pr. Soudour], *Steven s.n.* (lectotype, here designated, H!).

Perennial herbs with rootstock ca. 6–8 mm diam., branched, with fusiform-swollen roots and remains of stipules and petioles at apex; stem 40–60 cm tall, erect, usually branched from the base, pilose, with long eglandular hairs 1–2 mm long, and short glandular and eglandular hairs < 0.5 mm long. Basal leaves in a deciduous rosette; lamina 2.3–5.2 × 3–4.5 cm, divided for 0.65–0.75 of its length, pilose, with eglandular, appressed hairs; segments 4–7 mm wide at the base, 7–9-lobed in distal half; petioles to 11 cm long, with patent long eglandular hairs 1–1.5 mm long and short glandular and eglandular hairs < 0.5 mm long; cauline leaves opposite; stipules 4–6 × 2–3 mm, pilose with eglandular hairs on abaxial surface, glabrous adaxially. Bracts 3–4 × 1.5–2 mm, lanceolate, sometimes lobed, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 1–4.8 cm long, pilose, with eglandular, patent hairs ca. 1 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 3–4 × 0.5–1 mm, pilose with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–4 cm long, pilose, with eglandular patent hairs 1–1.5 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals 6–9 × 2.5–3 mm, mucronulate (with mucro 0.3–0.6 mm long), with scarious margins 0.1–0.2 mm wide, with eglandular hairs 1–1.3 mm long and some shorter (< 0.5 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 12–14 × 8–9 mm, emarginate (with notch ca. 1 mm deep), bright purple. Stamen filaments 5–6 mm long, with spreading glandular hairs and a tuft of eglandular hairs at the base on the abaxial side, without ciliae; anthers 1.5–1.6 × 0.8–0.9 mm, purple. Gynoecium 6–7 mm long; stigma pink-purple. Fruit 15–17 mm long; mericarps 6–7 × 3–3.5 mm, with 3–4 transverse ribs and a longitudinal crest, pilose, with appressed-eglandular hairs up to 0.5 mm long, not ciliate at the base; rostrum 9–10 mm long, pilose (with erect-patent, eglandular and glandular hairs ca. 0.1 mm long); stigmatic remains 1–2 mm long, with 5 pilose lobes. Seeds 2.8–3 × 1.8–1.9 mm; hilum ⅕ as long as the perimeter. Chromosome number: $n = 14$; $2n = 20$?. Figure 13. *Additional illustrations.* Karjagin (1955: 39 tab. 2); Grossheim (1962: 11 tab. 1 fig. 3); Tokarski (1972: 59, pl. 1).

*Distribution* (Fig. 14). Northern Iran and Caucasus; meadows, stony places, and forest margins, between 100 and 2600 m. *Additional maps.* Grossheim (1962, map no. 4); Meusel et al. (1978: 263).

*Phenology.* Flowering June–August.

*Representative specimens examined.* AZERBAIJAN. Lankoran, 38°45′N, 48°50′E, 1836, *Hohenacker s.n.* (BM, M, W); Elisabethpol, Schuscha, pr. Chan-Kendy, 39°17′N, 46°23′E, June 1900, *Fedossejew s.n.* (LE). GEORGIA. Georg. Cauc., m. Wilnser, 1838, *Kalm s.n.* (G); in dumosis circa Telav, Kachetia, 41°55′N, 45°29′E, 20 June 1918, *Pastuchov s.n.* (K, W); Transcaucasia, Georgia Orient., Steppa Shiraki, m. Schavi-mta, 41°42′N, 46°15′E, 600 m, 8 May 1940, *Sachokia s.n.* (MA-575069); pr. Sihuscha Georg. Cauc., 1838, *Hohenacker s.n.* (K, M). IRAN. 59 km S of Shahi, 1500 m, 36°27′N, 52°51′E, *Furse 2979* (K, W); Ardabil-Astara, 1200 m, 38°24′N, 48°52′E, *Bowles Scholarship Bot. Exped. 2312* (K); East Azerbaijan, W side of Hasi Amir Pass, on Russian border, 28 km NE of Ardabil, 1600 m, *Grant 16229* (W); Gilan, around the village Damash-E of Rudbar, 1700 m, 36°48′N, 49°23′E, *Ala 17143G* (W); Gilan, in collibus 10–20 km W Astara, ad viam versus Heyran ducentem, 500 m, 38°22′N, 48°38′E, *Rechinger 39902* (B, G, W); Gorgan, 37°00′N, 54°30′E, *Sharif 545* (W); Gozlu, Mazenderan, *Koelz 16221* (W); Guilan, *Lindsay 741* (BM, K, W); Mazanderan, Haraz valley, Karehsang, 100 m, 36°18′N, 52°0′E, *Wendelbo 584* (W); Ostan 1, Hassankif, 1070 m, 36°29′N, 51°9′E, *F. Schmid 6636* (G); Ostan 2, Dimelo, sommet du versant caspien, peu en dessous de la crête, 2600 m, *F. Schmid 5986* (G, W); Ostan 2, entre Amol et Siavicheh, 1800 m, 36°28′N, 52°21′E, *F. Schmid 5853* (G, W); Persia borealis, in dumetis prope Rascht, 37°16′N, 49°35′E, *J. Bornmüller & A. Bornmüller 6507* (BM, G, K, W); Persia borealis, Elburz, Pole-Zangulé, *Gauba 1553* (B); Persia borealis, Elburz, Kandaran, 1900 m, 36°16′N, 49°42′E, *Gauba 1453* (B); prov. Talysh et Korabach, m. Kohenaker, 38°29′N, 48°27′E, 1838, *Kalm s.n.* (G). RUSSIA. North Caucasus, Dagestan, pr. urb. Derbent, 130 m, 42°3′N, 48°17′E, *Alexeenko 7437* (LE); distr. Kurinskij, pr. st. Diviczi, 41°35′N, 47°45′E, *Alexeenko 7428* (LE).

*Geranium albanum* is a perennial species endemic to northern Iran and the Caucasus. It has a singular mericarp, with a very thick wall and a well-developed dorsal crest. Features shared with *G. divaricatum* are the inoperative discharge mechanism and the ribbed mericarp.

The chromosome number in this species is not fully clarified. Warburg (1938: 145) and Van Loon (1984a: 276) have given different numbers, with only that of the first author concording with data for *G. divaricatum.*

**6. Geranium divaricatum** Ehrh., Beitr. Naturk. 7: 164. 1792. *Geranium winterlii* Roth ["winterli"], Catal. Bot. 2: 78. 1800, nom. illeg. TYPE: Hungary. *Ehrhart Plant. Select. 69* (lectotype, here designated, M!).

*Geranium divaricatum* var. *ambiguum* Rochel ex Schult., Oestr. Fl. Ed. 2, 2: 285. 1814. *Geranium divaricatum*

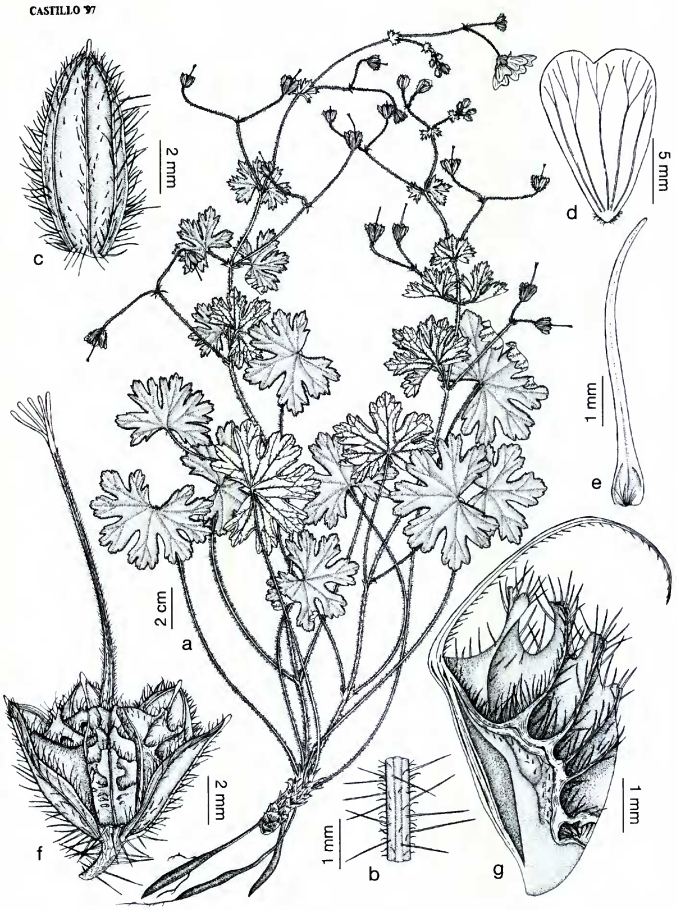


Figure 13. *Geranium albanum*. —a. Habit. —b. Peduncle. —c. Sepal. —d. Petal. —e. Stamen. —f. Fruit and sepals. —g. Mericarp. (a–e based on *Kalm s.n.* (G); f, g based on *Schmid 6636* (G).)

[B] *ambiguum* (Rochel ex Schult.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 51. 1913. TYPE: Cultivated, *Rochel 292* (lectotype, here designated, M!; isolectotype, W!).

Annual herb 20–50 cm tall; stem erect, usually branched from the base, pilose, with long eglandular hairs 1–3 mm long and short glandular and

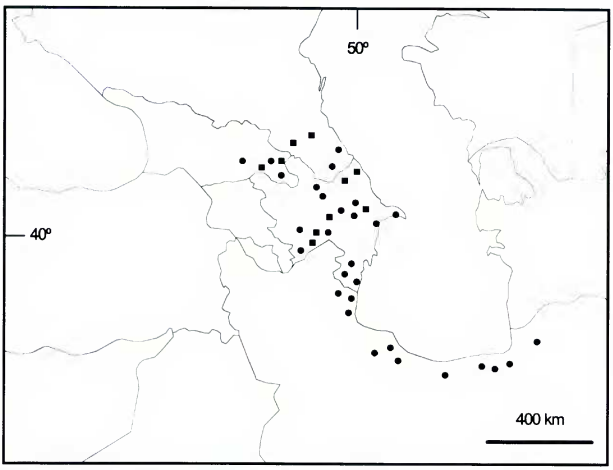


Figure 14. Distribution of *Geranium albanum* (longitude = 50°E; latitude = 40°N). Dots correspond to herbarium records, and squares indicate literature records from Grossheim (1962).

eglandular hairs < 0.5 mm long. Basal leaves in a ± persistent rosette; lamina 2.5–7 × 3.1–7.9 cm, divided for 0.65–0.85 of its length, pilose, with glandular and eglandular, appressed hairs; segments 4–9 mm wide at the base, 7–12(–15)-lobed in distal half; petioles to 15 cm long, with patent long eglandular hairs 1–2.8 mm long and short glandular and eglandular hairs < 0.5 mm long; cauline leaves alternate; stipules 4–7 × 1–2 mm, pilose with glandular and eglandular hairs on abaxial surface, glabrous adaxially. Bracts 4–5 × 1.5–2 mm, linear-lanceolate, sometimes lobed, pilose with glandular and eglandular hairs on abaxial surface and on the margin, glabrous adaxially; peduncles 0.6–3.5 cm long, pilose, with eglandular patent hairs 1–3.5 mm long and short (< 0.5 mm) glandular and eglandular hairs; bracteoles 3–4 × 0.5–1 mm, pilose with glandular and eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1–2.8 cm long, pilose, with eglandular patent hairs 1–2.5 mm long and short (< 0.5 mm) glandular and eglandular hairs. Sepals 4–4.5 × 1.8–2 mm, mucronulate (with mucro ca. 1 mm long), with scarious margins ca. 0.1 mm wide, with short (< 0.8 mm) eglandular and glandular hairs on the abaxial side, glabrous on the adaxial side. Petals 4.5–6.5 × 2.5–3 mm, emarginate (with notch ca. 1 mm deep), bright purple. Stamen filaments 1–2.5 mm long, pilose on the abaxial side, ciliate on the proximal half; anthers 0.4–0.6 × 0.3–0.4 mm, purple. Gynoecium 3–3.5 mm long; stigma purple. Fruit 7–11 mm long; mericarps 2.8–3.5 × 2–1.8 mm, with 3–4 transverse ribs, without a longitudinal rib or crest, pilose, with appressed-eglandular hairs up to 0.5 mm long, not ciliate at the base; rostrum 5–8 mm long, pilose (with erect-patent, eglandular and glandular hairs ca. 0.1 mm long); stigmatic remains 0.5–1 mm long, with 5 pilose lobes. Seeds 2.4–2.6 × 1.3–1.4 mm; hilum 1/6 as long as the perimeter. Chromosome number: $2n = 28$. Figure 15. *Additional illustrations.* Reichenbach (1841–1842: tab. 188 fig. 4873); Gams (1924: 1695, fig. 1637e–h); Tokarski (1972: 63, pl. 13).

*Distribution* (Fig. 16). Europe to central Asia, China, and the Indian subcontinent; waste places, meadows, stony dry slopes, field margins, and shady wood borders, between 0 and 2100 m.

*Phenology.* Flowering March–September.

*Representative specimens examined.* AFGHANISTAN. Farkhar-Tal, Takhar, 1250 m, 36°34′N, 69°51′E, *Podlech 10484* (M). ARMENIA. Ararat, montes Gegamski khrebet, in vicinitate ruinarum pagi Akhkeng, 2100 m, 39°47′N,

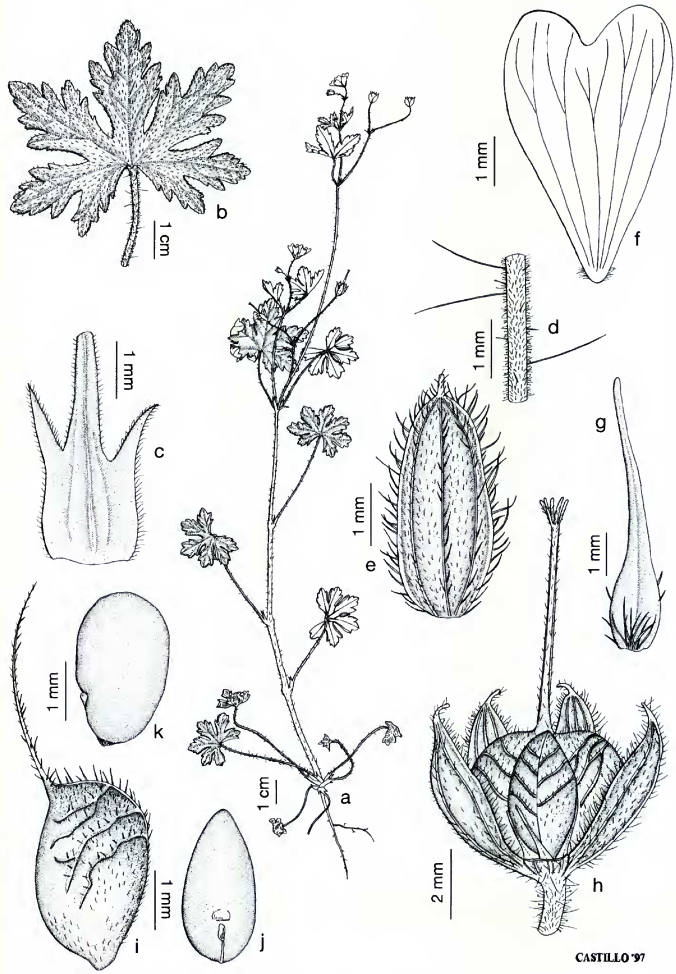


Figure 15. *Geranium divaricatum.* —a. Habit. —b. Leaf. —c. Stipule. —d. Peduncle. —e. Sepal. —f. Petal. —g. Stamen. —h. Fruit and sepals. —i. Mericarp. —j, k. Seeds. (a, c–g based on *Popov & Vvedensky s.n.* (MA-71170); b based on *Fritzsche s.n.* (BC-825281); h–k based on *Koch 46/348* (MA).)

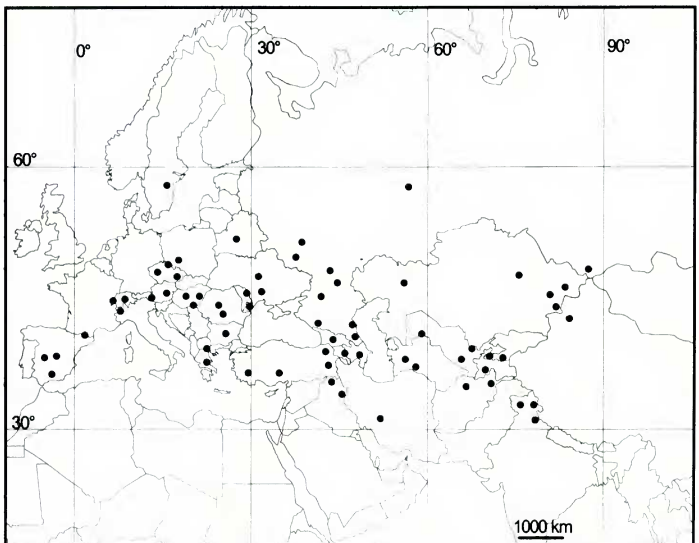


Figure 16. Distribution of *Geranium divaricatum*, based on herbarium records.

44°46′E, 10 July 1975, *Vasák s.n.* (B). AUSTRIA. Lienz, Tirolis, 46°15′N, 12°50′E, 19 May 1869, *Gander s.n.* (K). BELARUS. Minsk, Khojni, Mozyrskago, 53°54′N, 27°34′E, 1902, *Bordzilowski s.n.* (LE). BULGARIA. In graminosis ad Sofia, June 1924, *Stefanoff s.n.* (BM). CHINA. **Xinjiang**: Songarei, *Schrenk s.n.* (G); Tian-schan, Aktasch in montibus Karshan-tau, 43°0′N, 84°0′E, 15 May 1928, *Popov & Vvedensky s.n.* (MA-71170). FRANCE. Cerdagne, vallée de Carol à Porta, 1500 m, 13 Aug. 1916, *Sennen s.n.* (MA-155028). GERMANY. Pr. Francfort-sur-l'Oder, 52°20′N, 14°32′E, 27 June 1847, *Buek s.n.* (K). GREECE. Macedonia, Pisoderion, 1200 m, *Alston & Sandwith 970* (K). HUNGARY. Pest, in dumetis insula Cspel, 19 June 1900, *Degen s.n.* (G). INDIA. Chamba, W Himalaya, 2000 m, 32°N, 76°E, *Watt 2067* (K); Gaon, Bashahr, NW Himalaya, *Lace 882* (K). IRAN. Noa-kuh, Nawa, nr. Karend, W of Kermanshah, 2000 m, 31°28′N, 54°54′E, *Furse 1892* (K). IRAQ. Jebel Sinjar, Mosul liwa, 1000 m, *Gillet 11134* (K). ITALY. Oulx, ad saepes secundum viam quae est inter Borgata superiore di Oulx et S. Marco, Torino, 1200 m, 45°02′N, 6°50′E, 25 June 1906, *Ferrari & Vallino s.n.* (K). JAMMU-KASHMIR. Preslang near Pahlgam, Kashmir, 43°1′N, 75°25′E, *Stewart 21676* (K). KAZAKSTAN. Turkestania, Wernoje, 43°17′N, 68°16′E, 24 Sep. 1876, *Kuschakewitz s.n.* (K). KYRGYZSTAN. Turkestania, prov. Fergana, distr. Osch, pr. Gulcza, 40°21′N, 73°26′E, 30 May 1900, Tranzschel s.n. (LE). POLAND. Breslau, 51°5′N, 17°0′E, June 1860, *Uechtriz s.n.* (W). ROMANIA. Oltenia, Dolj, pr. Timburesti, 70 m, 9 May 1971, *D. Cîrtu & M. Cîrtu s.n.* (MA-252485). RUSSIA. North Caucasus, Dschmagat-Tal nordöstlich Teberda, 43°28′N, 41°46′E, *Stohr 9* (B); Russia Central, Kursk, Bielgorod, 50°38′N, 36°36′E, 5 June 1900, *Sukaczew s.n.* (LE); Russia East, Bashkiria Autonomous SSR, Zilairskij rajon, Userganskaya, 54°N, 56°E, *Grebner 241* (LE); Russia South, Saratov, Sarepta, 48°31′N, 44°29′E, 1 June 1894, *Becker s.n.* (M). SLOVAKIA. In mte. Zobor, Nitriam, 48°21′N, 18°7′E, 1836, *Láng s.n.* (K). SPAIN. Granada, Sierra Nevada, loc. dumetes inter Cerro Trevenque et Aquilones de Dilar, 1800 m, *Porta & Rigo 104* (K). SWEDEN. Sodermanland, Nacka, 4 Sep. 1915, *Vestergren s.n.* (W). SWITZERLAND. Cantou des Grisons, Engadine, ruine Steinsberg Ardez, 1490 m, 22 July 1933, *Huber s.n.* (BC-79174). TADZHIKISTAN. Pendjhakent, 1000 m, 39°29′N, 67°37′E, 23 May 1892, *Komarov s.n.* (LE). TURKEY. Babadagh Dobrudscha, bei Cucarova, 36°32′N, 29°10′E, *Sintenis 524* (K). TURKMENISTAN. Ashabad, in angustiis Karanky, 37°58′N, 58°24′E, *Litwinow 1129* (G). UKRAINE. Charkov pr. Walki, 50°0′N, 36°15′E, *Lindeman s.n.* (W). UZBEKISTAN. Pr. Tashkent, 41°16′N, 69°13′E, *Kuschakewitz s.n.* (K).

The most distinctive feature of this annual species is the transversely ribbed mericarp, which has thin walls and no longitudinal crest.

The eastern limit of *Geranium divaricatum* in

Europe is not well established, because it is quite difficult to obtain material from Russian herbaria. In Asia, this species reaches the Chinese Xinjian (84°E) and the western Himalayas to 76°E. It is known from Sweden by only one collection, which could be an introduction; the nearest locality is in Germany, almost 1000 km southward.

## Dubious Names

*Geranium brutium* [b] *micranthum* N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 122. 1913. TYPE: Italy. "Pisterola a Signa sopra Vallesega," *N. Terracciano s.n.* (no authentic material located). = *G. molle?*

*Geranium* ×*luganense* Chenevard, Bull. Herb. Boissier sér. 2, 3: 427. 1903. TYPE: Switzerland. "Crocefisso, Mt S. Giorgio," *Chenevard s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* f. *candidum* Beck, Fl. Nieder-Österreich. 563. 1892. TYPE: Austria. "Auf bebauten und wüsten Stellen, unter Buschwerk hie und da um Wien und bis gegen Baden, bei Laxenburg, Hainburg, Melk, Schenkenbrunn, Retz. V–IX," *Beck s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* var. *grandiflorum* Viv. ["*grandiflora*"], Fl. Libyc. Spec. 39. 1824. TYPE: Libya. "H. in totâ Cyrenaicâ," *Viviani s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* var. *grandiflorum* Vis., Fl. Dalmat. 3: 212. 1851, nom. illeg., non Viv. (1824). TYPE: Italy. "Hab in agris, cultis et ruderatis circa Zara, Sebenico, Traù, Spalato, Ragusa, var. praecipue in saxosis ad Scagliari prope Cattaro et in Montenegro," *Visiani s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* var. *grandiflorum* Lojac., Malpighia 20: 194. 1906, nom. illeg., non Viv. (1824). TYPE: Italy. "In herbidis Palermo. Herb. Pan.!," *Lojacono s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* var. *minus* Chevall. ["*minus*"], Fl. Gén. Env. Paris Ed. 1, 2: 802. 1828. TYPE: France. "Commun dans les bois et les décombres," *Chevallier s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* subsp. *pollinense* A. Terracc., Malpighia 4: 198. 1890. *Geranium pollinense* N. Terracc. ex A. Terracc., Malpighia 4: 198. 1890. TYPE: Italy. "Del monte Pollino alle Neviere ed all'Affircata," *A. Terracciano s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* var. *suaveolens* Boenn. ex Rchb., Fl. Germ. Excurs. 778. 1832. *Geranium pusillum* f. *suaveolens* (Boenn. ex Rchb.) Gams, in Hegi, Ill. Fl. Mitt.-Eur. Ed. 1, 4: 1702. 1924. *Geranium molle* [l] *suaveolens* (Boenn. ex Rchb.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Germany. "Auf bebautem Boden, Schutt, an Mauern, Planken" (no authentic material located). = *G. molle?*

*Geranium molle* f. *pinguis* K. Malý, Verh. K.K. Zool.-Bot. Ges. Wien 54: 229. 1904. *Geranium molle* [B] *pinguis* (K. Malý) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Yugoslavia. "Novibazar: kljeznicatal zwischen Prijepolje und Jabuka (Weisbach)," *Weisbach s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* var. *montanum* A. Terrac. ex N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 123. 1913. TYPE: Italy. "Acquanera," *N. Terracciano s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* [II] *tenuisecta* A. Terracc. ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Nei colli sino a che sui monti. . .," *A. Terracciano s.n.* (no authentic material located). = *G. molle?*

*Geranium molle* [I] *triviale* A. Terracc. ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 52. 1913. TYPE: Italy. "Porto d'Anzio," *A. Terracciano s.n.* (no authentic material located). = *G. molle?*

*Geranium punctatum* Kanitz, Linnaea 32: 569. 1863, nom. illeg., non Andrews (1799). TYPE: Hungary. "Habitat inter frutices Syrmii, unde a Wolny pro G. umbroso missum," *Kanitz s.n.* (no authentic material located). = *G. molle?*

*Geranium pusillum* var. *exsertum* Peterm., Fl. Lips. Excurs. 512. 1838. TYPE: Germany. ". . . ad praedium Pfaffendorf, ad pagos Leutzsch, Anger, Reudnitz, ad oppidum Delitzsch etc.," *Petermann s.n.* (no authentic material located). = *G. pusillum?*

*Geranium pusillum* var. *luxurians* A. Terracc., Malphigia 4: 206. 1890. TYPE: Italy. ". . . che ho qui di Carlsbaad e dell'Alpe Gebbo (1165 m) in val Cairasca (Ossola) Frizzi!," *A. Terracciano s.n.* (no authentic material located). = *G. pusillum?*

*Geranium pusillum* f. *subcalvum* Casp. ex Abrom., Fl. Ost- & Westpreussen 154. 1898. TYPE: Germany. "Westpreussen, Fl. zw. Kamin u. Obkaser Mühle, Abhang am Mochelsee (Km. 70)," *Abromeit s.n.* (no authentic material located). = *G. pusillum?*

*Geranium pusillum* var. *villosum* F. Saut., Oesterr. Bot. Z. 49: 402. 1899. *Geranium pusillum* [?] *villosum* (F. Saut.) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 42. 1913. TYPE: Italy. "Bozen: an Weinbergsmauern in St. Johann, Guntschna, St. Magdalena, bei Caslar," *Sauter s.n.* (no authentic material located). = *G. pusillum?*

*Geranium pyrenaicum* var. *depilatum* Sommier & Levier, Trudy Imp. S.-Peterburgsk. Bot. Sada 16: 102. 1900. *Geranium depilatum* (Sommier & Levier) Grossh., in Grossh. & Schischk., Sched. Herb. Pl. Or. Exsicc. 14: 36. 1928. TYPE: Georgia. "Rekom, fl. fr. (Lojka)," *Lojka s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

*Geranium pyrenaicum* var. *leiocarpum* Guss. ex Lojac., Malpighia 20: 195. 1906. TYPE: Italy. "Lojac. exsicc. pl. Pizzuta. Herb. Pan.!," *Lojacono s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

*Geranium pyrenaicum* var. *montanum* A. Terracc., Malpighia 4: 208. 1890. TYPE: Italy. "Monte Pollino all'Afforcata N. Terracciano!, sommità del Coccorello in Abruzzo Cherici! Velino Sanguinetti!," *N. Terracciano s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

*Geranium pyrenaicum* var. *mutilum* Beck, Fl. Nieder-Österreich. 563. 1892. *Geranium pyrenaicum* [4] *mutilum* (Beck) Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913. TYPE: Austria. "Bei Hütteldorf, Laxemburg," *Beck s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

*Geranium pyrenaicum* [b] *murense* N. Terracc., Bull. Orto Bot. Regia Univ. Napoli 3: 122. 1913. TYPE: Italy. "S. Vito vecchio, e nei pressi del Piscone di Pister-

ola," *N. Terracciano s.n.* (no authentic material located). = *G. pyrenaicum* subsp. *pyrenaicum?*

## Excluded Names

*Geranium bifidum* Ehrenb. ex R. Knuth, in Engl., Pflanzenr. IV.129 (Heft 53): 152. 1912, nom. nud., pro syn.

*Geranium calabrum* Ten., nom. nud., in sched. (NAP: photocopy!).

*Geranium divaricatum* var. *tenuisectum* Sennen, Pl. Espagne 1916, no. 2575 (1916), nom. nud., in sched. (BC-825282).

*Geranium molle* subf. *abortiva* (De Not. ex Ces.) A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium molle* f. *albiflorum* R. Uechtr., Jahresber. Schles. Ges. Vaterl. Cult. 60: 254. 1883, nom. nud.

*Geranium molle* var. *caucasicum* Regel ex Woronow, in Kusn., N. Busch & Fomin, Fl. Cauc. Crit. 7(3): 66. 1909, nom. nud., pro syn.

*Geranium molle* var. *diffusum* Ten. ex A. Terracc., Malpighia 4: 202. 1890, nom. nud.

*Geranium molle* var. *elatum* Ten. ex A. Terracc., Malpighia 4: 202. 1890, nom. nud.

*Geranium molle* f. *glabrata* A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium molle* var. *graecum* A. Terracc., Malpighia 4: 202. 1890, nom. nud.

*Geranium molle* var. *lucanum* Gasp. ex Nyman, Consp. Fl. Eur. 138. 1878, nom. nud., pro syn.

*Geranium molle* var. *maioriflorum* Borbás, Oesterr. Bot. Z. 40: 382. 1890, nom. nud.

*Geranium molle* var. *maritimum* Lojac., Malpighia 20: 194. 1906, nom. nud., pro syn.

*Geranium molle* var. *montanum* A. Terracc., Malpighia 4: 202. 1890, nom. nud.

*Geranium molle* subsp. *normale* A. Terracc., Malpighia 4: 202. 1890; nom. inval. (see Greuter et al., 1994, Art. 24.3).

*Geranium molle* f. *pygmaea* A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium molle* f. *sepincola* A. Terracc., Malpighia 4: 200, 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium molle* f. *tenuisecta* A. Terracc., Malpighia 4: 199–200, 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium molle* f. *trivialis* A. Terracc., Malpighia 4: 199–200, 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium molle* [a] *triviale* A. Terracc. ex Gortani & M. Gortani, Fl. Friulana 2: 300. 1906, nom. nud.

*Geranium molle* var. *typicum* Posp., Fl. Oesterr. Küstenl. 2: 31. 1898, nom. inval. (see Greuter et al., 1994, Art. 24.3).

*Geranium molle* f. *villosissima* A. Terracc., Malpighia 4: 202. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium molle* var. *vulcanicum* A. Terracc., Malpighia 4: 202. 1890, nom. nud.

*Geranium multiflorum* Lang ex Schur, Oesterr. Bot. Z. 18: 317. 1868, nom. nud., pro syn.

*Geranium novum* Winterl, Index Hort. Bot. Univ. Hung., fig. 2. 1788, nom. inval. (see Greuter et al., 1994, Art. 23.6).

*Geranium pseudovillosum* Schur ["*pseudo-villosum*"], Enum. Pl. Transsilv. 921. 1866, nom. nud., pro syn.

*Geranium pusillum* var. *albiflorum* Opiz, Seznam 47. 1852, nom. nud.

*Geranium pusillum* var. *album* Lindm., Bot. Soc. Exch. Club Brit. Isles 7: 766. 1925, nom. nud.

*Geranium pusillum* f. *major* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium pusillum* f. *minor* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium pusillum* [α] *genuinum* Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 41. 1913, nom. inval. (see Greuter et al., 1994, Art. 24.3).

*Geranium pusillum* subf. *humifusa* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium pusillum* f. *humile* Bueck ex Prahl, Krit. Fl. Schlesw.-Holst. Ed. 1 2: 37. 1889, nom. nud., pro syn.

*Geranium pusillum* subsp. *normale* A. Terracc., Malpighia 4: 212. 1890, nom. inval. (see Greuter et al., 1994, Art. 24.3).

*Geranium pyrenaicum* f. *algeriensis* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium pyrenaicum* var. *diffusum* Ten. ex A. Terracc., Malpighia 4: 211. 1890, nom. nud., pro syn.

*Geranium pyrenaicum* var. *grandiflorum* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1876, nom. nud.

*Geranium pyrenaicum* var. *heterotrichum* Sennen, nom. nud., in sched. (PH!).

*Geranium pyrenaicum* f. *maior* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium pyrenaicum* f. *minor* A. Terracc., Malpighia 4: 208. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium pyrenaicum* subsp. *normale* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 24.3).

*Geranium pyrenaicum* var. *parviflorum* Schur, Verh. Naturf. Vereins Brünn 15: 161. 1876, nom. nud.

*Geranium pyrenaicum* f. *sicula* A. Terracc., Malpighia 4: 211. 1890, nom. inval. (see Greuter et al., 1994, Art. 33.5).

*Geranium pyrenaicum* var. *typicum* Woronow, in Kusn., N. Busch & Fomin, Fl. Cauc. Crit. 3(7): 56. 1908, nom. inval. (see Greuter et al., 1994, Art. 24.3).

*Geranium pyrenaicum* [a] *typicum* Woronow ex Graebn., in Asch. & Graebn., Syn. Mitteleur. Fl. 7: 33. 1913, nom. inval. (see Greuter et al., 1994, Art. 24.3).

*Geranium pyrenaicum* var. *velutinum* Buhse, Aufzähl. Transkauk. 48. 1860, nom. nud.

*Geranium subdivaricatum* Schur, Verh. Naturf. Vereins Brünn 15: 160. 1877, nom. inval. (see Greuter et al., 1994, Art. 34.1).

*Geranium villosum* f. *albiflorum* Sennen, Pl. Espagne, no. 2994. 1917, nom. nud., in sched. (BM!, W!).

*Geranium villosum* var. *gracile* Sennen, Pl. Espagne, no. 2994. 1917, nom. nud., in sched. (BM!, W!).

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## Appendix 1

Chromosome numbers of *Geranium* sects. *Batrachioidea* and *Divaricata*.

*Geranium* sect. *Batrachioidea*

*G. aequale*, $2n = 26$ (Gauger, 1937: 529).

*G. molle*, $n = 13$ (Warburg, 1938: 142); $2n = 26$ (Gauger, 1937: 529; Warburg, 1938: 142; Löve & Löve, 1956: 209; Böcher & Larsen, 1958: 19; Mulligan, 1959: 83; Gadella & Kliphuis, 1966: 548; Löve & Kjellqvist, 1974: 163; Alves & Leitão, 1976: 233; Skalińska et al., 1976: 120; Natarajan, 1978: 529; Májovský, 1978: 25; Franzén & Gustavsson, 1983: 104; Van Loon, 1984b: 295; Hill, 1989: 18).

*G. pusillum*, $2n = 26$ (Gauger, 1937: 529; Löve & Löve, 1945: 11; Pólya, 1950: 51; Shaw, 1952: 299; Löve & Löve, 1956: 209; Gadella & Kliphuis, 1966: 548; Fritsch, 1973: 460; Májovský, 1974: 10; Alves & Leitão, 1976:

233; Skalińska et al., 1976: 121; Fernández Casas et al., 1978: 109; Arohonka, 1982: 5; Van Loon, 1984b: 295; Buttler, 1989: 13); $2n = 34$? (Warburg, 1938: 142).
*G. pyrenaicum* subsp. *pyrenaicum*, $n = 11–12$ (Heitz, 1926: 642, 678; Tischler, 1934: 10); $n = 13$ (Galland, 1988: 144); $2n = 20$ (Chatterjee & Sharma, 1970: 183); $2n = 26$ (Gauger, 1937: 530; Májovský, 1974: 11; Skalińska et al., 1978: 42; Strid, 1980: 710; Strid & Franzén, 1981: 836; Van Loon & Van Setten, 1982: 591; Van Loon, 1984a: 277; Semerenko, 1985: 993; Galland, 1988: 144; Baltisberger, 1991: 167); $2n = 28$? (Warburg, 1938: 151; Van Loon et al., 1971: 159; Mizianty et al., 1983: 208).
*G. pyrenaicum* subsp. *lusitanicum*, $2n = 26$ (Alves & Leitão, 1976: 232; Van Loon, 1984a: 277).

*Geranium* sect. *Divaricata*

*G. albanum*, $n = 14$ (Warburg, 1938: 145); $2n = 20$ (Van Loon, 1984a: 276).
*G. divaricatum*, $2n = 28$ (Májovský, 1974: 10; Dersch, 1974: 77; Van Loon, 1984b: 294; Jankun et al., 1996: 12).

## Index to Scientific Names

Accepted names are in roman type; the main entry for each is in **boldface**. Synonyms are in *italics*.