

Taxonomic revision of *Geranium* sect. *Gracilia* (Geraniaceae)

CARLOS AEDO, JUAN JOSÉ ALDASORO, L. SÁEZ, AND
CARMEN NAVARRO

Aedo, C. and J. J. Aldasoro (Real Jardín Botánico, Consejo Superior de Investigaciones Científicas, Plaza de Murillo 2, 28014 Madrid, España; aedo@ma-rjb.csic.es, aldasoro@ma-rjb.csic.es), L. Sáez (Unitat de Botànica, Facultat de Ciències, Universitat Autònoma de Barcelona, 08193-Bellaterra, Barcelona, España; Llorens.Saez@uab.es) & C. Navarro (Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, 28040 Madrid, España; cnavar@farm.ucm.es). Taxonomic revision of *Geranium* sect. *Gracilia* (Geraniaceae). *Brittonia* 55: 93–126. 2003.—*Geranium* sect. *Gracilia* (Geraniaceae) comprises nine species in the Andes of Venezuela and Colombia. *Geranium lindenianum* and *G. gracilipes* are synonymized with *G. holosericeum*. The identity of *G. multiceps* is clarified. Its differences from the two Colombian species, *G. santanderiense* and *G. lainzii*, are discussed. *Geranium lignosum*, *G. sebosum*, *G. stoloniferum*, *G. subnudicaule*, and *G. velutinum* are now considered to be members of sect. *Gracilia*. The identity of *G. pilgerianum* could not be clarified because the type was destroyed and other collections have not been found. Micromorphological leaf and seed characters are discussed. Six lectotypes and one neotype are designated.

Key words: Geraniaceae, *Geranium*, *Gracilia*, Colombia, Venezuela.

Aedo, C. y J. J. Aldasoro (Real Jardín Botánico, Consejo Superior de Investigaciones Científicas, Plaza de Murillo 2, 28014 Madrid, España; aedo@ma-rjb.csic.es, aldasoro@ma-rjb.csic.es), L. Sáez (Unitat de Botànica, Facultat de Ciències, Universitat Autònoma de Barcelona, 08193-Bellaterra, Barcelona, España; Llorens.Saez@uab.es) & C. Navarro (Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, 28040 Madrid, España; cnavar@farm.ucm.es). Taxonomic revision of *Geranium* sect. *Gracilia* (Geraniaceae). *Brittonia* 55: 93–126. 2003.—Se revisa *Geranium* sect. *Gracilia* (Geraniaceae), un grupo formado por nueve especies distribuidas por los Andes de Venezuela y Colombia. Se sinonimizan *G. lindenianum* y *G. gracilipes* a *G. holosericeum*. Se aclara la identidad de *G. multiceps*, y se establecen sus diferencias con *G. santanderiense* y con *G. lainzii*, ambas esencialmente colombianas. Se aceptan en esta sección *G. lignosum*, *G. stoloniferum* y *G. sebosum*, propuestos tras la descripción de la sect. *Gracilia*, y *G. subnudicaule* y *G. velutinum*, ya tratados por otros autores en como pertenecientes a este grupo. Por el contrario, la identidad de *G. pilgerianum* no ha podido ser aclarada tras la destrucción del tipo y ante la falta de otros materiales de la especie. Se estudian diversos caracteres micromorfológicos, especialmente algunos referibles a la anatomía foliar y la de la semilla. Se designan seis lectótipos y un neótipo.

The genus *Geranium* L. comprises ca. 420 species in temperate areas and tropical mountains throughout most of the world (Aedo et al., 1998a). A brief history of the

generic delimitation and infrageneric classification, as well as a description of the genus, can be found in Aedo (1996). In addition, a key for subgenera and sections can

be found in Aedo et al. (1998b) and Aedo et al. (1998a), respectively.

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

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

South America is the richest area of the world for *Geranium*, with over 150 species, most of them provisionally included in sect. *Geranium*. It is the region that requires more taxonomic work on the genus. For many species, taxonomic information is deficient and they are only known by their short original descriptions. In other cases, local catalogues, floras, or checklists provide additional interesting information (Barboza & Correa, 1988; Bono, 1996; Brako & Zarucchi, 1993; Lasser, 1947; Marticorena & Quezada, 1985; Sánchez, 1998; Vareschi, 1970). The only recent monographic study covers the stemless species included in sects. *Azorelloida*, *Neoandina*, and *Paramensia*, and comprises 27 taxa (Aedo et al., 2002).

Knuth's (1912) monograph of *Geranium* provided the sole description of sect. *Gracilia*. His account was based on the limited material available at that time. He knew only three of the seven recognized species firsthand: *G. holosericeum*, *G. multiceps*, and *G. pilgerianum* (represented by two, seven, and one specimen, respectively). For the remaining accepted species, he transcribed the original descriptions of *G. gracilipes*, *G. lindenianum*, *G. subnudicaule*, and *G. velutinum*. As a consequence of the scarcity of plant material, the descriptions and key are incomplete, lacking some important features. In this present revision we have added three species (*G. lignosum*, *G. sebosum*, and *G. stoloniferum*) described since his monograph. We have clarified the identity of *G. multiceps*, in which Knuth (1912) included three different species: *G. lainzii*, *G. multiceps*, and *G. santanderiense*.

Following our recent revisions of several *Geranium* sections (Aedo, 2001; Aedo et al., 2002), and in pursuit of the aim to comprehensively monograph the genus, we present here a revision of section *Gracilia*.

The species of this group have \pm vertical rootstock (not turnip-shaped), well-developed aerial stems, palmatifid leaves without an abscission zone between lamina and petiole, and an inflorescence that is a dichasial cyme. They are restricted to the Andes of northern and central Colombia and Venezuela.

Materials and Methods

This revision is based on more than 400 herbarium specimens from the following herbaria: B, BM, BR, C, COL, E, F, G, GH, K, LE, M, MA, MER, MO, MPU, NY, P, PORT, S, U, US, VEN, W, and Z. Microfiche, photographs, and other data have been examined from the following additional herbaria: B, FI, and KW. Curators from AAU and H reported that their herbaria did not have any specimens from this section.

For epidermal studies, dried leaves were rehydrated in water for 48–96 hours, depending on the leaf's condition, and cleared in a commercial solution of sodium hypo-

clorite for 3–8 hours until they were totally transparent (Stace, 1965). After being washed with distilled water, the adaxial and abaxial epidermical surfaces were separated and studied under a Nikon Photolab microscope equipped with a drawing tube. Twenty measurements of stomatal guard cells and trichomes were done for each specimen.

For scanning electron microscopy (SEM), samples were critical-point dried (Cohen, 1974), mounted on aluminium stubs, coated with 40–50 nm gold, and examined with a JEOL-TSM T330A scanning electron microscope at 15 kV.

Seeds were cut transversely to reveal their internal structure. Thin hand-cut sections were taken with a SLEE-MAINZ-MTC microtome in the micropylar third, stained with Malachite green, and photographed under magnification.

Morphology

LIFE SPAN AND HABIT

All species of *Geranium* sect. *Gracilia* are small, perennial, and usually herbaceous plants. The unique exception is *G. lignosum*, a shrub. The basal part of the plant is unknown; herbarium specimens of this species only show portions of one or two branches. Consequently, it is difficult to determine the size of the whole plant. The size of the remaining species of this section varies from 8 cm high in the smaller specimens of *G. lainzii* to 100 cm high in the largest specimens of *G. holosericeum*. They usually have a \pm vertical and branched rootstock (but \pm horizontal in *G. santanderiense*), being neither tuberculate nor turnip-shaped. The rootstock is more or less slender (3–10 mm diam.). Roots are fusiform in *G. lainzii*, *G. multiceps*, and *G. santanderiense*, and unknown in the remaining species.

The upper part of rootstock branches are not subterranean and are often covered by remains of the stipules. Each branch ends in a rosette of leaves from which erect or decumbent (in *Geranium lainzii*, *G. multiceps*, and *G. santanderiense*) aerial stems arise directly. *Geranium holosericeum* has a basal structure, unique in sect. *Gracilia*,

which we have named as “vegetative stems.” These vegetative stems are slender, covered by young stipules, without any vestiges of the petiole, more or less horizontal, and not rooting (shown in Fig. 5a). At the apex of each vegetative stem, new leaf rosettes are developed; during the next year, new fertile and erect stems arise.

Each rootstock branch bears several fertile stems in all species but *Geranium stoloniferum*, which has solitary fertile stems. *Geranium stoloniferum* also has an unusual character, perhaps unique: the presence of epigeal stolon.

INDUMENTUM

Three trichome types have been found, all of them simple and uniseriate (terminology of Theobald et al., 1979). A) Eglandular, unicellular hairs of variable length, 0.1–2.3 mm. They are usually wider at the base, and sometimes with a basal constriction. They have an ornamented surface of isodiametric papillae (Fig. 1a) but sometimes are smooth. According to Payne’s (1978) terminology, they could be included in the subulate type. Type A is found in all species, widespread for nearly all organs of the plant. B) Long glandular hairs, of 3–5 cells, smooth, of variable length (0.2–1.2 μ m). Two subtypes can be distinguished: the foot consisting of decussated cells (Fig. 1b) or of cylindric cells (Fig. 1c). They can be found in *Geranium holosericeum*, *G. lignosum*, *G. sebosum*, *G. stoloniferum*, *G. subnudicaule*, and *G. velutinum*, restricted to the inflorescence or throughout the whole plant. C) Short glandular hairs (43–64 μ m long), smooth, usually consisting of two cells (Fig. 1d), although they sometimes have a bicellular foot (which occurs occasionally in *G. santanderiense*, and *G. holosericeum*). They are present in all species studied here but they are not mentioned in the descriptions and key because they are only evident at high magnification (30 \times). These three types of hairs have also been found in other groups of *Geranium* (Aedo, 1996; Aedo et al., 1998b).

LEAVES

In sect. *Gracilia*, basal leaves occur in persistent rosettes. The first pair of cauline

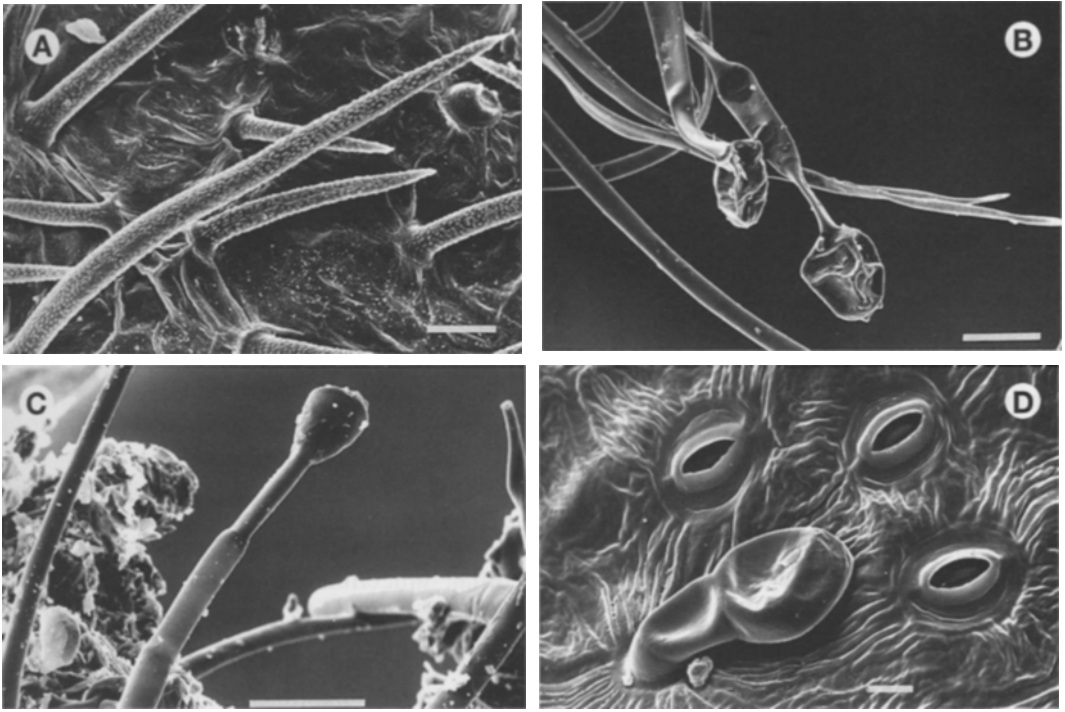


FIG. 1. Trichome types found in *Geranium* sect. *Gracilia* (SEM photographs). **A.** Eglandular trichome on the mericarp surface of *Geranium multiceps* (Oberwinkler 12799, M). **B.** Long glandular trichome with the stalk formed by decussate cells on the peduncle of *G. holosericeum* (Uribe 6787, COL). **C.** Long glandular trichome with the stalk formed by cylindrical cells on the abaxial leaf surface of *G. sebosum* (Farenholtz s.n., B). **D.** Adaxial leaf surface of *G. lainzii* showing several anomocytic stomata and one short glandular trichome (Hatheway & Idrobo 1083, COL). Scale bar: A = 300 μ m; B, C = 50 μ m; D = 10 μ m.

leaves is found at the point where the inflorescence branches arise. Cauline leaves are similar to basal ones but are progressively less divided. Thus, basal leaves have usually been used to prepare descriptions.

The leaves are polygonal in outline except in *Geranium santanderiense*, which has orbicular leaves. *Geranium lainzii* has subtruncate leaf bases, and *G. multiceps* cuneate to subtruncate leaf bases, whereas the remaining species have cordate leaf bases. All species but *G. holosericeum*, *G. lignosum*, *G. multiceps*, and *G. subnudicaule* have coriaceous leaves. The number of main divisions or segments varies between 5 and 7 in most species. Only *G. lainzii* has usually 3 segments (rarely 5). Most species have obtriangular middle segments except *G. holosericeum* and *G. lignosum*, in which they are rhombic. The secondary divisions or lobes vary between 3 (in *G. lainzii* and *G. stoloniferum*) and 13 (*G. holosericeum*).

All species in sect. *Gracilia* have palmate leaf lamina. The main division in the descriptions is indicated by the ratio between the length of the main sinus and the length of the middle segment. This ratio is high *G. holosericeum* (0.77–0.9) and *G. lignosum* (0.8–0.9), and relatively low in *G. santanderiense* (0.45–0.55). The secondary leaf division is measured at the main lobe of the middle segment. It is indicated by the ratio between the length of the main sinus of this lobe and the length of the middle segment. All species but *G. holosericeum* and *G. lignosum* have relatively low values for the secondary divisions.

Main anatomic features of sect. *Gracilia* leaves are the following: **A) Shape of cells.** Epidermal cells are, in most cases, irregularly polygonal, with straight or slightly curved anticlinal walls on the adaxial leaf surface, and more curved on abaxial face. The anticlinal cell walls of *Geranium sub-*

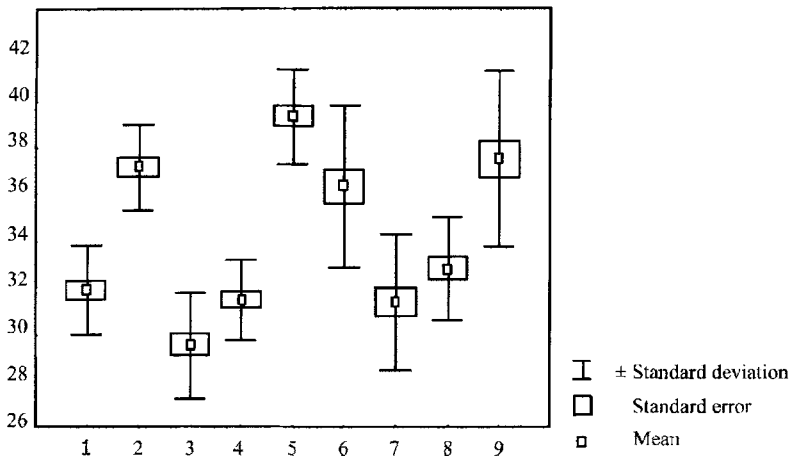


FIG. 2. Variation of the length (in μm , vertical axis) of guard cells in *Geranium* sect. *Gracilia*. Horizontal axis: 1) *G. lignosum*, 2) *G. santanderiense*, 3) *G. lainzii*, 4) *G. multiceps*, 5) *G. subnudicaule*, 6) *G. sebosum*, 7) *G. stoloniferum*, 8) *G. holosericeum*, and 9) *G. velutinum*.

nudicaule are strongly sinuous. The thickness of these anticlinal walls varies among the species, ranging from 2.5 to 8 μm . Most species show thickenings in the anticlinal walls, which are more marked on the adaxial leaf surface. This character appears at random and is difficult to use for taxonomic purposes. The surface of the outer periclinal walls is slightly convex and smooth; only in *G. lignosum* and *G. subnudicaule* is the surface striated. B) *Stomata*. Most of sect. *Gracilia* species bear hypostomatic leaves, except *G. multiceps*, *G. sebacum*, and *G. santanderiense*, which have amphistomatic leaves. All of the species present anomocytic stomata (Fig. 1d), which confirms the results of Metcalfe & Chalk (1979: 201) for the Geraniaceae. C) *Stomatal distribution*. In all taxa, stomata are regularly distributed on leaf surface, but are lacking along the main nerves. In the group of taxa with amphistomatic leaves, the stomata are scanty on the adaxial surface (hypoamphistomatic distribution). Stomata generally show an irregular pattern in distribution, although adaxial surface guard cells in *G. multiceps* show a parallel disposition with respect to the midvein. D) *Size of guard cells*. The length of guard cells range from 29.6 $\mu\text{m} \pm 2.2 \mu\text{m}$ in *G. lainzii*, to 39.3 $\mu\text{m} \pm 2.02 \mu\text{m}$ in *G. subnudicaule* (Fig. 2).

The only species showing glandular hairs on the leaf surface is *Geranium sebosum*,

although they can be rarely found in *G. subnudicaule*. The remaining species have only scattered to velutinous eglandular hairs. Four species (*Geranium lainzii*, *G. multiceps*, *G. santanderiense*, and *G. stoloniferum*) are glabrous or have scattered hairs on the adaxial surface. In these species, hairs usually are present near the margin or on the nerve channels. On the abaxial surface, *G. lainzii* is glabrous, whereas *G. multiceps*, *G. santanderiense*, and *G. stoloniferum* are hairy, mainly along the nerves. *Geranium santanderiense* shows a single unique feature: a densely ciliate leaf margin of antrorse, appressed hairs. The remaining four species of sect. *Gracilia* (*G. holosericeum*, *G. lignosum*, *G. subnudicaule* and *G. velutinum*) are hairy on both surfaces. *G. velutinum* is remarkable in having an abaxial surface covered by a velutinous indumentum of short and patent hairs.

The cauline leaves of this section are opposite. There is a progressive simplification of leaf dissection, and reduction in size towards the plant apex, for both the leaf lamina and the petiole. This is very conspicuous in the *G. lainzii*, *G. multiceps*, and *G. santanderiense*, which have very small cauline leaves, with cuneate or truncate base, and entire segments.

Geranium multiceps and *G. stoloniferum* have the shortest petioles in sect. *Gracilia*, with 5 cm and 7 cm, respectively. *Gerani-*

um santanderiense has the longest petioles, sometimes ca. 40 cm long. *Geranium sebosum* is unique in bearing glandular hairs on the petiole. The other species have only eglandular hairs. They are patent except in *G. multiceps* and *G. santanderiense*, which have retrorse and appressed hairs.

Stipule features have been examined for the basal pair of cauline leaves. The stipules are lanceolate, except in *Geranium lainzii* and *G. stoloniferum* (and occasionally in *G. holosericeum*), which have subulate stipules. The stipules are usually glabrous adaxially and eglandular hairy on the abaxial surface and margin. However, *G. lainzii* and *G. santanderiense* have stipules that are subglabrous on the abaxial surface and *G. sebosum* has stipules that are hairy on both surfaces.

INFLORESCENCE AND BRANCHING

The inflorescence is a dichasial cyme, with the lateral branches being much longer than the central one. Sometimes, one of the lateral branches is more developed than the other, resulting in a dichasial cyme that is asymmetric. Cymules are always 2-flowered, bracteolate, and solitary. They are not in umbellate aggregates at the end of the branches.

The peduncles and pedicels of *Geranium holosericeum*, *G. lignosum*, *G. sebosum*, *G. subnudicaule*, and *G. velutinum* have both glandular and eglandular hairs. The remaining species have only eglandular hairs. In all species, the pedicel and peduncle together usually overtop the subtending leaf.

SEPALS

Length varies from 4.5 to 10 mm. The mucro is usually short (0.15–0.5 mm long), but in *Geranium lignosum* it is a bit longer (1–1.5 mm). All species have 3-nerved sepals but in *G. holosericeum* and *G. lignosum*, there can be 3–5 nerves. Three taxa (*G. lainzii*, *G. multiceps*, and *G. santanderiense*) have eglandular hairs on the abaxial surface. The remaining species have also glandular hairs. All species but *G. lignosum* are glabrous adaxially.

PETALS

Petals generally range from 9 to 14 mm long. However, two species have smaller petals: *Geranium subnudicaule* (8–9 mm) and *G. sebosum* (6–7 mm). The apex is entire (in *G. lignosum*) or can be slightly emarginate (0.5–1 mm deep), as in the remaining species. In most of the species, the petals taper uniformly toward the base, without a claw, except in *G. lainzii*, *G. lignosum*, *G. multiceps*, and *G. santanderiense*, which possess a short claw 1–2 mm long. Petals are always glabrous in *G. lainzii*, *G. multiceps*, and *G. subnudicaule*. *Geranium lignosum* has hairs on both surfaces (at base) and on the margin. The remaining species are hairy on the margin and at the base of adaxial surface. The petals are purplish in all species, but vary from purplish to white in *G. multiceps* and *G. velutinum*.

STAMENS AND POLLEN

The ten stamens (all fertile) are disposed in two whorls. Staminal filaments are short, 3 to 6 mm long and not exerted. *Geranium lignosum* has longer filaments, 9–10 mm, that are not exerted. Filaments are lanceolate to subulate in *G. stoloniferum* and lanceolate in the remaining species. Staminal filaments are usually hairy on the abaxial surface (mainly towards the base) and short-ciliate on the basal margin. The cilia can be up to 1 mm long in *G. lignosum*. Two species, *G. lainzii* and *G. sebosum*, have glabrous filaments except for a few marginal hairs. The filaments are usually yellowish, except in *G. lignosum*, which has purplish filaments.

Pollen is tricolpate and more or less isodiametric. The exine is thin, semitectate, and reticulate with distinctly baculate, clavate, or gemmate supracteal elements. Two main types can be found: a) with gemmate (3 μ m), and baculate (1–2 μ m) supracteal elements as in *Geranium lignosum* (Fig. 3a); and b) with only baculate (1–1.5 μ m) supracteal elements as in *G. lainzii* or *G. multiceps* (Fig. 3b). There are intermediate cases, as in *G. velutinum*, which have gemmate and baculate supracteal elements of similar size (1–2.5 μ m). Exine ornamentation is similar to that found in previously-

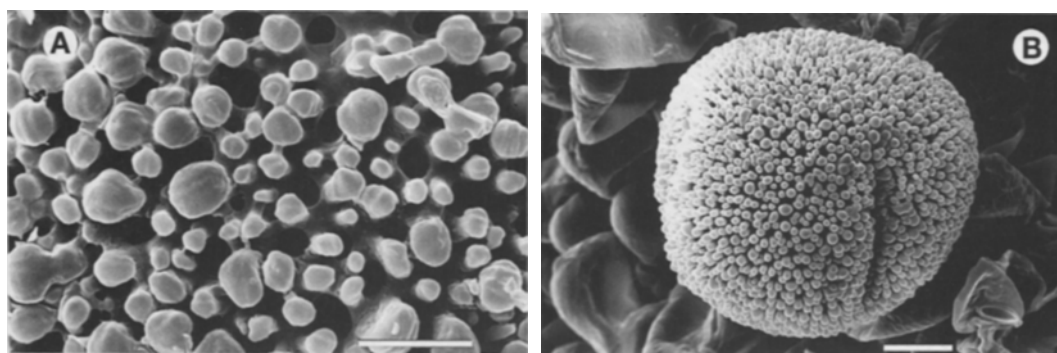


FIG. 3. Pollen of *Geranium* sect. *Gracilia* (SEM photographs). A. Exine of *Geranium lignosum*, with separate baculate and gemmate supracteal elements (*Simons s.n.*, BM). B. Pollen grain of *G. multiceps*, with more packed baculate and gemmate supracteal elements (*Stergios & Taphorn 2123*, PORT). Scale bar: A = 5 μ m; B = 10 μ m.

studied species of the genus (Bortenschlager, 1967; Stafford & Blackmore, 1991; Verhoeven & Marais, 1990).

NECTARIES

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

FRUITS

Fruits exhibit the “seed ejection-type” of discharge, which characterizes the subgenus *Geranium* (Yeo, 1984). In this type, a single seed is actively discharged by the explosive recurvature of the awn of the fruit, which remains together with the mericarp, attached to the columella. The seed ejection-type is found in all native species of South America except those of sect. *Brasiliensia* (Aedo et al., 1998a).

Geranium lignosum has the longest fruit in the section, to 30 mm long, and *G. lainzii* and *G. multiceps* have the shortest fruits, 13–18 mm long. In four species (*G. lainzii*, *G. santanderiense*, *G. stoloniferum*, and *G. velutinum*) the fruits are reflexed, whereas the remaining species possess erect fruits.

The mericarps are brownish, smooth, with a basal callus, without a longitudinal rib, and without a basal beak. The basal callus has some setae standing erect over the lower part of the orifice (formed by abscission), which prevent the seed from dropping during the pre-explosive interval. Glandular hairs are present in all species,

although *G. subnudicaule* has mericarps with scattered hairs. *Geranium holosericeum* is unique with long glandular hairs, to 0.5 mm on the mericarp.

The rostrum tapers gradually to the remains of the stigmas. The alternate condition, a columnar rostrum abruptly narrowed at the apex, is only found in three species: *G. holosericeum*, *G. lignosum*, and *G. subnudicaule*. The rostrum is hairy with patent to antrorse, eglandular and usually glandular hairs. Stigmatic remains are 2 to 4 mm long, much shorter than the fruit, and usually glabrous or subglabrous.

SEEDS

The seeds are more or less ellipsoid, finely reticulate, without spots, and with scattered stomata. They are usually reddish, except in *Geranium lignosum*, which has blackish seeds. *Geranium holosericeum*, *G. subnudicaule*, and *G. velutinum* have seeds longer than the other species. The hilum is $\frac{1}{2}$ as long as the perimeter except in *G. lainzii* and *G. subnudicaule*, which have a hilum $\frac{1}{4}$ as long as the perimeter.

The seed coat seems to be finely reticulate at a magnification of 30 \times , but SEM shows that reticulate surface is due to the prominence of outer and middle layers of the outer integument (Fig. 4a). The outer layer has cells with thickened walls and collapsed lumina, forming a polygonal structure; the inner layer is lignified and has tannins and crystals. The next layer (the outer

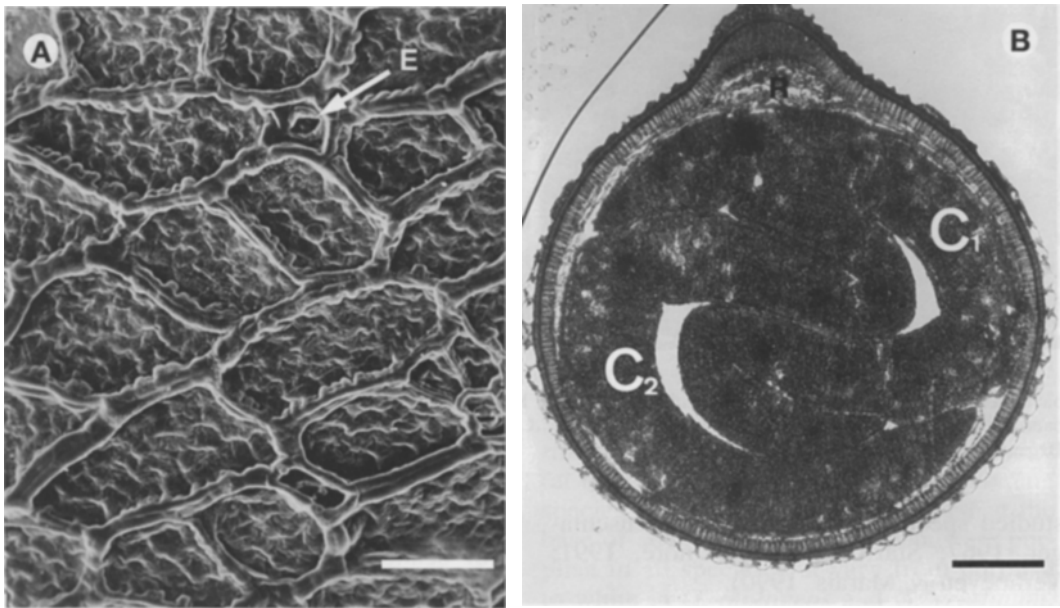


FIG. 4. Seed of *Geranium* sect. *Gracilia* (A, SEM photographs; B, optical microscope photographs). A. Seed-coat of *Geranium velutinum* (Steyermark & Manara 125442, VEN) with some scattered stomata. B. Transverse section of *G. santanderiense* seed (Cleef 4458, COL) showing conduplicate arrangement of cotyledons. C₁, and C₂ = cotyledons; E = stoma; R = radicle. Scale bar: A = 50 μ m; B = 300 μ m.

layer of the inner integument) is also sclerified, but the cells are not so compacted, being prismatic with undulate anticlinal walls. The seed coat is uniform in structure and thickness, 25 to 30 μ m thick, similar to that found in other species (Aedo et al., 1998b).

The cotyledons are always conduplicate, one half of each cotyledon lying in the primary fold of the opposite cotyledon (Fig. 4b). The cotyledons have entire margins, truncate bases, and short petioles, as found in sect. *Batrachioidea* (Aedo et al., 1998b).

Distribution

Section *Gracilia* occurs in the Andes of Colombia and Venezuela (Figs. 6, 8, 11, 14, and 18). *Geranium lignosum*'s northernmost localities are in Sierra Nevada de Santa Marta, Magdalena, Colombia, whereas *G. santanderiense* is furthest to the South in the Páramo de Chaquiro, Antioquia-Bolívar, Colombia.

The area of highest diversity is the Cordillera de Mérida, Venezuela, with five endemic species. Three of them (*Geranium*

sebosum, *G. stoloniferum*, and *G. subnudicaule*) are only known from the type localities; *G. multiceps* and *G. velutinum* are more widely distributed.

Two species, *Geranium lignosum* and *G. lainzii*, are endemic to Colombia. The former is restricted to Sierra Nevada de Santa Marta, northern Colombia, whereas the latter occurs in two separate areas, Cordillera Oriental and Cordillera Occidental, of central Colombia. *Geranium holosericeum* and *G. santanderiense* are mainly Colombian but also occur in adjacent southwestern Venezuela.

The plants are found at 2600 to 4800 m, in damp páramo (pool shores and bogs), roadside banks, rocky or dry areas, brushy slopes, or in the montane rain forest.

Taxonomic Treatment

GERANIUM sect. GRACILIA R. Knuth in Engl., Pflanzenr. IV. 129 (Heft 53): 45, 104. 1912. TYPE: *Geranium multiceps* Turcz.

Geranium sect. *Fruticulosa* R. Knuth, Repert. Spec.

Nov. Regni Veg. 28: 10. 1930. TYPE: *Geranium lignosum* R. Knuth

Perennial *herbs* or *shrubs*. *Rootstock* 3–10 mm diam., \pm vertical to horizontal; fusiform roots, sometimes unknown; *aerial stems* 8–100 \times 0.1–0.5 cm, leaved (sometimes scapiform), erect or decumbent, with eglandular and glandular hairs, eglandular hairs, or glabrous, usually without stolon, sometimes with vegetative stems, \pm horizontal, and covered with imbricate stipules. *Basal leaves* in a persistent rosette, venation actinodromous; lamina orbicular to polygonal, cordate, or subtruncate, palmatifid, sometimes coriaceous, glabrous to velutinous; segments 3–7, obtriangular or rhombic, 3–13-lobed in the distal half; *cauline leaves* opposite; stipules lanceolate or subulate, free, papery, hairy. *Inflorescence* in dichasial cymes, with lateral branches longer than the central branch; cymules 2-flowered, solitary; peduncles erect or reflexed, with glandular and eglandular hairs, or only eglandular hairs; bracteoles lanceolate or subulate, papery; pedicels with glandular and eglandular hairs, or only eglandular hairs; pedicel and peduncle together usually overtopping the subtending leaf. *Sepals* ovate, erect patent during anthesis and erect in fruit, shortly mucronate, with scarious margins, hairy abaxially (with eglandular or glandular hairs), usually glabrous adaxially. *Petals* erect patent, \pm obovate, entire or emarginate, without a claw or with a short claw, glabrous or hairy at the base, purplish (sometimes white). *Stamens* 10, both whorls bearing anthers; filaments not exerted, usually lanceolate, per-

sistent in fruit, \pm ciliate, usually hairy abaxially, yellowish. *Nectaries* hemispherical, glabrous. *Stigmas* yellowish to purplish. *Fruit* of the seed-ejection type; mericarps smooth, without longitudinal rib, without basal beak, callus basal, without a basal prong, hairy; rostrum with or without a narrowed apex; stigmatic remains of 5 usually hairy lobes. *Seeds* ellipsoid, reddish or blackish; hilum 1/6–1/4 as long as the perimeter. *Cotyledons* entire.

Section *Gracilia* is readily distinguished from the other South American sections by the combination of the following characters: rootstock \pm vertical and not turnip-shaped, obvious aerial stems, palmatifid leaves without an abscission zone between lamina and petiole, and inflorescences in a dichasial cyme of 2-flowered cymules. Section *Fruticulosa* was described by Knuth (1930) from the sole species, *G. lignosum*, and it was characterized by a ligneous stem, which is unusual in the genus. We have preferred to include this species in sect. *Gracilia*, because it shares important inflorescence features with the other species of this section. Another woody *Geranium*, *G. loxense*, was described as a new species from Ecuador. Halfdan-Nielsen (1996) suggested that it should be included in sect. *Fruticulosa* on the basis of the presence of a ligneous stem. However, it can be distinguished from species of sect. *Gracilia* by its 1-flowered cymules, which are axillary and solitary. In *Geranium*, the ligneous stem condition has arisen in several groups such as sect. *Neurophyllodes* and sect. *Parramensia* (Standley, 1915; Aedo et al., 1998a).

Key to the species of *Geranium* sect. *Gracilia*

1. Pedicels without glandular hairs.
 2. Basal leaves cordate, densely ciliated with antrorse, appressed, eglandular hairs; petals ciliate on the basal margin. *G. santanderiense*
 2. Basal leaves subtruncate or cuneate; margin glabrous or with spread patent hairs; petals glabrous.
 3. Basal leaves coriaceous, with 3(–5) segments, subtruncate; with some eglandular hairs at the end of each segment and near the margin (sometimes with patent cilia); stipules of cauline leaves subulate. *G. lainzii*
 3. Basal leaves not coriaceous, with 5 segments, cuneate to subtruncate; with spread patent eglandular hairs on the margin; stipules of cauline leaves lanceolate. *G. multiceps*
1. Pedicels with glandular hairs 0.15–1.2 mm long (rarely without glandular hairs, then leaves velutinous abaxially).
 4. Aerial stem ligneous, 0.4–0.5 cm diam.; lateral branches with groups of stipules and persistent rosettes of leaves. *G. lignosum*

4. Aerial stem herbaceous, 0.1–0.3(0.35) mm diam.; lateral branches without groups of stipules and persistent rosettes of leaves.
5. Petioles of basal leaves densely covered by patent hairs; eglandular hairs 0.5–2.5 mm long, glandular hairs 0.3–0.5 mm long. *G. sebosum*
5. Petioles of basal leaves only with eglandular hairs (to 1 mm long).
6. Vegetative stems 5–20(–50) cm long, ± horizontal, covered with imbricate stipules, usually without petiole remains. *G. holosericeum*
6. Without vegetative stems.
 7. Basal leaves glabrous abaxially (sometimes with short eglandular hairs on nerve channels); stolon present. *G. stoloniferum*
 7. Basal leaves hairy abaxially; stolon absent.
 8. Fruit reflexed; leaves coriaceous, velutinous abaxially. *G. velutinum*
 8. Fruit erect; leaves not coriaceous, eglandular hairs on the nerves of abaxial surface. *G. subnudicaule*

1. GERANIUM HOLOSERICEUM Willd. ex Spreng., Syst. Veg. 3: 72. 1826. (Fig. 5).

TYPE: "Amer. austr.," *F. W. Humboldt s.n.* (LECTOTYPE, designated by Knuth, 1912: 105: B, photo).

Geranium lindenianum Turcz., Bull. Soc. Imp. Naturalistes Moscou 31: 418. 1858. TYPE: VENEZUELA. Páramo del Portachuelo, 1843, *J. Linden 1394* (LECTOTYPE, here designated: KW, photocopy at MA; ISOLECTOTYPES: K, LE, MPU).

Geranium gracilipes Triana & Planch., Ann. Sci. Nat. Bot. (Paris) ser. 5, 17: 113. 1873, nom. illeg.? TYPE: COLOMBIA. Quindío, A. J. Bonpland *s.n.* (LECTOTYPE, here designated: P).

Geranium holosericeum var. *stuebelii* R. Knuth in Engl., Pflanzenr. IV. 129 (Heft 53): 105. 1912. TYPE: COLOMBIA. Cundinamarca. Páramo de Pasca, M. A. Stuebel 146 p.p. (HOLOTYPE: B, destroyed).

Geranium holosericeum var. *typicum* R. Knuth in Engl., Pflanzenr. IV. 129 (Heft 53): 105. 1912; nom. inval. (Greuter et al., 1994, Art. 24.3).

Herbs perennial. *Rootstock* 5–10 mm diam., ± vertical; roots unknown; with vegetative stems 5–20(–50) cm long, ± horizontal, covered with imbricate stipules, usually without petiole remains, stolon absent; *aerial stems* 20–60(–100) × 0.1–0.25(–0.35) cm, herbaceous, leaved, erect, with eglandular, patent hairs 0.2–1.4 mm long and glandular (only on the inflorescence), patent hairs 0.3–1 mm long. *Basal leaves* in a persistent rosette; lamina 2.9–4.2(–6) × 3.2–5.2(–7) cm, polygonal in outline, cordate, palmatifid (divided for (0.77–)0.85–0.9 of its length), not coriaceous, not projected, pilose, with eglandular, appressed hairs; segments 5(–7), rhombic, 3–5(–9) mm at the base, 5–7(–13)-lobed in distal half (main sinus length of the middle

segment/middle segment length = 0.16–0.31), usually obtuse, mucronate; *cauline leaves* opposite, similar to the basal; petioles to 25 cm long, with eglandular, patent hairs 0.2–1 mm long; stipules 7–9 × 3 mm, lanceolate to subulate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. *Peduncles* 3–10(–13) cm long, with eglandular, patent to retrorse hairs 0.15–0.5 mm long and glandular, patent hairs 0.3–1(–1.2) mm long; bracteoles 5–10 × 2–2.5 mm, lanceolate to subulate, with eglandular hairs on both surfaces and on the margin; pedicels 1.5–3 cm long, with eglandular, patent to retrorse hairs 0.15–0.5(–1.9) mm long and glandular, patent hairs 0.3–1(–1.2) mm long. *Sepals* 7–9 × 3.5–4.5 mm, with mucro 0.4–0.5 mm long, with scarious margins 0.2–0.35 mm wide, with eglandular, ± patent hairs 0.3 mm long on the abaxial surface and glandular, erect patent hairs 0.4–0.9 mm long, glabrous adaxially. *Petals* 10–14 × 8–11 mm, entire or slightly emarginate (notch ca. 1 mm deep), without claw, glabrous on the adaxial surface, hairy on the base of abaxial surface, ciliate on the basal margin, purplish. *Staminal filaments* 5–6 mm long, lanceolate, pilose on the abaxial surface, ciliate on all of its length, with eglandular hairs 0.3–0.9 mm long and some minute glandular hairs; anthers 1–1.2 × 0.7–0.8 mm. *Gynoeceium* 6–7 mm long. *Fruit* 21–29 mm long, erect; mericarps 3–4 × 1.3–2 mm, with eglandular, patent hairs 0.15–0.4 mm long and glandular, ± patent hairs 0.3–0.5 mm long; rostrum 16–24 mm long, with a narrowed apex 1–2 mm long, with eglandular, patent hairs 0.15–0.5 mm long and gland-

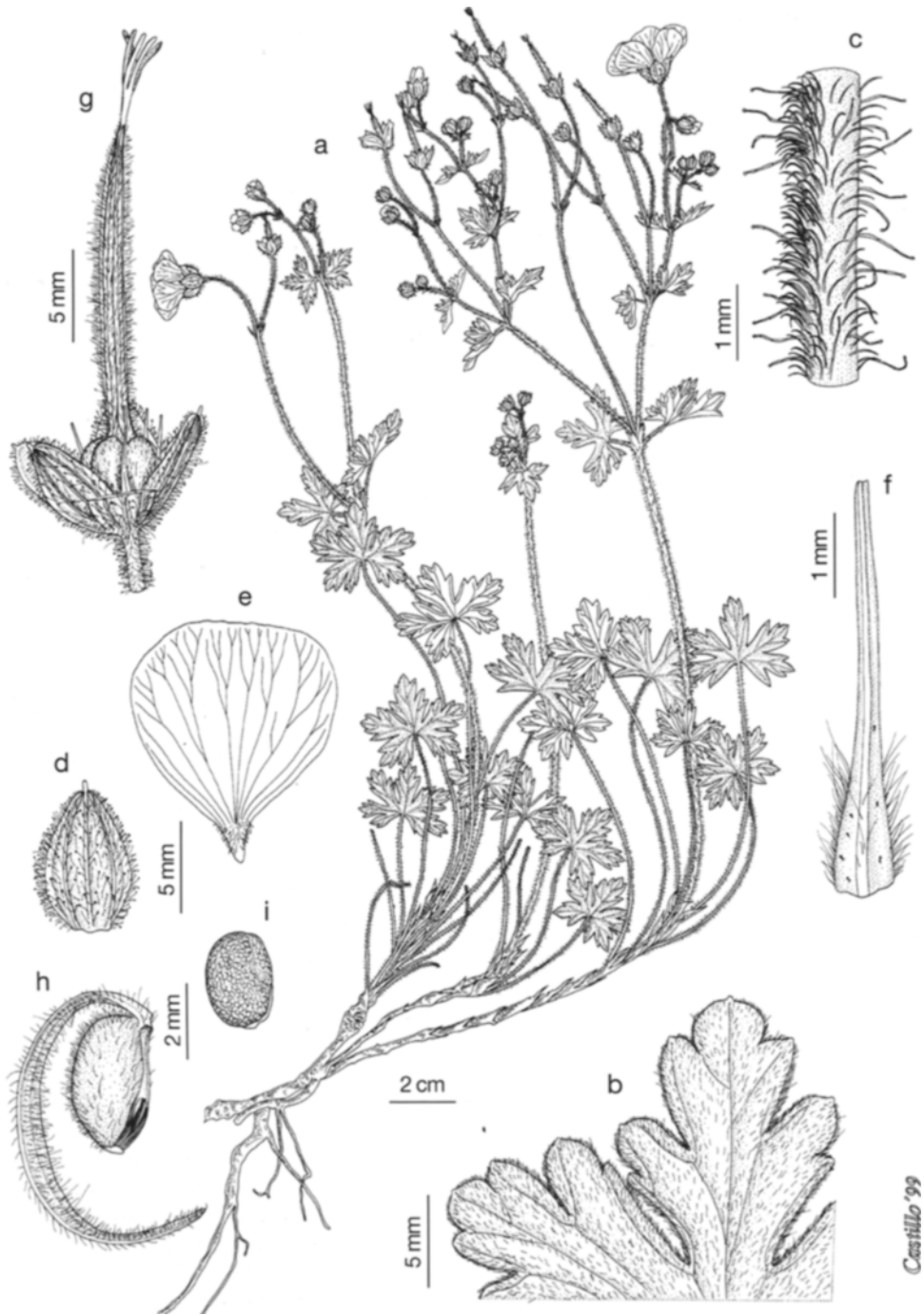


FIG. 5. *Geranium holosericeum*. A. Habit. B. Adaxial leaf surface. C. Peduncle. D. Sepal. E. Petal. F. Filament of stamen. G. Fruit. H. Mericarp. I. Seed. (a-i: from Uribe 6787, COL)

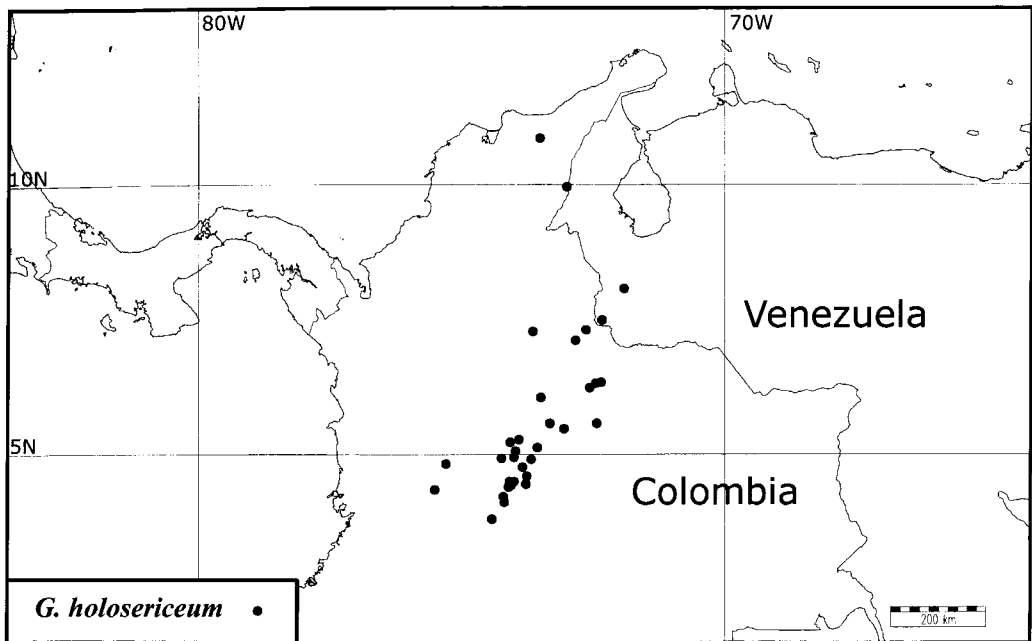


FIG. 6. Distribution of *Geranium holosericeum*.

dular, \pm patent hairs 0.3–0.5 mm long; stigmatic remains 2–4 mm long, with 5 glabrous lobes. Seeds $2.3\text{--}2.5 \times 1.2\text{--}1.3$ mm, reddish; hilum $\frac{1}{2}$ as long as the perimeter.

Distribution and habitat.—Colombia: Cordillera Central (Caldas-Tolima and Quindío), Cordillera Oriental (Depts. Boyacá, Cundinamarca, Meta, Norte de Santander, and Santander), Sierra de Perijá (Dept. César), and Sierra Nevada de Santa Marta (Dept. La Guajira). Venezuela: (State of Táchira). It is found in pool shores, wet meadows, and bogs areas; 2700–3800 m (Fig. 6).

Phenology.—Flowering from February to November.

Additional specimens examined: COLOMBIA. **Boyacá:** Alto del Sote, $5^{\circ}39'N$, $73^{\circ}19'W$, 15 May 1996, *Rangel et al. 13268 OR* (COL); Nevado del Cocuy, Quebrada de San Paulino, el Morrón, $6^{\circ}24'N$, $72^{\circ}27'W$, 11 Sep 1938, *Cuatrecasas & García Barriga 1375* (COL, F, US); valle Ritacueva, $6^{\circ}24'N$, $72^{\circ}27'W$, 4 Apr 1959, *Barclay & Juajibioy 7215* (MO); entre Arcabuco y Tunja, cruce de la carretera a Cómbita, 5 Jun 1989, *Castroviejo et al. 10686* (MO); hacia La Cueva, en la Zanja, $6^{\circ}25'N$, $72^{\circ}21'W$, 13 Sep 1938, *Cuatrecasas 1640* (F, US); La Uvita, vereda el Hatíco, zona de la Quebrada Honda, $6^{\circ}19'N$, $72^{\circ}34'W$, 26 Jul 1996, *Fernández Alonso et al. 14472* (COL); Pesca,

Páramo de la Cortadera, vereda La Peña, $5^{\circ}33'N$, $73^{\circ}3'W$, 14 Aug 1982, *Bejarano 222* (COL). **Caldas-Tolima:** carretera al Nevado del Ruiz, 30 Aug 1966, *Panchón et al. 65* (COL). **César:** Sierra de Perijá, 25 km east of Codazzi, on the Venezuelan border, $10^{\circ}2'N$, $73^{\circ}0'W$, 16 Feb 1945, *Grant 10960* (COL, NY). **Cundinamarca:** Estación Agrícola Experimental Usme, $4^{\circ}28'N$, $74^{\circ}6'W$, 9 Jun 1950, *Idobro et al. 310* (COL); Páramo de Sumapaz, después de la laguna de Chisacá, cerca del Río Taquecito, $4^{\circ}11'N$, $74^{\circ}11'W$, 9 Nov 1987, *Fernández Alonso et al. 7742* (MA); Carupa, cerca al boquerón de Peña de Sumangá, $5^{\circ}21'N$, $73^{\circ}54'W$, 4 Aug 1967, *Uribe 5908* (COL, NY); cerca de San Cayetano, $5^{\circ}18'N$, $74^{\circ}4'W$, 21 Oct 1977, *Uribe 7027* (COL); entre los municipios de Tausa y Cogua, zona del embalse de Neusa, $5^{\circ}8'N$, $73^{\circ}58'W$, 18 Oct 1982, *Ballesteros 45* (COL); Fómique, alrededores de la laguna de Chingaza, $4^{\circ}31'N$, $73^{\circ}46'W$, *Franco 382* (COL); laguna de Verjón, above Bogotá, $4^{\circ}30'N$, $74^{\circ}3'W$, Oct 1922, *Ariste 755* (US); macizo de Bogotá, Quebrada de San Cristóbal, $4^{\circ}34'N$, $74^{\circ}5'W$, 28 May 1939, *Cuatrecasas 5123* (F, US); Moquentiva valley, 22 km NW of Gachetá, $4^{\circ}59'N$, $73^{\circ}40'W$, 25 Jun 1944, *Grant 9481* (NY); on road to Villavicencio, above Chipaqué, just below Páramo de Cruz Verde, $4^{\circ}30'N$, $74^{\circ}3'W$, 28 Feb 1943, *Fosberg 20249* (NY); Páramo de Choachi, abajo Peñazul, $4^{\circ}34'N$, $74^{\circ}0'W$, 22 Jul 1963, *Soejarto 257* (COL); Páramo de Guasca, cumbre, $4^{\circ}50'N$, $73^{\circ}50'W$, 4 Oct 1948, *Uribe 1814* (COL); Páramo de La Siberia, NE de Bogotá, $4^{\circ}40'N$, $73^{\circ}45'W$, 24 May 1959, *Barclay & Juajibioy 7707* (MO); Páramo de Neusa, 50 km N of Bogotá, $5^{\circ}8'N$, $73^{\circ}58'W$, 1 Mar 1975, *Burbidge 75/240* (NY); Páramo

Tablazo, 5°0'N, 74°14'W, 6 Jul 1990, *Pipoly & Orozco 12069* (COL, MO); valle del Río San Cristobal, alto de la Horqueta, 4°34'N, 74°5'W, 16 Nov 1958, *García Barriga 16141* (COL); Yomasa, near Bogota, 26 May 1948, *Camilo s.n.* (US); Cundinamarca, Zipaquirá, en Pantano Redondo, 5°1'N, 74°0'W, 23 Oct 1949, *Romero Castañeda 1831* (COL). **Guajira:** above Macotama, 10°55'N, 73°30'W, 16 May 1939, *Hanbury-Tracy 441* (K). **Meta:** Macizo de Sumapaz, Hoya de la quebrada El Buque, 9 Jul 1981, *Diaz et al. 2733* (COL). **Norte de Santander:** Pamplona SW de la ciudad, por el Piñuelal, 7°24'N, 72°38'W, 30 Jun 1945, *Garganta Fábrega 1039* (F). **Santander:** near Mutisqua, 6°8'N, 73°29'W, 1848, without collector (K); Páramo del Almorzadero, 7°22'N, 73°38'W, 20 Jul 1940, *Cuatrecasas & García Barriga 9972* (COL). **Santander-Norte de Santander:** Cordillera Oriental, páramo cerca de la carretera Pamplona-Bucaramanga, 7°12'N, 72°50'W, 18 Jun 1966, *Schulz et al. 439* (U).

VENEZUELA. **Táchira:** Páramo de Portachuelo, 8°10'N, 71°55'W, 23 Oct 1978, *Luteyn et al. 6025* (MO); Páramo del Zumbador, carretera Táriba-El Coebre, 7°35'N, 72°20'W, 25 Jul 1976, *Stergios 636* (MO, PORT).

This species has a feature unique in the section: the long, more or less horizontal vegetative stems that are covered by young stipules but without remaining petiole. Similar stems are found in some species of sect. *Neoandina* Aedo, e.g., *G. sibbaldioides* Benth. However, those plants can readily be distinguished by the stemless habit and the 1-flowered cymules.

Many specimens had been previously identified as *Geranium lindenianum*, but after studying the type we have concluded that species is not distinct.

We only could study a photograph of the Lectotype of *Geranium holosericeum* at the Willdenow herbarium (B), but the detail of the indumentum was not clear. Dr. Vogt kindly confirmed the presence of glandular hairs on the inflorescence. The earliest name *G. holosericeum*, has been long neglected, possibly because of the imprecise locality: "Amer. austr." Considering the route of Humboldt's journey, it was likely collected in central Colombia (Stearn, 1968; Botting, 1981). We also presume that Humboldt's collection is a duplicate of original material of *G. gracilipes*, because both collectors were together along most of their trip and their specimens were later divided on their return to Europe (Botting, 1981).

Knuth (1912) distinguished *G. holosericeum* var. *stuebelii* from the type by its lon-

ger indumentum on the stems and abaxial leaf surface. The type of var. *stuebelii* was destroyed during the Second World War; unfortunately, no other duplicate of this collection has been found. We have found that *G. holosericeum* varies in such indumentum features, which makes us reluctant to accept taxonomically any forms based on indumentum.

A specimen (*Hanbury-Tracy 441*, K) collected on an isolated locality in Sierra Nevada de Santa Marta, Colombia, represents the northernmost point for this species. The leaves of this specimen are larger (6 × 7 cm) and more deeply divided (with more lobes per segment, and with lobes more deeply divided), but match *Geranium holosericeum* otherwise. Other specimens from Venezuela (*Luteyn et al. 6025*, MO; *Stergios 636*, MO, PORT), or from northern Colombia (Sierra de Perijá, *Grant 10960*, COL, NY; Dept. Santander, *Cuatrecasas & García Barriga 9972*, COL) are remarkable robust, but are not otherwise distinctive within *G. holosericeum*.

2. GERANIUM LAINZII Aedo, Anales Jard. Bot. Madrid 57: 162. 1999. (Fig. 7).

TYPE: COLOMBIA. Cundinamarca: Páramo de Guasca en el cerrito del Santuario, 25 Apr 1932, *J. Cuatrecasas 2273* (HOLOTYPE: MA-252510).

Herbs perennial. *Rootstock* 3–8 mm diam., ± vertical; with ± fusiform roots; without vegetative stems, stolon absent; aerial stems 8–42 × 0.1–0.2 cm, herbaceous, leaved (sometimes scapiform), decumbent, ± glabrous or with eglandular, patent to retrorse 0.15–0.35(–0.6) mm long (on a longitudinal line). *Basal leaves* in a persistent rosette; lamina 1.1–2.9 × 1.6–4.2 cm, polygonal in outline, subtruncate, palmatifid (divided for 0.6–0.8 of its length), coriaceous, projected on the abaxial surface, sunken adaxially, with some eglandular hairs at the end of each segment and near the margin (sometimes with patent cilia), abaxially glabrous; segments 3(–5), obtriangular, 3–7(–9) mm at the base, 3-lobed at apex (main sinus length of the middle segment/middle segment length = 0.11–0.23), obtuse, mucronate; *cauline leaves* opposite,

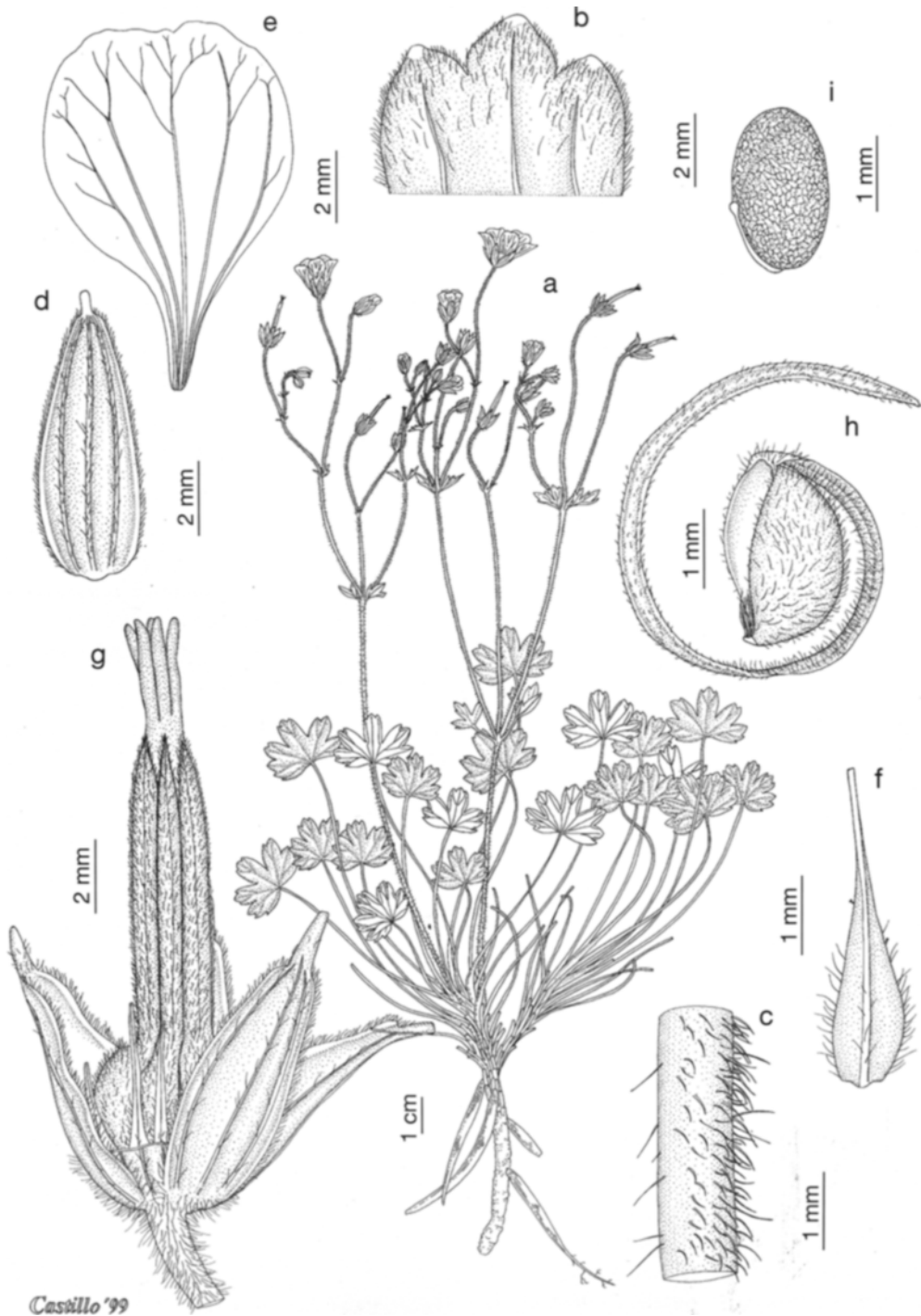


FIG. 7. *Geranium lainzii*. A. Habit. B. Adaxial leaf surface. C. Peduncle. D. Sepal. E. Petal. F. Filament of stamen. G. Fruit. H. Mericarp. I. Seed. (a: from Hatheway & Idobro 1083, COL; b-g: from Cuatrecasas 5550, US; h-i: from Langenheim et al. 3683, US)

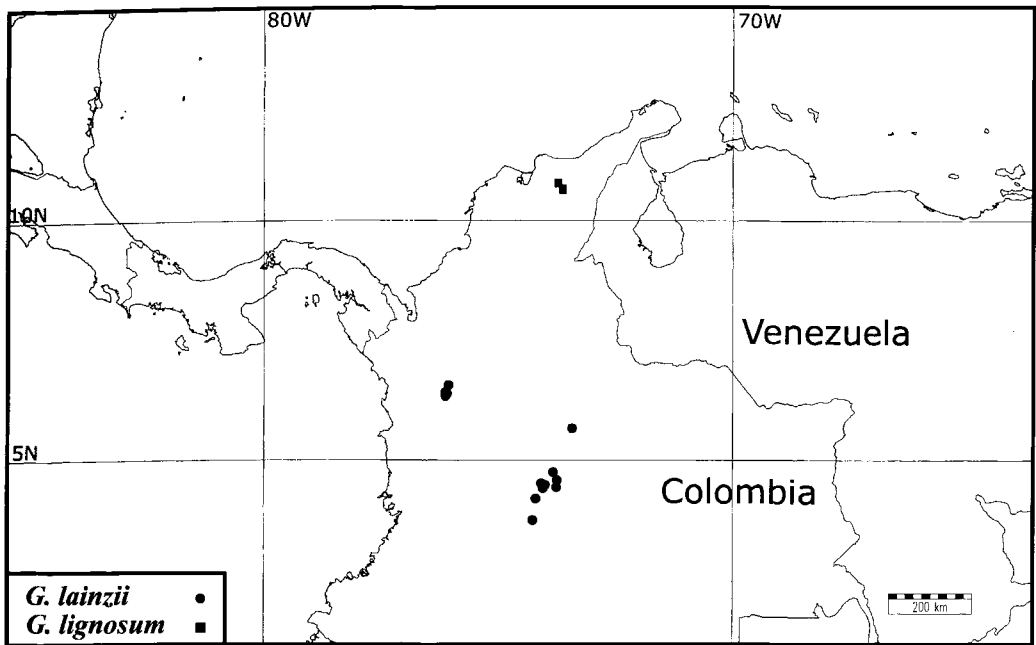


FIG. 8. Distribution of *Geranium lainzii* and de *Geranium lignosum*.

cuneate to truncate, with usually (1–)3 entire segments; petioles to 10(–20) cm long, with eglandular, patent hairs 0.15–0.35 mm long; stipules 5–6(–10) × 2(–4) mm, subulate, with eglandular hairs on the margin, subglabrous on abaxial surface and glabrous adaxially. *Peduncles* 4–7(–10) cm long, with eglandular, retrorse to patent hairs 0.3–0.5 mm long; bracteoles 5–7 × 1.5–2 mm, subulate, with eglandular hairs on the margin, subglabrous on abaxial surface and glabrous adaxially; pedicels 1.8–4 cm long, with eglandular, retrorse to patent hairs 0.3–0.5 mm long. *Sepals* 7–9 × 2–3 mm, with mucro 0.2–0.4 mm long, with scarios margins 0.15–0.25 mm wide, with eglandular, antrorse, ± appressed hairs 0.15–0.6 mm long, at least on the nerves and margin, glabrous adaxially. *Petals* 12–13 × 6–7 mm, entire or slightly emarginate (notch ca. 0.5 mm deep), with claw ca. 2 mm long, glabrous, purplish. *Staminal filaments* 5–6 mm long, lanceolate, glabrous on both surfaces, ciliate on the proximal half, with eglandular hairs 0.1–0.2 mm long and some minute glandular hairs; anthers 1–1.2 × 0.7–0.8 mm. *Gynoecium* 4–5.5

mm long. *Fruit* 15–18 mm long, reflexed; mericarps 3.2–3.9 × 1.5–2 mm, with abundant eglandular, erect patent hairs 0.15–0.5 mm long and some minute glandular hairs; rostrum 10 mm long, without a narrowed apex, with abundant eglandular, erect patent hairs 0.15–0.5 mm long, and some minute glandular hairs; stigmatic remains 2–3 mm long, with 5 subglabrous lobes. *Seeds* 1.8–2 × 0.9–1 mm, reddish; hilum 1/4 as long as the perimeter.

Distribution and habitat.—Colombia: Cordillera Oriental, Depts. Boyacá, Cundinamarca, and Meta, and Cordillera Occidental, Dept. Antioquia. It is found on pool shores, bogs, and other damp areas; 3000–3600 m (Fig. 8).

Phenology.—Flowering from February to December.

Additional specimens examined: COLOMBIA. **Antioquia**: at summit of Morro Pelado, along Anoccosca-Abriaqui camino, 6°39'N, 76°3'W, 15 Mar 1944, *Core 460* (US); Páramo of Morro Frontino, N Urrao, 6°25'N, 76°7'W, 11 Mar 1944, *Core 402* (US). **Boyacá**: Arcabuco, 5°45'N, 73°26'W, 6 Jun 1969, *Huertas & Camargo 6781* (COL). **Cundinamarca**: Guadalupe, 4°34'N, 74°3'W, 20 Apr 1947, *Haught 5640* (COL); La Calera, Páramo de la Siberia, 4°40'N, 73°45'W, 16

Sep 1953, *Langenheim et al.* 3683 (US); Páramo de Palacio, 4°40'N, 73°45'W, 14 Jul 1960, *Schultes* 22473 (COL); Parque Nacional Natural de Chingaza, Quebradas de Piedras Gordas, 4°31'N, 73°46'W, 5 May 1990, *Kubocz & Schmitt* 80 (COL); Alto de las Cruces-Guadalupe, 4°34'N, 74°3'W, 19 Jun 1939, *Cuatrecasas* 5550 (F; US); Páramo above Guasca, 4°50'N, 73°50'W, 13 Jun 1957, *Barclay* 4050 (COL); Páramo Cruz Verde, 4°30'N, 74°3'W, 6 Sep 1967, *Kirkbride & Idrobo* 346 (MO); Páramo de Chingaza, 4°31'N, 73°46'W, 26 Feb 1983, *Wood* 3526 (K); Páramo de Chisacá, 4°17'N, 74°12'W, 15 Oct 1966, *Soderstrom* 1345 (K, NY, P); Páramo de Choachí near Bogotá, 4°34'N, 74°0'W, 8 Aug 1922, *Killip & Ariste-Joseph* 11952 (US). **Meta:** Quebrada el Cariño, second main affluent of Río Arroz on S side, 3°50'N, 74°16'W, 28 Aug 1943, *Fosberg* 20904 (NY, US).

This species is endemic to Colombia. The specimens have been erroneously identified as *Geranium multiceps*, probably following Knuth's (1912: 105, fig. 18) drawing. Knuth included mixed material in *G. multiceps*, but only the Venezuelan specimens should be considered as the true *G. multiceps*. This fact was detected by Sandwith (1942: 220), who stated: "... the distinctive plant which is common around Bogotá in Colombia and has been identified with *G. multiceps* by all authors since Triana is certainly not the 'typical' form of that species. ..."

Geranium lainzii is easily distinguished from *G. multiceps* by its coriaceous, subtruncate leaves with 3 segments and by its reflexed fruits, when mature (vs. not coriaceous, cuneate to subtruncate leaves with 5 segments, and erect fruits).

Geranium lainzii superficially resembles *G. santanderiense*. However, *G. santanderiense* has cordate leaves with 5 segments, with antrorse, appressed cilia on the margin, and eglandular hairs on the abaxial surface (vs. subtruncate leaves with 3 segments, glabrous on the abaxial surface and with scattered patent cilia).

3. GERANIUM LIGNOSUM R. Knuth, Repert. Spec. Nov. Regni Veg. 28: 10. 1930. (Fig. 9). TYPE: "Colombia: Charakterpflanze der Páramos, Siminchuena, 3200 m, A. Schultze, Reise in die Sierra Nevada de Santa Marta a. 1928 n. 1232" (HOLOTYPE: B, destroyed). COLOMBIA. Nevada de Santa Marta, June 1844,

Hups? s.n. (NEOTYPE, here designated: K).

Shrubby perennial; (basal part of the plant unknown). *Aerial stems* ca. 50 × 0.4–0.5 cm, ligneous, leaved, erect, with lateral branches having groups of stipules and persistent rosettes of leaves, with eglandular, patent to retrorse 0.5–1.2 mm long. *Leaf lamina* 2.8–3.5 × 3.7–4 cm, polygonal in outline, cordate, palmatifid (divided for 0.8–0.9 of its length), not coriaceous, not projected, pilose, with ± appressed, eglandular hairs; segments 5(–7), rhombic, 2–3 mm at the base, 7–9-lobed in distal half (main sinus length of the middle segment/middle segment length = 0.1–0.33), acute; *cauline leaves* opposite; petioles to 9 cm long, with eglandular, patent to retrorse hairs 0.1–1 mm long; stipules 6–9 × 1.5–2 mm, lanceolate, with eglandular hairs on abaxial surface and on the margin, almost glabrous adaxially. *Peduncles* 4–9 cm long, with abundant eglandular, retrorse to patent hairs 0.1–1 mm long, and some glandular, patent hairs 0.3–0.6 mm long; bracteoles 4–5 × 1–1.5 mm, lanceolate, with eglandular hairs on both surfaces and on the margin; pedicels 2.5–3.5 cm long, with some eglandular, patent hairs 0.1–0.4 mm long and abundant glandular, patent hairs 0.2–0.6 mm long. *Sepals* 9–10 × 4 mm, with mucro 1–1.5 mm long, with scarious margins 0.3 mm wide, with eglandular, ± patent hairs 0.2–0.9 mm long and glandular, erect patent hairs 0.2–0.6 mm long on both surfaces. *Petals* 13–14 × 8–9 mm, entire, with claw 1 mm long, hairy on both surfaces (mainly on the base of adaxial surface), ciliate on the margin, purplish. *Staminal filaments* 9–10 mm long, lanceolate, pilose on the abaxial surface, ciliate on the proximal half, with eglandular hairs 0.8–1.2 mm long; anthers 1.3 × 0.6 mm. *Gynoecium* 9 mm long. *Fruit* 25–30 mm long, erect; mericarps 3–4 × 2 mm, with eglandular, erect patent hairs 0.5–1 mm long; rostrum 21–22 mm long, with a narrowed apex 3 mm long, with abundant eglandular, patent hairs 0.2–0.6 mm long and glandular hairs 0.3–0.5 mm long; stigmatic remains 4 mm long, with 5 glabrous lobes. *Seeds* 1.9 × 1 mm, blackish; hilum 1/6 as long as the perimeter.

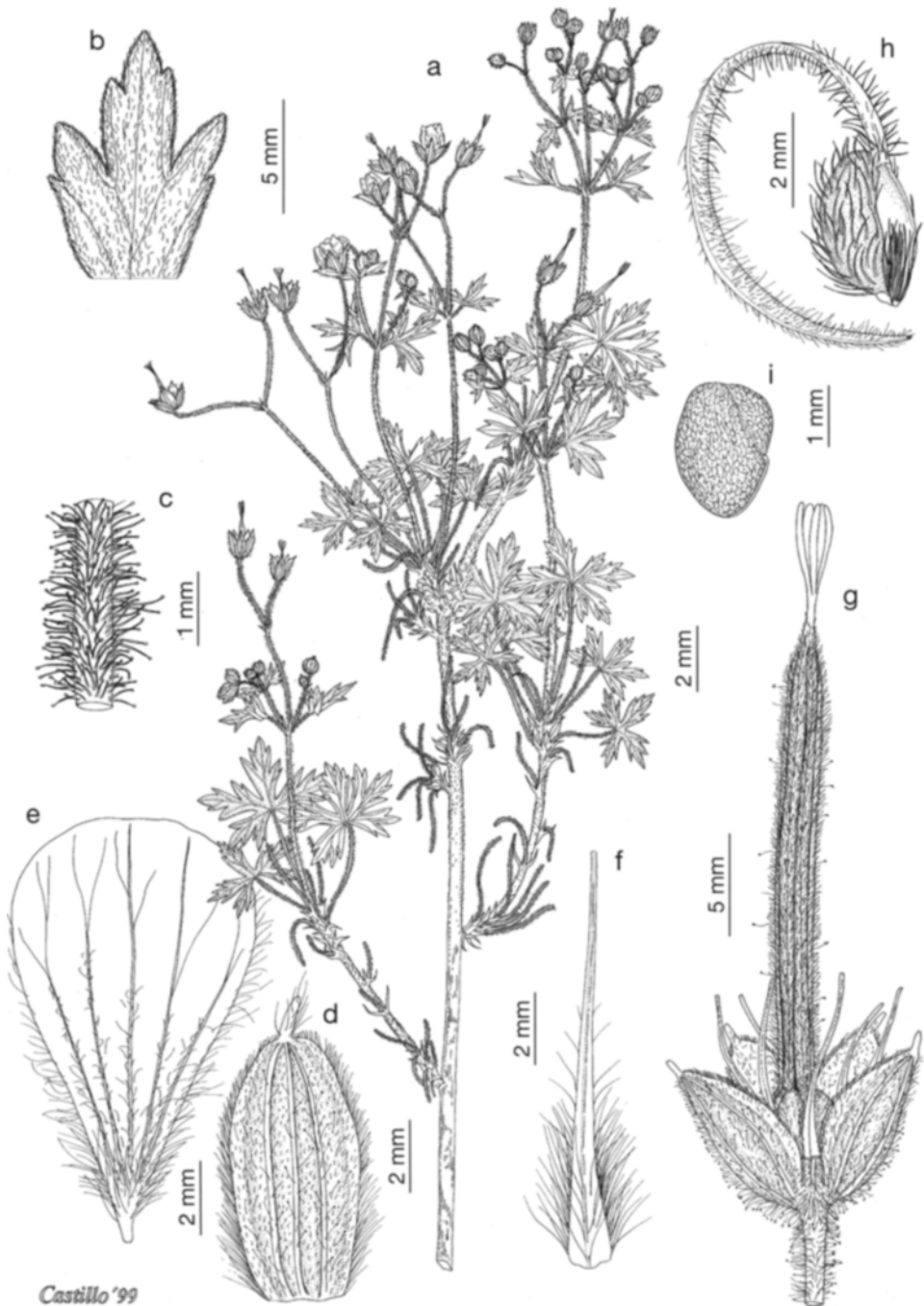


FIG. 9. *Geranium lignosum*. A. Flowering branch. B. Adaxial leaf surface. C. Peduncle. D. Sepal. E. Petal. F. Filament of stamen. G. Fruit. H. Mericarp. I. Seed. (a: from *Hups? s.n.*, K; b-i: from *Simons s.n.*, BM)

Distribution and habitat.—Colombia: Sierra Nevada de Santa Marta, Dept. Magdalena. It occurs on montane rain forest; 3300–4000 m (Fig. 8).

Phenology.—Flowering from May to June.

Additional specimens examined: COLOMBIA. **Magdalena:** vic. Río Mamancanaca, 10°43'N, 73°39'W, 26 May 1977, *White & Alverson 600* (NY); Magdalena, valley of Río Yebosimeina, 10°44'N, 73°39'W, 26 May 1977, *White & Alverson 601* (COL, NY); Sierra Nevada, Santa Marta, 1880, *Simons s.n.* (BM).

Geranium lignosum can be distinguished from all other species of sect. *Gracilia* by its ligneous fertile stems, and the lateral branches having stipules groups and persistent rosettes of leaves. Herbarium specimens are few; no specimens has the basal part of the plant. Thus, we can only describe the leaves from the lateral rosettes.

The Holotype was a unique specimen, according to H. E. Moore (on label, BM specimen). We have selected therefore, a Neotype, also collected in Sierra Nevada de Santa Marta.

4. GERANIUM MULTICEPS Turcz., Bull. Soc. Imp. Naturalistes Moscou 31: 417. 1858. (Fig. 10). TYPE: VENEZUELA. Mérida, Páramo de Muchuchí, *N. Funck & L. J. Schlim 861* (LECTOTYPE, here designated: KW, photocopy at MA; ISOLECTOTYPES: BM, G, LE, MPU, P, W).

Herbs perennial. *Rootstock* 5–7 mm diam., ± vertical; with ± fusiform roots; without vegetative stems, stolon absent; *aerial stems* 10–20 × 0.1–0.2 cm, herbaceous, leaved (sometimes scapiform), decumbent, with eglandular, usually retrorse, appressed 0.15–0.4 mm long. *Basal leaves* in a persistent rosette; lamina (0.7–)1.7–2.2 × (0.9–)2.4–3.1 cm, polygonal in outline, cuneate to subtruncate, palmatifid (divided for 0.65–0.83 of its length), not coriaceous, ± projected on the abaxial surface, sunken adaxially, with very short eglandular hairs (mainly on nerve channels) on adaxial surface, spread patent eglandular hairs on the margin, eglandular hairs on the nerves of abaxial surface (sometimes glabrous); segments 5, obtriangular, 2–4 mm at the base,

3(–5)-lobed at apex (main sinus length of the middle segment/middle segment length = 0.13–0.3), obtuse, mucronate; *cauline leaves* opposite, cuneate to truncate, with usually 3(–5) entire segments; petioles to 5 cm long, with eglandular, retrorse, appressed (sometimes patent), hairs 0.15–0.4 mm long; stipules 5–6 × 1.5–2 mm, lanceolate, subglabrous on abaxial surface, glabrous adaxially. *Peduncles* 2–5.5 cm long, with eglandular, usually retrorse, ± appressed hairs 0.1–0.4 mm long; bracteoles 2–4 × 1–2 mm, lanceolate, subglabrous on abaxial surface, glabrous adaxially; pedicels 1–3 cm long, with eglandular, usually retrorse, ± appressed hairs 0.1–0.4 mm long. *Sepals* 6–8 × 2.5–3.5 mm, with mucro 0.3–0.5 mm long, with scarious margins 0.15–0.2 mm wide, with eglandular, antrorse, appressed hairs 0.2–0.7 mm long at least on the nerves of abaxial surface and margin, glabrous adaxially. *Petals* 9–11(–12) × 4–5(–7.5) mm, entire or slightly emarginate (notch ca. 0.5 mm deep), with claw ca. 2 mm long, glabrous, purplish, sometimes white with purplish veins. *Staminal filaments* 4–5 mm long, lanceolate, pilose on the abaxial surface, ciliate on the proximal half, with eglandular hairs 0.2–0.3 mm long and some minute glandular hairs; anthers 0.85–1 × 0.6–0.8 mm. *Gynoecium* 5–5.5 mm long. *Fruit* 13–17 mm long, erect; mericarps 2.5–3 × 1.5–2 mm, with abundant eglandular, antrorse, appressed hairs 0.15–0.3 mm long, and some minute glandular hairs; rostrum 10–12 mm long, without a narrowed apex, with abundant eglandular, antrorse, appressed hairs 0.15–0.3 mm long, and some minute glandular hairs; stigmatic remains 2–3 mm long, with 5 subglabrous lobes. *Seeds* 1.7–1.9 × 0.9–1 mm, reddish; hilum 1/4 as long as the perimeter.

Distribution and habitat.—Venezuela: State of Mérida. It is found on pool and stream shores and other damp areas; 3200–4800 m (Fig. 11).

Phenology.—Flowering from February to December.

Additional specimens examined: VENEZUELA. **Mérida:** Aguila Pass, 80 km NE of Mérida, 8°45'N, 70°55'W, 8 Oct 1966, *Bruijin 1146* (VEN); Caserío Mifafí, camino quebrada Río Chama-caserío Mucupús,

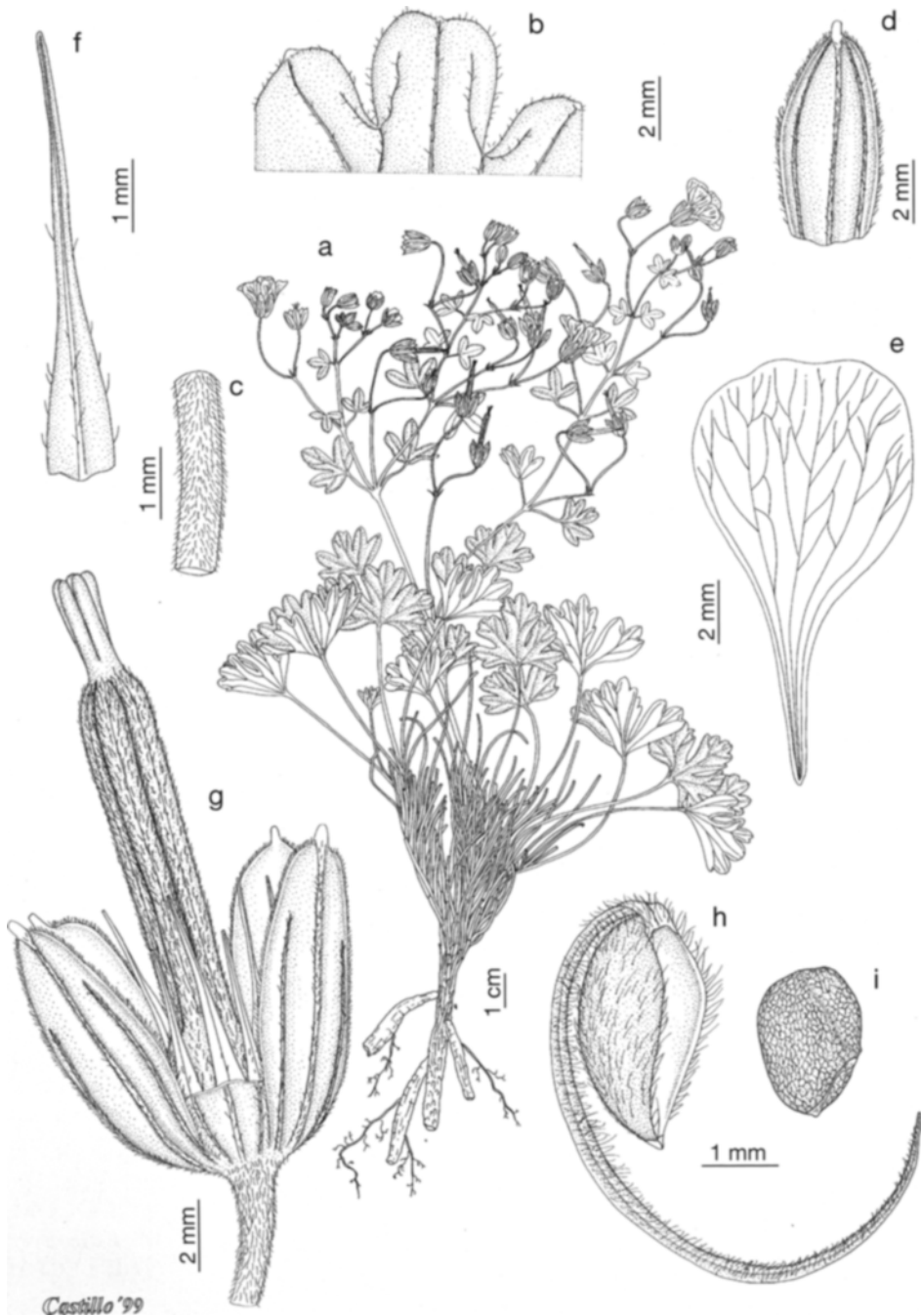


FIG. 10. *Geranium multiceps*. A. Habit. B. Abaxial leaf surface. C. Peduncle. D. Sepal. E. Petal. F. Filament of stamen. G. Fruit. H. Mericarp. I. Seed. (a-b: from Barreto 626, MER; c-i: from Oberwinkler 12799, M)

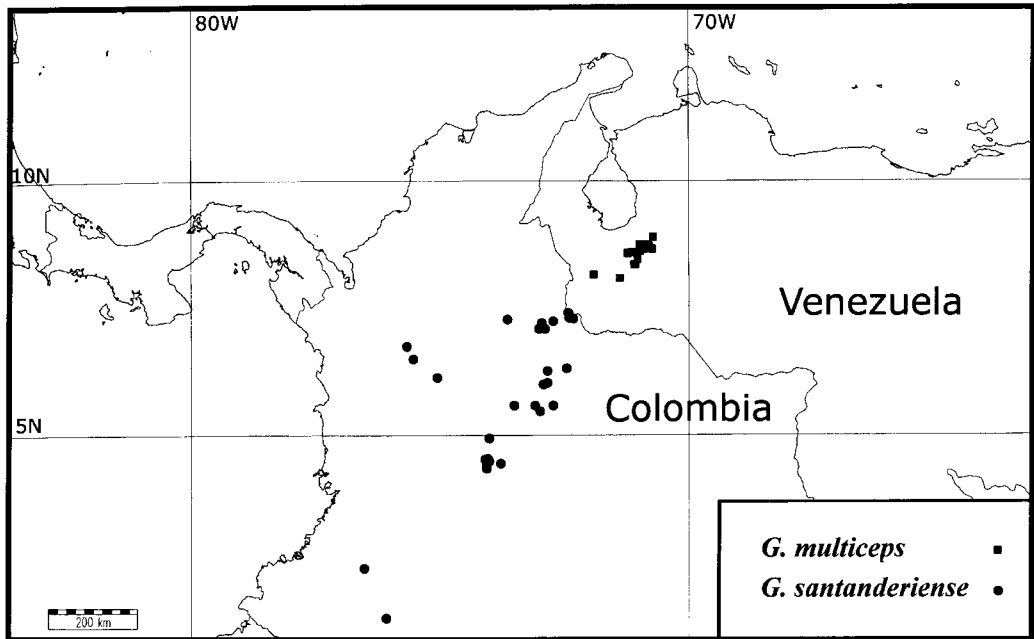


FIG. 11. Distribution of *Geranium multiceps* and *Geranium santanderiense*.

Páramo Piedra Blanca, entrada road Apartaderos-Pico Águila, 8°45'N, 70°55'W, 14 Aug 1980, *Stergios & Taphorn 2123* (MO, PORT); Miranda, entre Chachopo y Pico el Águila, 8°45'N, 70°55'W, 17 Oct 1972, *Badillo 5137* (F); Justo Briceño, Páramo de Piedras Blancas, 8°50'N, 71°0'W, 18 Jun 1982, *Briceño et al. 553* (MER); Rangel, cascada SE of laguna de Mucubají and below Pico Mucuñuque, 8°48'N, 70°49'W, 15 Jun 1988, *Dorr & Barnett 5536* (NY, PORT, VEN); laguna de Santo Domingo, 8°48'N, 70°49'W, 19 Nov 1939, *Müller & Barras 1011* (VEN); laguna Negra, 8°15'N, 71°55'W, 18 May 1952, *Vareschi 979* (VEN); Páramo de la Sal, 2 Sep 1921, *Jahn 591* (VEN, US); Páramo de los Conejos, 8 km NE Mérida, 8°40'N, 71°15'W, 27 Dec 1967, *Wessels Boer 2121* (U); Páramo de los Leones al W del Mucurubá, La Lagunita, La Cañada Grande, 8°41'N, 71°10'W, 31 May 1930, *Gehriger 139* (F); Páramo de Mucuchíes, 8°45'N, 70°55'W, *Moritz 1247* (BM); Páramo de Santo Domingo, massif des P. Bolivar, von der Loma Redonda gegen den P. Espejo, 8°33'N, 71°3'W, 13 Aug 1967, *Merxmüller 22874* (M); Páramo de Timotes, 8°59'N, 70°44'W, 4 Jul 1934, *Farenholtz s.n.* (B); Parque Nacional Sierra Nevada, Páramo Media Luna, 8°27'N, 71°5'W, 27 Oct 1994, *Berg 186* (VEN); Pasa del Toro, Sierra Nevada above Mérida, 8°27'N, 71°7'W, Feb 1939, *Chenery s.n.* (BM); Pico Bolivar, 8°33'N, 71°3'W, 1951, *Croizat 15* (VEN); Quebrada de Saisay, 8°11'N, 71°24'W, 10 Apr 1930, *Gohrger 48* (VEN); Rangel, alrededores de la laguna del Humo o del Bartolo, al pie del pico Bartolo, N Mucuchíes, 8°50'N, 70°55'W, 13 Oct 1965, *Ruiz Terán 198* (MO); Sierra Nevada, de Loma Redonda a laguna de los Antojos, 8°27'N, 71°5'W, 2 Nov 1976, *Bernardi et al. 17036* (C); trail leading from La Ne-

grita to the Boquerón of the Quebrada de las Cañas, 31 Oct 1978, *Luteyn et al. 6137* (MO).

The differences between *Geranium multiceps* and *G. lainzii* are addressed in the discussion under *G. lainzii*. The leaves on herbarium specimens are notable because the lateral leaf segments are usually folded on the central one; thus the cuneate appearance of the leaf base is accentuated.

According to Vareschi (1970) this species is also present in the State of Trujillo, but we could not examine any collections from this area.

5. GERANIUM SANTANDERIENSE R. Knuth, *Repert. Spec. Nov. Regni Veg.* 18: 291. 1922. (Fig. 12). TYPE: COLOMBIA. Ocaña to Pamplona, *W. Kalbreyer 715* (HOLOTYPE: B, destroyed; LECTOTYPE, here designated: K).

Herbs perennial. *Rootstock* 5–10 mm diam., ± horizontal; with fusiform roots; without vegetative stems, stolon absent; *aerial stems* (10–)15–60 × 0.1–0.2 cm, herbaceous, leaved, decumbent, with retrorse, appressed, eglandular hairs 0.3–0.5 mm long. *Basal leaves* in a persistent rosette;

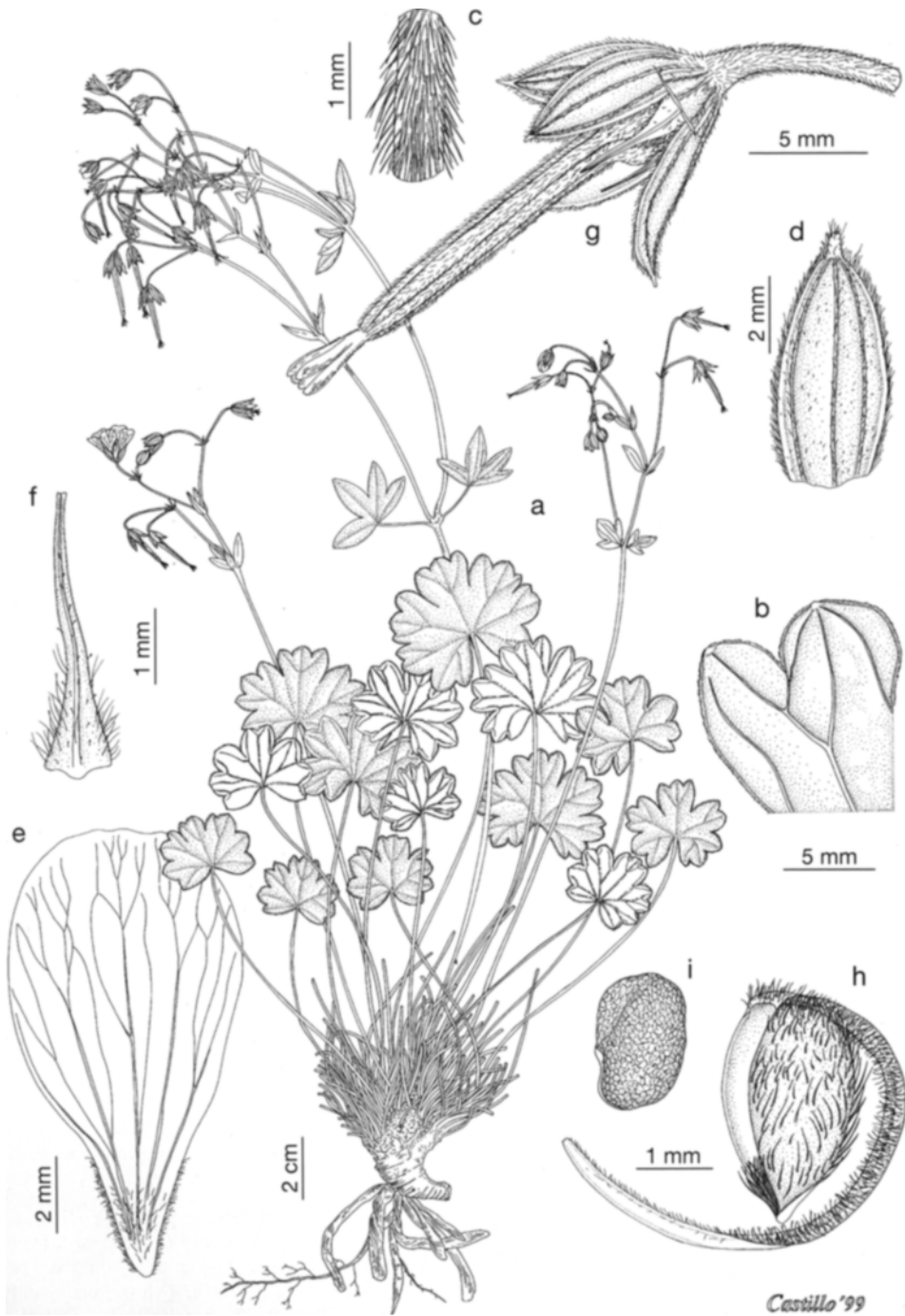


FIG. 12. *Geranium santanderiense*. A. Habit. B. Adaxial leaf surface. C. Peduncle. D. Sepal. E. Petal. F. Filament of stamen. G. Fruit. H. Mericarp. I. Seed. (a: from Fernández Alonso et al. 5156, COL; b–g, h: from Fernández Alonso et al. 5156, MA; i: from St. John 20754, NY)

lamina 2.5–3.9(–5.5) × 3–4.9(–6) cm, orbicular in outline, cordate, palmatifid (divided for 0.45–0.55 of its length), coriaceous, projected on the abaxial surface, sunken adaxially, usually glabrous beneath (sometimes hairy, mainly on nerve channels), densely ciliated (with antrorse, appressed, eglandular hairs), and with eglandular hairs on the nerves of abaxial surface; segments 5(–7), obtriangular, 8–9 mm at the base, 3-lobed in distal half (main sinus length of the middle segment/middle segment length = 0.07–0.13), usually obtuse, mucronate; *cauline leaves* opposite, cuneate to truncate, with usually 1(–3) entire segments; petioles 15(–40) cm long, with eglandular, retrorse, appressed hairs 0.15–0.3 mm long; stipules 2–3 × 1–1.2 mm, lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. *Peduncles* 3–7(–9) cm long, with eglandular, retrorse, appressed hairs 0.3–0.5 mm long; bracteoles 2–4 × 1–1.5 mm, lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 2.1–5 cm long, with eglandular, retrorse, appressed hairs 0.3–0.5 mm long. *Sepals* 5–6(–9) × 1.8–2 mm, with mucro 0.2–0.4 mm long, scarious margins 0.15–0.3 mm wide, eglandular, antrorse, appressed hairs 0.15–0.6 mm long at least on nerves and margin, glabrous adaxially. *Petals* 12–16 × 6–9 mm, entire or slightly emarginate (notch ca. 0.5 mm deep), with claw 1–2 mm long, hairy on the base of adaxial surface, glabrous on the abaxial surface, ciliate on the basal margin, purplish. *Staminal filaments* 3–5 mm long, lanceolate, pilose on the abaxial surface, ciliate on the proximal half, with eglandular hairs 0.2–0.4 mm long and some minute glandular hairs; anthers 0.8–1.1 × 0.5–0.8 mm. *Gynoecium* 4–5 mm long. *Fruit* 19–21 mm long, reflexed; mericarps 3–3.5 × 1.5–2 mm, with abundant eglandular, erect patent hairs 0.3–0.5 mm long, and some minute glandular hairs; rostrum 17 mm long, without a narrowed apex, with abundant eglandular, erect patent hairs 0.15–0.5 mm long, and some minute glandular hairs; stigmatic remains 2–3 mm long, with 5 subglabrous lobes. *Seeds* 1.8–1.9 × 0.9–1 mm, reddish; hilum 1/2 as long as the perimeter.

Distribution and habitat.—Colombia: Cordillera Oriental (Depts. Boyacá, Cundinamarca, Norte de Santander, and Santander), Cordillera Central (Depts. Antioquia, and Cauca); Venezuela: (States of Apure and Táchira). It grows on roadside banks, pajonales, dry areas of páramo, grassy areas, open rocky hillsides, brushy slopes, and bogs; 2800–4000 m (Fig. 11).

Phenology.—Flowering from January to December.

Additional specimens examined: COLOMBIA. **Antioquia:** Belmira, Páramo El Morro, 6°35'N, 75°32'W, 22 Apr 1993, *Fonnegra & Tuberquia 4621* (MO); Páramo de Chaquiro, 6°13'N, 75°3'W, 23 Feb 1918, *Pennell 4275* (NY, US); San Andrés de Cuerquia, 6°50'N, 75°40'W, 31 Jul 1958, *Garganta 2188* (US). **Antioquia-Bolívar:** Páramo de Chaquiro, 1°28'N, 76°5'W, 23 Feb 1918, *Pennell 4275* (MO). **Boyacá:** 25 km S of Socha, Las Mesas, headwaters of Río Pauto, NE Quebrada Laja, 5°40'N, 72°43'W, 11 Nov 1944, *Fosberg 22268* (US); Páramo de Hüina entre Belén y Susacón, 6°7'N, 72°50'W, 6 May 1959, *Barclay & Juajibioy 7599* (MO); Duitama, trayecto Vereda El Carmen a el Páramo de La Rusia, 5°40'N, 73°5'W, 19 Nov 1994, *Fernández Alonso et al. 11956* (COL); Páramo de la Rusia about 18 km from Duitama on road to Charalá, 5°40'N, 73°5'W, 11 Aug 1953, *Langenheim 3409* (COL, F); Nevado del Cocuy, alto valle de Las Lagunillas, 6°24'N, 72°27'W, 12 Sep 1938, *Cuatrecasas 1441a* (F); Páramo al NW de Belén, cabeceras Quebrada Minas, Hoya Collada Larga, 6°5'N, 72°55'W, 28 Feb 1975, *Cleef 2011* (U); Páramo de Pisva, carretera Socha-La Punta, Km 61, 6 km E Los Pinos, Alto de Granados, 12 Jun 1972, *Cleef 4458* (COL, U); Santuario de Iguaque, near Laguna de Iguaque, 5°40'N, 73°30'W, 3 Jul 1980, *Melampy 1003* (MO); Sierra Nevada del Cocuy, Páramo Cóncavo, fondo del valle del Río Cóncavo, 6°24'N, 72°27'W, 6 Jun 1973, *Cleef 10008* (U); Sierra Nevada del Cocuy, valle de los Corralitos, 6°24'N, 72°27'W, 31 Jul 1957, *Grubb et al. 195* (COL, F, K); Tota, 5°33'N, 72°59'W, Dec 1951, *Yepes Agredo 3299* (COL). **Boyacá-Santander:** Charalá, Páramo de La Rusia, 5°40'N, 73°5'W, 7 May 1986, *Fernández Alonso et al. 6134a* (COL). **Cauca:** Popayán, 2°27'N, 76°32'W, 21 Jul 1960, *Schultes 22501a* (COL, K). **Cundinamarca:** Bogotá-Choachí road, repetidora La Viga, 4°34'N, 74°0'W, 7 Jan 1974, *Gentry et al. 8930* (MO); Montserrate, above Bogotá, 4°37'N, 74°2'W, 6 Jan 1974, *Gentry et al. 8895* (MO); Chipaque, 4°25'N, 74°3'W, s.d., *Triana 3754* (BM); Cruz Verde, 4°30'N, 74°3'W, 27 Aug 1967, *Dwyer & Idrobo 8161* (MO); Fómeque, Parque Natural Nacional de Chingaza, 4°31'N, 73°46'W, 7 Feb 1981, *Franco & Rangel 62* (COL); Guadalupe, 4°34'N, 74°3'W, 1845, *Goudot s.n.* (G); in pass along highway from Bogotá to Villavicencio, 4°25'N, 74°3'W, 7 Nov 1943, *Core 30* (US); Quebrada Chico, hills above Bogotá, 4°36'N, 74°5'W, 11 Jul 1943, *Allen 2990* (MO); Zipaquira, en Pantano Redondo, 5°1'N, 74°0'W, 12 Dec 1948, *Romero Castañeda 1325*

(COL); Zuqué near Bogotá, 4°31'N, 74°3'W, 4 Sep 1948, *Regis s.n.* (US). **Norte de Santander:** de La Laguna a Nariz de Judío, Mutiscua, 7°20'N, 72°43'W, 19 Jun 1946, *Garganta 1201* (F); Santander, a 2 km del paraje Berlín, 7°11'N, 72°53'W, 18 Dec 1948, *Molina & Barkley 18S.407* (US); **Santander:** edge of Páramo de las Vegas, 7°11'N, 73°0'W, 20 Dec 1926, *Killip & Smith 15705* (NY); edge of Páramo de Santurbán, near Vetás, 7°12'N, 72°59'W, 17 Jan 1927, *Killip & Smith 17946* (US); Onzaga, vereda de Chaguacá, alto de la laguna de los Bobos, filo divisorio con Bocayá, 6°21'N, 72°50'W, 7 Aug 1958, *Jaramillo et al. 926* (COL); Páramo de Mogotocoro, near Vetás, 7°12'N, 72°59'W, 18 Jan 1927, *Killip & Smith 17597* (NY); Páramo de Santurbán, en route from Toma to Mutiscua, 7°12'N, 72°59'W, 18 Feb 1927, *Killip & Smith 19554* (NY, US); Páramo del Almorzadero, extremo sur en Peralonso, 7°22'N, 73°38'W, 28 Nov 1941, *Cuatrecasas 13519* (COL, US); Páramo del Romeral, 29 Jan 1927, *Killip & Smith 18538* (NY); Páramo Rico, 5 km S of California, 7°18'N, 72°57'W, 15 Sep 1944, *St. John 20754* (NY, P, US).

VENEZUELA. Apure: Páramo de Pata de Judío, frontera Colombia-Venezuela, 30 km S San Vicente de la Revancha, al S Alquitrana, 7°23'N, 72°19'W, 19 Jan 1968, *Steyermark et al. 101141* (NY, US, VEN). **Táchira:** NE side of Páramo de Tamá from Cave to top, 7°30'N, 72°25'W, 18 Oct 1978, *Luteyn et al. 5896* (NY, VEN); Páramo de Tamá, 7°30'N, 72°25'W, Jul 1935, *Cardona 295* (VEN).

Geranium santanderiense is easily distinguished from other species of sect. *Gracilia* by its leaves with antrorse, appressed cilia on the margin, which gives a scarious aspect to the leaf border. Other differences between *G. santanderiense* and *G. lainzii* are addressed in the discussion under *G. lainzii*.

Some specimens from Sierra Nevada de Cocuy, Bocayá, Colombia (*Cuatrecasas 1441a*, F; *Grubb et al. 195*, US; *Cleef 10008*, U), and Páramo de la Pata del Judío, Apure, Venezuela (*Steyermark & Dunster-ville 101141*, NY, US, VEN) show an unusual leaf indumentum: eglandular, appressed hairs 1.3 mm long on the adaxial surface, and eglandular hairs only on the nerves of the abaxial surface. Otherwise, they are similar to the other specimens of *G. santanderiense*.

6. GERANIUM SEBOSUM S. F. Blake, Contr. U.S. Natl. Herb. 20: 526. 1924. (Fig. 13). TYPE: VENEZUELA. Mérida, Páramo de Timotes, s.d., A. Jahn 5 (HOLOTYPE: US-602198).

Herbs perennial. *Rootstock* 5–8 mm diam., ± vertical; roots unknown; without

vegetative stems, stolon absent; *aerial stems* 15–25 × 0.1–0.2 cm, herbaceous, leaved, erect, with eglandular, patent hairs 0.5–2.3 mm long, and glandular, patent hairs 0.3–0.5 mm long. *Basal leaves* in a persistent rosette; lamina 2.5–3.5 × 3.4–4.1 cm, polygonal in outline, cordate, palmatifid (divided for 0.5–0.6 of its length), not coriaceous, not projected, densely hairy, with glandular and eglandular, appressed hairs on both surfaces; segments 5, obtriangular, 5–8 mm at the base, 3–5-lobed at apex (main sinus length of the middle segment/middle segment length = 0.15–0.2), usually obtuse, mucronate; *cauline leaves* similar to basal leaves; petioles to 10 cm long, with eglandular, patent hairs 0.5–2.5 mm long, and glandular, patent hairs 0.3–0.5 mm long; stipules 5–6 × 2 mm, lanceolate, with eglandular hairs on both surfaces and on the margin. *Peduncles* 2–2.5 cm long, with eglandular, ± patent hairs 0.5–2 mm long, and glandular, patent hairs 0.5–1 mm long; bracteoles 4–5 × 1 mm, lanceolate, with eglandular hairs on both surfaces and on the margin; pedicels 1–2 cm long, with eglandular, ± patent hairs 0.5–2 mm long, and glandular, patent hairs 0.5–1 mm long. *Sepals* 4.5–5.5 × 2 mm, with mucro 0.2–0.3 mm long, with scarious margins ca. 0.1 mm wide, with eglandular, ± patent hairs 0.3–0.5 mm long and glandular, ± patent hairs 0.5–0.7 mm long on the abaxial surface, glabrous adaxially. *Petals* 6–7 × 5 mm, entire or slightly emarginate (notch ca. 0.5 mm deep), without claw, hairy on the base of adaxial surface, glabrous on the abaxial surface, ciliate on the basal margin (with eglandular hairs and minute glands), and with minute glands at the apex, purplish. *Staminal filaments* 4–5 mm long, lanceolate, glabrous on both surfaces, ciliate on the proximal half, with eglandular hairs 0.3–0.8 mm long and some minute glandular hairs; anthers 0.9–1 × 0.5 mm. *Gynoecium* 5–6 mm long. *Fruit* 16–18 mm long, erect; mericarps 3–3.5 × 1.5–2 mm, with eglandular, ± patent hairs 0.3–0.5 mm long; rostrum 11–12 mm long, without a narrowed apex, with eglandular, patent hairs 0.15–0.6 mm long and glandular, patent hairs 0.5–0.7 mm long; stigmatic remains 2 mm long, with 5 glabrous

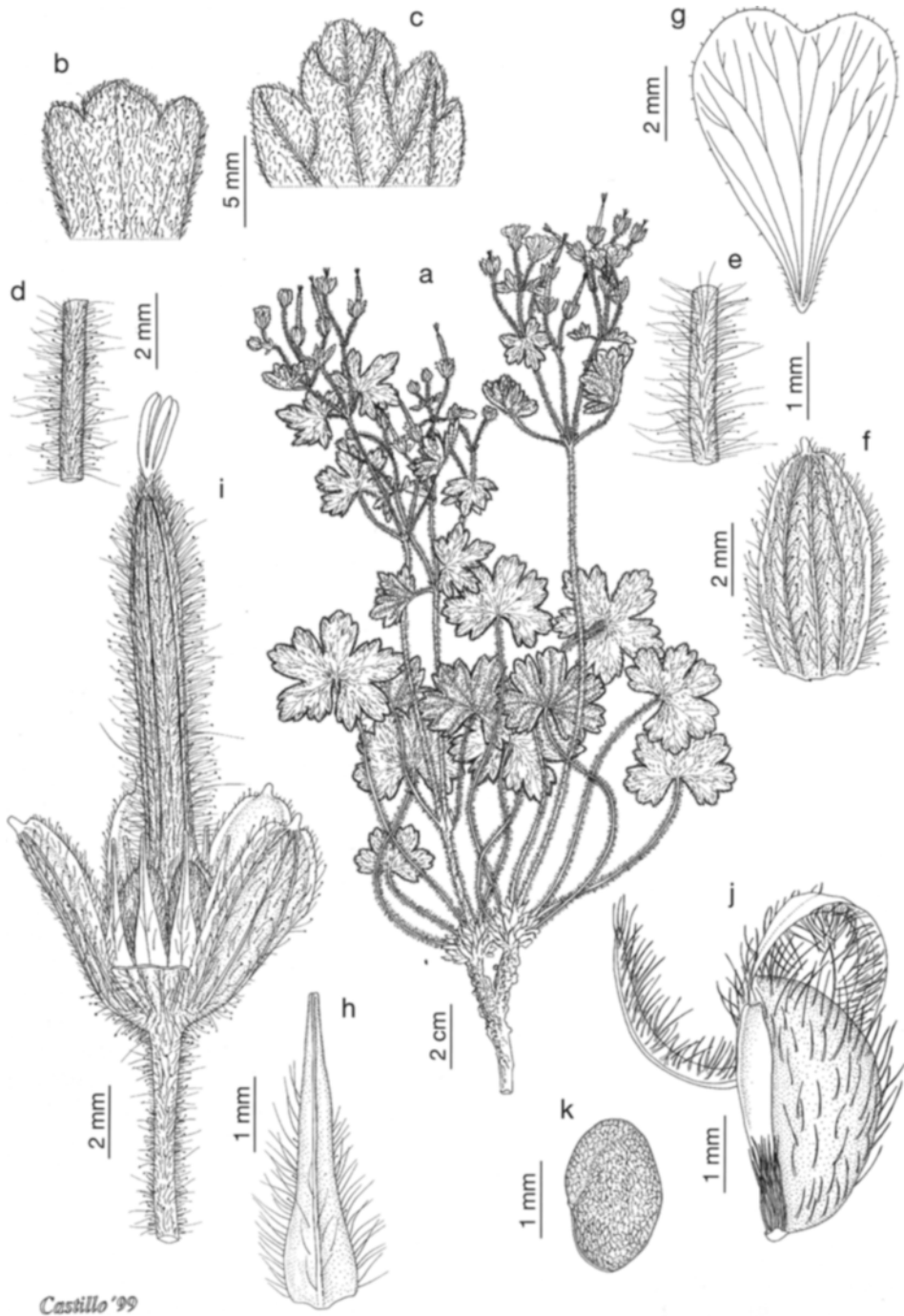


FIG. 13. *Geranium sebosum*. A. Habit. B. Adaxial leaf surface. C. Abaxial leaf surface. D. Pedicel. E. Peduncle. F. Sepal. G. Petal. H. Filament of stamen. I. Fruit. J. Mericarp. K. Seed. (a-h: from Farenholtz s.n., B; i-k: from Jahn 5, US)

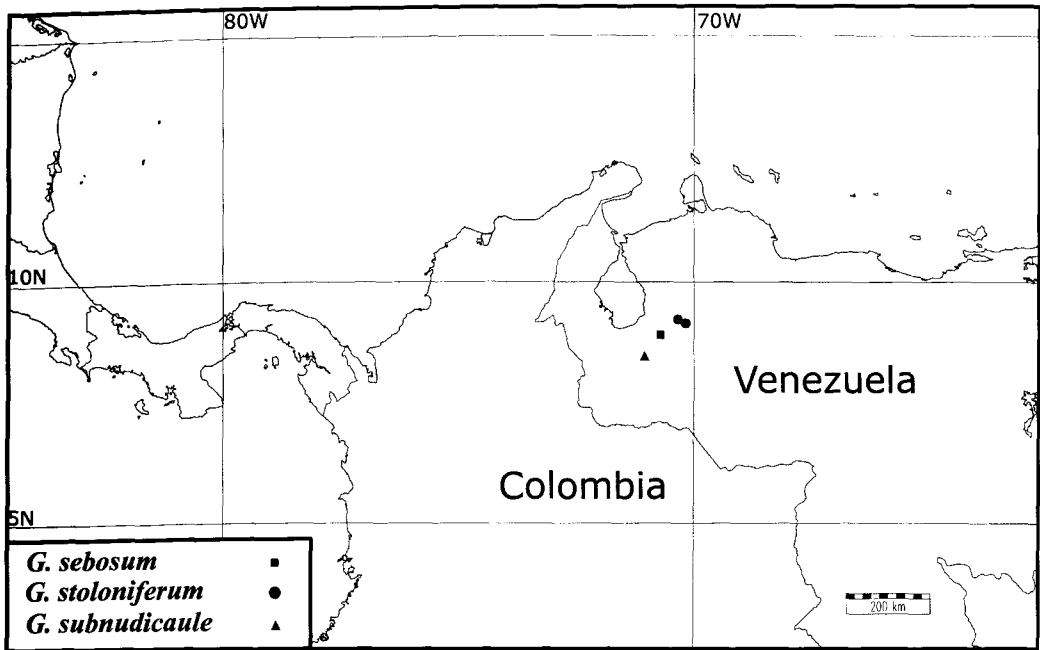


FIG. 14. Distribution of *Geranium sebosum*, *Geranium stoloniferum*, and *G. subnudicaule*.

lobes. Seeds 2.2×1.2 mm, brownish; hilum $\frac{1}{2}$ as long as the perimeter.

Distribution and habitat.—Venezuela: eastern Mérida; 3000–4000 m (Fig. 14).

Phenology.—Flowering from March to July.

Additional specimens examined: VENEZUELA. Mérida: Páramo de Timotes, $8^{\circ}59'N$, $70^{\circ}44'W$, 4 Jul 1934, Farenholtz s.n. (B).

This species is characterized by the dense indumentum of long, glandular and eglandular hairs. *Geranium sebosum* can be distinguished from the other species by the presence of glandular hairs on the petioles.

Geranium sebosum is a rare species only collected in two localities. The herbarium specimens lack information about habitat. Pittier (1929) recorded this species on Páramo de Mucuchíes, State of Mérida, Venezuela, on the basis of the *Gutzwiller 19* (NY); but it is *G. velutinum*.

7. GERANIUM STOLONIFERUM Standl., Contr. U.S. Natl. Herb. 18: 110. 1916. (Fig. 15). TYPE: VENEZUELA. Trujillo, Páramo de la Cristalina, 20 Dec 1910, A. Jahn 126 (HOLOTYPE: US–602320).

Herbs perennial. **Rootstock** 3–6 mm diam., \pm vertical; roots unknown; without vegetative stems, stolon present (10–40 cm long); **aerial stems** 20–25 \times 0.1–0.2 cm, herbaceous, leaved, erect, with eglandular, patent hairs 0.1–0.3 mm long. **Basal leaves** in a persistent rosette; lamina 1.8–2.6 \times 2.2–3.1 cm, polygonal in outline, cordate, palmatifid (divided for 0.7–0.75 of its length), coriaceous, projected on the abaxial surface, sunken adaxially, usually glabrous adaxially (sometimes with eglandular hairs on nerve channels), densely ciliated (with patent, eglandular hairs), and with eglandular hairs on the nerves of abaxial surface; segments 5, obtriangular, 3–6 mm at the base, 3-lobed at apex (main sinus length of the middle segment/middle segment length = 0.11–0.16), obtuse, mucronate; **cauline leaves** opposite, similar to basal; petioles to 7 cm long, with eglandular, patent hairs 0.1–0.5 mm long; stipules 8–9 \times 2 mm, subulate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. **Peduncles** 1.2–2.5 cm long, with eglandular, patent hairs 0.1–0.6 mm long, and glandular, patent hairs 0.3–0.5 mm

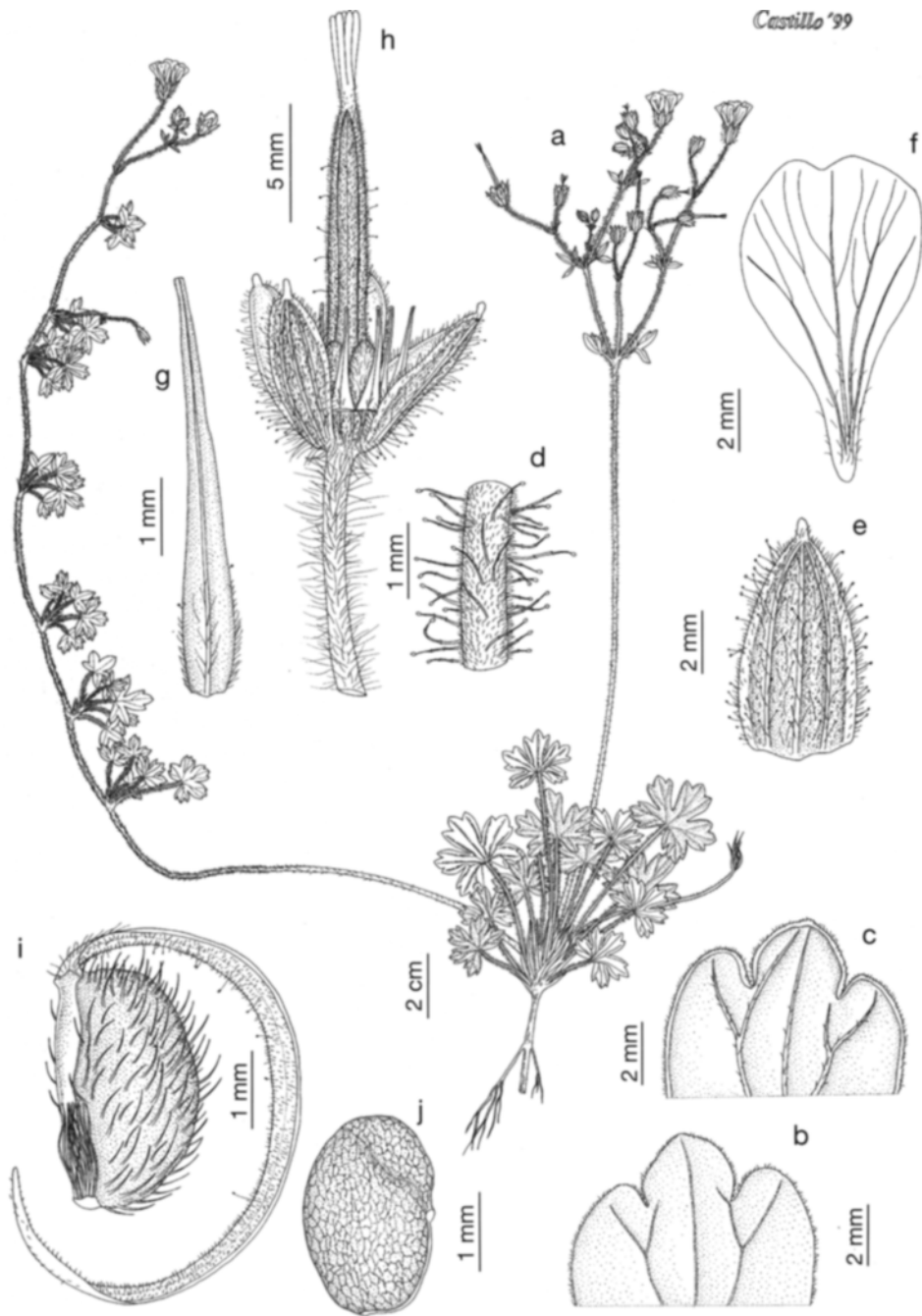


FIG. 15. *Geranium stoloniferum*. A. Habit. B. Adaxial leaf surface. C. Abaxial leaf surface. D. Peduncle. E. Sepal. F. Petal. G. Filament of stamen. H. Fruit. I. Mericarp. J. Seed. (a, e-j: from Dorr *et al.* 4955, NY; b-d: from Dorr *et al.* 7381, NY)

long; bracteoles 5–6 × 1 mm, subulate, with eglandular hairs on both surfaces and on the margin; pedicels 0.8–2.2 cm long, with eglandular, ± patent hairs 0.1–0.6 mm long, and glandular, patent hairs 0.3–0.5 mm long. *Sepals* 5–6 × 2 mm, with mucro 0.15–0.2 mm long, with scarious margins 0.2–0.3 mm wide, with eglandular, appressed hairs 0.1–0.2 mm long and glandular, patent hairs 0.3–0.9 mm long on the abaxial surface, glabrous adaxially. *Petals* 11–12 × 7 mm, entire or slightly emarginate (notch ca. 0.5 mm deep), without claw, hairy on the base of adaxial surface, glabrous on the abaxial surface, ciliate on the basal margin, purplish. *Staminal filaments* 4–5 mm long, lanceolate to lanceolate with an abruptly narrowed apex, pilose on the abaxial surface, ciliate on the proximal half, with eglandular hairs 0.2–0.5 mm long and some minute glandular hairs; anthers 1 × 0.6 mm. *Gynoecium* 5–6 mm long. *Fruit* 15–16 mm long, reflexed; mericarps 3–3.5 × 1.5–2 mm, with eglandular, ± patent hairs 0.1–0.3 mm long; rostrum 12–13 mm long, without a narrowed apex, with eglandular, patent hairs 0.1–0.4 mm long, and glandular, patent hairs 0.3–0.5 mm long; stigmatic remains 2 mm long, with 5 glabrous lobes. *Seeds* 2 × 1.3 mm, reddish; hilum 1/2 as long as the perimeter.

Distribution and habitat.—Venezuela: Sierra Nevada de Mérida, State of Trujillo. It is found in disturbed areas of the páramo; 2800–3450 m (Fig. 14).

Phenology.—Flowering in January, and from April to July.

Additional specimens examined: VENEZUELA. **Trujillo:** entre Boconó y Guaramacal, cumbre del Páramo de Guaramacal, 25 Feb 1971, *Steyermark 104856* (VEN); Páramo de Guaracamal, 3 Feb 1987, *van der Werff et al. 8863* (MO), 18 July 1990, *Dorr et al. 7381* (C, NY); Bocono, Páramo de Guaramacal, below television towers, 9°14'N, 70°11'W, 18 July 1990, *Dorr et al. 4955* (NY); Fila de Agua Fría, 9°16'N, 70°8'W, Jan 1996, *Stergios & Zambrano 17694* (MA).

This rare species is easily recognized by its epigeal stolon, which is probably unique in the whole genus.

Bono (1996: 554) recorded *G. stoloniferum* from Páramo de Tamá, State of Táchira, Venezuela, on limestone (*Steyermark*

57348). Unfortunately, we have not located any specimens of this collection.

8. *GERANIUM SUBNUDICAULE* Turcz., Bull. Soc. Imp. Naturalistes Moscou 31: 418. 1858. (Fig. 16). Type: VENEZUELA. Mérida, Sierra Nevada, 1846, *N. Funck & L. J. Schlim 1127* (LECTOTYPE, here designated: KW, photocopy at MA; ISOLECTOTYPES: BM, BR, G, LE, MPU, P, W).

Herbs perennial. *Rootstock* 3–5 mm diam., ± vertical; roots unknown; without vegetative stems, stolon absent; *aerial stems* 30–60 × 0.2–0.3 cm, herbaceous, leaved, erect, with scattered eglandular, patent hairs 0.15–0.6 mm long and glandular (only on the inflorescence), patent hairs 0.3–1 mm long. *Basal leaves* in a persistent rosette; lamina 3.1–4.1 × 3.5–5.4 cm, polygonal in outline, cordate, palmatifid (divided for 0.65–0.75 of its length), not coriaceous, not projected, pilose, with ± appressed, mostly eglandular hairs beneath, and with eglandular hairs on the nerves of abaxial surface; segments 5, obtriangular, 5–8 mm at the base, 7–11-lobed in distal half (main sinus length of the middle segment/middle segment length = 0.13–0.14), usually obtuse, mucronate; *cauline leaves* opposite, similar to the basal; petioles to 26 cm long, with scattered eglandular, patent hairs 0.15–0.4 mm long; stipules 8–10 × 4 mm, lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. *Peduncles* 2–5 cm long, with eglandular, patent hairs 0.15–0.4 mm long and glandular, patent hairs 0.3–0.8 mm long; bracteoles 2–3 × 1–1.5 mm, lanceolate, glabrous on both surfaces, ciliate (with eglandular hairs); pedicels 1.1–2.7 cm long, with eglandular, patent hairs 0.15–0.4 mm long and glandular, patent hairs 0.3–0.8 mm long. *Sepals* 7–8 × 3–3.5 mm, with mucro 0.4–0.5 mm long, with scarious margins 0.15–0.2 mm wide, with eglandular, ± patent hairs 0.2–0.7 mm long and glandular, erect patent hairs 0.3–0.9 mm long on the abaxial surface, glabrous adaxially. *Petals* 8–9 × 5 mm, entire or slightly emarginate (notch ca. 0.5 mm deep), without claw, glabrous, purplish. *Staminal filaments* 3–4 mm

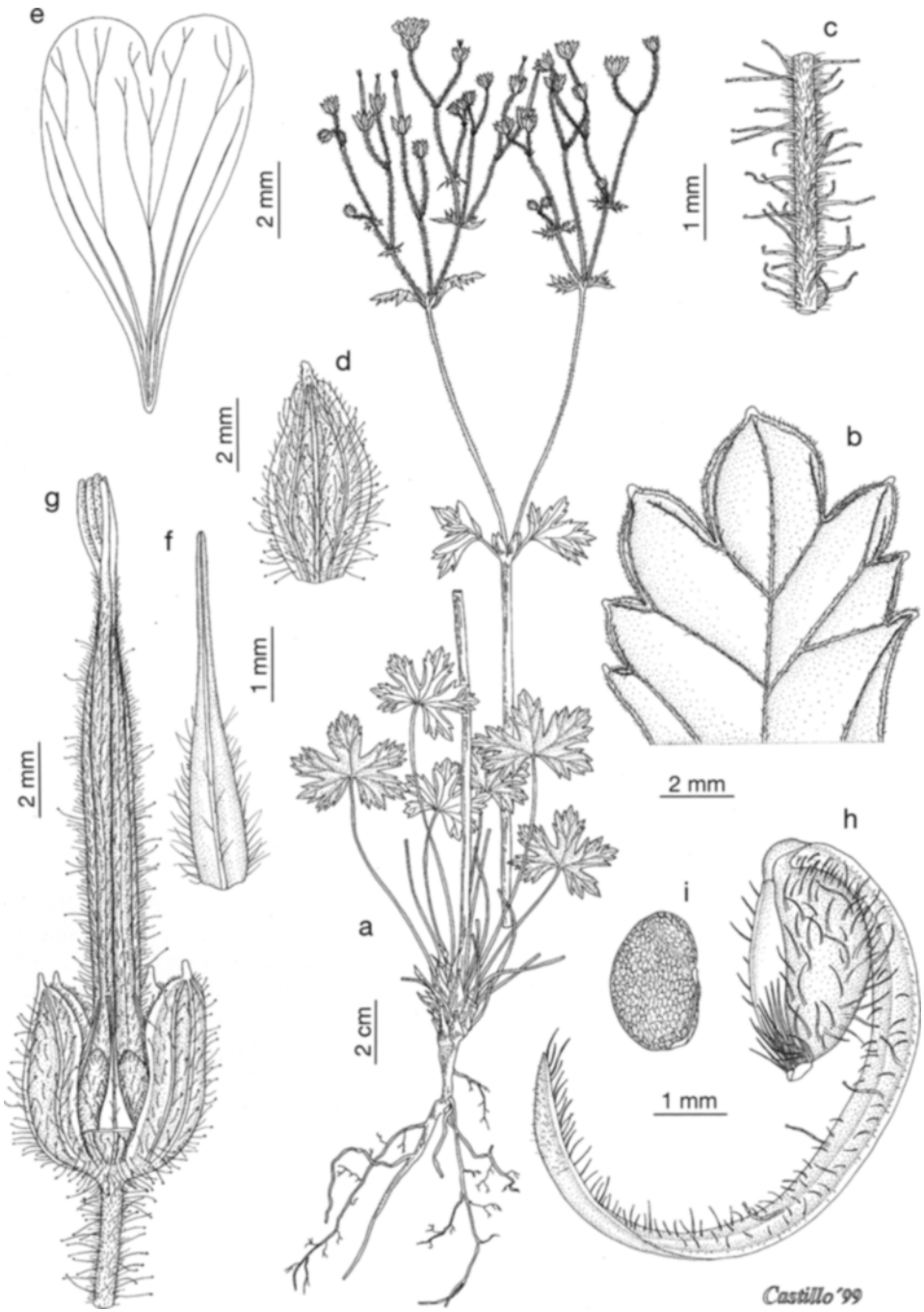


FIG. 16. *Geranium subnudicaule*. A. Habit. B. Abaxial leaf surface. C. Peduncle. D. Sepal. E. Petal. F. Filament of stamen. G. Fruit. H. Mericarp. I. Seed. (a, c, d-f: from *Funk & Schlim 1127*, G; b: from *Liden 413*, K; g: from *Funk & Schlim 1128*, BM)

long, lanceolate, pilose on the abaxial surface, ciliate on the proximal half, with eglandular hairs 0.2–0.5 mm long and some minute glandular hairs; anthers 0.7×0.3 mm. *Gynoecium* 4–5 mm long. *Fruit* 19–20 mm long, erect; mericarps $3\text{--}3.5 \times 2$ mm, with scattered, eglandular, erect patent hairs 0.3–0.8 mm long; rostrum 16 mm long, with a narrowed apex 1–2 mm long, with eglandular, erect patent hairs 0.15–1 mm long, and sometimes glandular, patent hairs 0.5–0.6 mm long; stigmatic remains 2–3 mm long, with 5 hairy lobes. *Seeds* 2.4×1.5 mm, reddish; hilum $\frac{1}{4}$ as long as the perimeter.

Distribution and habitat.—Venezuela: Sierra Nevada de Mérida, State of Mérida; ca. 3000 m (Fig. 14).

Phenology.—Flowering from April to September.

Additional specimens examined: VENEZUELA. Caracas, S América, Apr 1842, *Linden 413* (K); Prov. de Mérida, Aug 1842, *Linden 413* (W); Sierra Nevada de Mérida, Aug 1849, *Linden 413* (MPU); Hautes Andes de Trujillo & de Mérida, 1842, *Linden 413* (G); Venezuela, 1846, *Funck & Schlim 1128* (BM, P, W); Mérida, Sierra Nevada, 1846, *Funck & Schlim 1128* (G, MPU).

Geranium subnudicaule is similar to *G. velutinum*. However, *G. velutinum* has coriaceous leaves, is velutinous abaxially, and has mature fruit reflexed (vs. not coriaceous leaves, with eglandular hairs on the nerves of abaxial surface, and mature fruit erect).

There are few herbarium specimens of *G. subnudicaule*; it seems to occur on the Sierra Nevada de Mérida; however, some duplicates have different labels (see: Additional specimens examined). Some labels bear the questionable locality of "Caracas," which might be dubious.

9. GERANIUM VELUTINUM Turcz., Bull. Soc. Imp. Naturalistes Moscou 31: 417. 1858. (Fig. 17). TYPE: VENEZUELA. Mérida, Páramo de Portechuelo, 1846, *N. Funck & L. J. Schlim 1251* (LECTOTYPE, here designated: KW, photocopy at MA).

Herbs perennial. *Rootstock* 6–9 mm diam., \pm vertical; roots unknown; without vegetative stems, stolon absent; *aerial stems* $20\text{--}40 \times 0.2\text{--}0.3$ cm, herbaceous, leaved, erect, with eglandular, patent (some-

times retrorse, appressed) hairs 0.15–1.1 mm long, and glandular, patent hairs 0.3–1 mm long only on the inflorescence. *Basal leaves* in a persistent rosette; lamina $3.6\text{--}5 \times 3.9\text{--}5.4$ cm, polygonal in outline, cordate, palmatifid (divided for 0.5–0.7(–0.8) of its length), coriaceous, projected on the abaxial surface, sunken adaxially, pilose, with eglandular, appressed hairs beneath, and velutinous (with eglandular hairs, longer on the nerves) abaxially; segments 5 (–7), obtriangular, 7–9 mm at the base, 3–5(–7)-lobed in distal half (main sinus length of the middle segment/middle segment length = 0.09–0.18), usually obtuse, mucronate; *cauline leaves* opposite, similar to the basal; petioles to 20 cm long, with eglandular, usually patent hairs 0.15–0.7 mm long; stipules $7\text{--}9 \times 3\text{--}3.5$ mm, lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially. *Peduncles* 2.5–7 cm long, with eglandular, usually patent hairs 0.15–0.8 mm long, and usually glandular, patent hairs 0.3–1 mm long; bracteoles $2\text{--}4 \times 1\text{--}1.5$ mm, lanceolate, with eglandular hairs on abaxial surface and on the margin, glabrous adaxially; pedicels 1.5–3.1 cm long, with eglandular, usually patent hairs 0.15–0.8 mm long, and usually glandular, patent hairs 0.3–1 mm long. *Sepals* $6\text{--}8 \times 2.5\text{--}4$ mm, with mucro 0.3–0.5 mm long, with scarious margins 0.15–0.2 mm wide, with eglandular, \pm patent hairs 0.2–0.6 mm long and usually glandular, erect patent hairs 0.2–0.9 mm long and on the abaxial surface, glabrous adaxially. *Petals* $11\text{--}12.5 \times 7$ mm, entire or slightly emarginate (notch ca. 0.5 mm deep), without claw, glabrous or hairy on the base of adaxial surface, and ciliate on the basal margin, purplish, sometimes white. *Staminal filaments* 4.5–5.5 mm long, lanceolate, pilose on the abaxial surface, ciliate on the proximal half, with eglandular hairs 0.1–0.4 mm long and some minute glandular hairs; anthers $1.1\text{--}1.2 \times 0.6$ mm. *Gynoecium* 6–7 mm long. *Fruit* 18–21 mm long, reflexed; mericarps $2.5\text{--}3.3 \times 1.5\text{--}2$ mm, with eglandular, erect patent hairs 0.3–0.5 mm long; rostrum 15–17 mm long, without a narrowed apex, with eglandular, erect patent hairs 0.3–0.5 mm long, and sometimes glandular, patent hairs

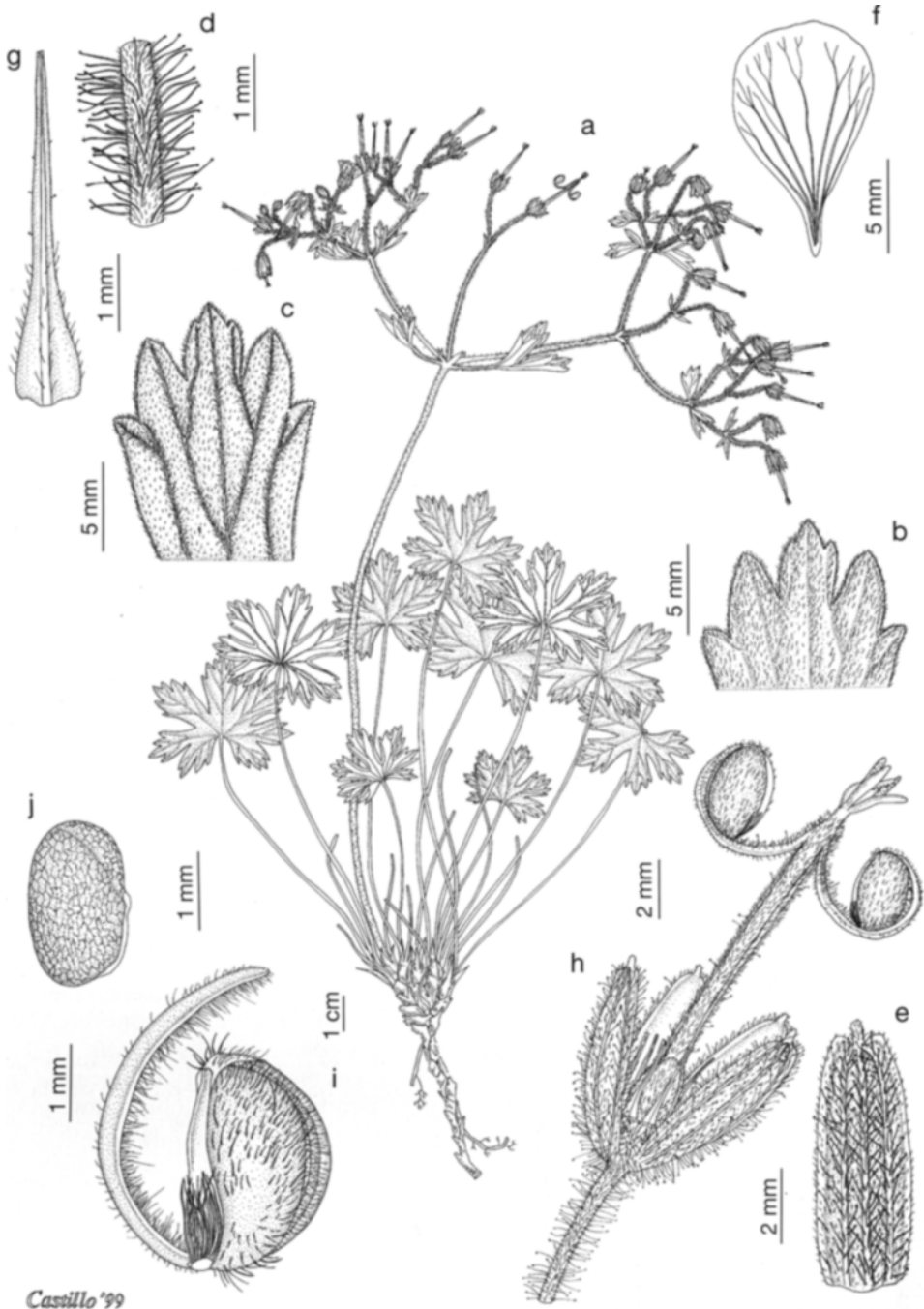


FIG. 17. *Geranium velutinum*. A. Habit. B. Adaxial leaf surface. C. Abaxial leaf surface. D. Peduncle. E. Sepal. F. Petal. G. Filament of stamen. H. Fruit. I. Mericarp. J. Seed. (a-c: from *Alston 7028*, BM; d-e, g-j: from *Breteler 4620*, US; f: from *Stergios 763*, PORT)

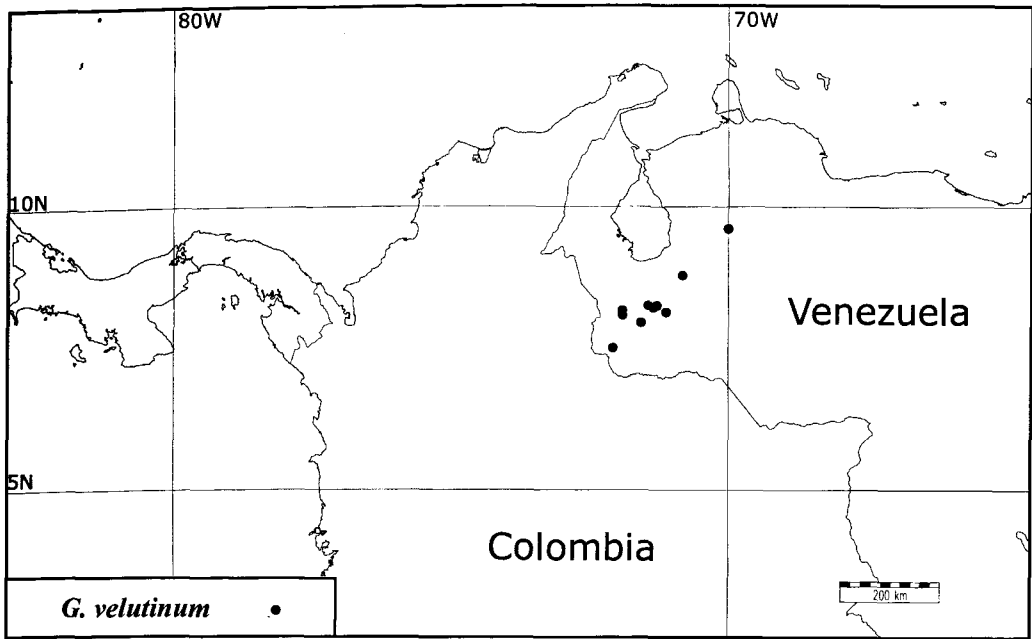


FIG. 18. Distribution of *Geranium velutinum*.

0.3–0.4 mm long; stigmatic remains 2–3 mm long, with 5 glabrous lobes. Seeds 2.2–2.3 × 1.2 mm, reddish; hilum $\frac{1}{2}$ as long as the perimeter.

Distribution and habitat.—Venezuela: Cordillera de Mérida (States of Mérida, Táchira, and Trujillo). It occurs on roadside banks, páramo, brushy slopes, and montane forest; 2600–3300 m (Fig. 18).

Phenology.—Flowering from February to December.

Additional specimens examined: VENEZUELA. **Mérida:** Páramo de Mucuchíes, 8°52'N, 70°50'W, Dec 1927, *Gutzwiller 19* (NY); Sucre, Estanques, estribaciones del páramo de Quirorá, 8°20'N, 71°27'W, 19 Feb 1970, *Ruiz-Terán & López-Figueras 11* (MO, NY, VEN); Páramo de Pozo Negro, between San José and Beguilla, 8°20'N, 71°18'W, 3 May 1944, *Steyermark 56266* (F); Páramo La Negra between Tovar and La Grita, 8°15'N, 71°55'W, 7 Oct 1965, *Breteler 4620* (K, MO, NY, S, US); Páramo de Mucucuí, sobre Pueblo Nuevo, 8°18'N, 71°22'W, 7 Dec 1952, *Bernardi 90* (NY); Páramo Quirorá, 8°20'N, 71°27'W, 8 Oct 1921, *Jahn 724* (GH); Páramo de Aricagua, 8°13'N, 71°8'W, 31 Mar 1922, *Jahn 1004* (GH, VEN); Páramo El Batallón, 8°10'N, 71°55'W, 18 Nov 1976, *Charpin et al. 13532* (C). **Táchira:** Páramo Portachuelo, 8°10'N, 71°55'W, 23 Oct 1978, *Luteyn & Lebrón-Luteyn 6025* (F, VEN); de civitate La Grita ad civitatem Pregonero, 8°2'N, 71°35'W, 9 Oct 1965, *Bernardi 10969* (K); Pá-

ramo del Batallón, sector de las Antenas, entrando por Portachuelo y las Porqueras, 8°10'N, 71°55'W, 27 Dec 1976, *Stergios 773* (PORT); Jáuregui, entre el Portachuelo y la antena de CANTV, Páramo Batallón, 8°10'N, 71°55'W, 8 Aug 1976, *Benítez 2044* (MO); Jáuregui, Páramo La Negra, 8°45'N, 71°55'W, 19 Aug 1988, *Badillo et al. 7964* (F); Uribante, cabeceras del Río Uribante, 44 km SW de Pregonero, 7°35'N, 72°5'W, 28 Sep 1981, *Steyermark & Manara 125442* (VEN). **Trujillo:** La Quebrada Cortijo, by boundary line Lara-Trujillo, above Humocaró Bajo, 9°41'N, 70°0'W, 6 Feb 1944, *Steyermark 55345* (F, NY, VEN).

Geranium velutinum has usually patent, glandular hairs (to 1 mm long) on the upper part of the stem, inflorescence (peduncles, pedicels, sepals), and fruit rostrum. However, in some specimens glandular hairs are scarce, and rarely specimens lack glandular hairs (*Ruiz Terán & López Figueiras 11*, NY). Otherwise, they are quite similar to the other specimens of *G. velutinum*.

Pittier (1929: 180) considered *Geranium velutinum* to be not distinctive from *G. multiceps*. We disagree with this opinion after having studied the types and many other specimens. In our opinion, *G. velutinum* can be easily distinguished from *G. multiceps* by the glandular hairs on the peduncles,

pedicels, and sepals. The few specimens with scarce glandular hairs might be identified as *G. velutinum* by the coriaceous leaves that are velutinous on the abaxial surface. *Geranium multiceps* does not show coriaceous leaves, but the leaves have eglandular hairs only on nerves of abaxial surface or are rarely glabrous. There are also differences in petal and fruit features. See the discussion of *G. subnudicaule* for additional comparisons.

We have examined three duplicates of *Luteyn et al.* 6025 collection: two of them (F, and U) are *G. velutinum*; the third (MO) is *G. holosericeum*. This suggests a possible labeling mistake.

Doubtful Names

Geranium pilgerianum R. Knuth in Engl., Pflanzentr. IV.129 (Heft 53): 106. 1912.

TYPE: COLOMBIA. Cundinamarca, Páramo de Pasca, *M. A. Stuebel 146*, p.p. (HOLOTYPE: B, destroyed, photos F, G, GH, NY).

The holotype of this species was destroyed during the 1943 fire of the Berlin herbarium (B). Neither type photographs nor original description permit a conclusive interpretation of this taxon. The two fragments in the photographs do not show the important inflorescence features so it is not possible to include the species in sect. *Gracilia*. No other specimen from the type locality (Páramo de Pasca) has been seen which could be identified as *G. pilgerianum*.

Acknowledgments

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ing our visits and for loan of specimens. This work was partly financed by the Spanish Dirección General de Investigación Científica y Técnica (DGICYT) through the research project PB96-0849, and the Spanish Agency of International Cooperation (AECI) through the project 99GN0001.

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Index of Scientific Names

The accepted names are in bold type, and synonyms are in *italics*.

Geranium

- sect. *Fruticulosa* R. Knuth =
sect. **Gracilia**
sect. **Gracilia** R. Knuth
gracilipes Triana & Planch. =
G. holosericeum
holosericeum Willd. ex Spreng.
var. *stuebelii* R. Knuth =
G. holosericeum
var. *typicum* R. Knuth =
G. holosericeum
lainzii Aedo
lignosum R. Knuth
lindenianum Turcz. =
G. holosericeum
multiceps Turcz.
pilgerianum R. Knuth =
nomen dubium
santanderiense R. Knuth
sebosum S.F. Blake
stoloniferum Standl.
subnudicaule Turcz.
velutinum Turcz.

Exsiccatae

Each specimen is cited by the first collector surname. The number in parentheses refers to the corresponding species in the text, and in the following list of species.

1. *Geranium holosericeum* Willd. ex Spreng.
2. *Geranium lainzii* Aedo
3. *Geranium lignosum* R. Knuth
4. *Geranium multiceps* Turcz.
5. *Geranium santanderiense* R. Knuth
6. *Geranium sebosum* S. F. Blake
7. *Geranium stoloniferum* Standl.
8. *Geranium subnudicaule* Turcz.
9. *Geranium velutinum* Turcz.

Allen 2990 (5); Alston 6845 (4), 7028 (9), 7475 (2); Arietseguieta 2827 (4); Ariste 755 (1), 1919 (2).

Badillo 530 (4), 5137 (4), 7964 (9); Ballesteros 45 (1); Barclay 21 (2), 4050 (2), 4373 (5), 7215 (1), 7599 (5), 7707 (1), 7733 (5), 9541 (4), 9681 (4), 9783 (4); Barreto 626 (4); Bejarano 222 (1), 89 (1); Ballard 255 (4); Benítez 2044 (9); Berg 93 (4), 186

(4); Bernardi 90 (9), 603 (4), 690 (4), 10725 (5), 10787 (4), 10969 (9), 17036 (4), 17150 (4); Breteler 4620 (9); Briceño 553 (4); Bruijij 1146 (4); Burbidge 75/240 (1).

Cardona 295 (5); Castroviejo 10686 (1); Charpin 13201 (5), 13532 (9); Cleef 457 (2), 2011 (5), 2758 (2), 2910 (2), 3074 (2), 3391 (2), 3737 (2), 4458 (5), 4914 (1), 10008 (5); Core 30 (5), 402 (2), 460 (2); Croizat 15 (4); Cuatrecasas 22 (5), 372 (5), 1375 (1), 1441a (5), 1640 (1), 2273 (2), 5123 (1), 5550 (2), 9499 (2), 9972 (1), 10456 (2), 12611 (5), 13519 (5), 25614 (2); Cuatrecasas & Jaramillo 25992 (1); Curran 283 (4), 289 (4), 292 (4).

Dennis 2090 (4); Díaz et al. 2733 (1); Dorr 4955 (7), 5536 (4), 7381 (7); Dumont 100 (2); Dwyer 8161 (5).

Fernández Alonso 5156 (5), 5410 (3), 6134a (5), 6341 (1), 7742 (1), 11956 (5), 14472 (1); Fonnegra 4621 (5); Fosberg 20249 (1), 20839 (1), 20904 (2), 22268 (5); Franco 62 (5), 382 (1); Funck 861 (4), 1127 (8), 1128 (8).

García 39 (1); García Barriga 16141 (1); 16180 (1), 16181 (1); Garganta 1039 (1), 1201 (5), 2188 (5); Garzon 11 (1), 67 (1); Gehriger 114 (4), 139 (4); Gentry 8895 (5), 8930 (5); Gohrger 48 (4); Grant 9481 (1), 10960 (1); Grubb 2 (2), 53 (1), 195 (5); Gutiérrez 254 (1); Gutzwiller 19 (9).

Hammen 382 (2), 402 (5), 407 (5); Hanbury-Tracy 441 (1), 76 (4); Hatheway 1083 (2); Haught 5051 (5), 5640 (2); Huertas 6781 (2); Humbert 26889 (2); Hups? s.n (3).

Idrobo 310 (1).

Jahn 5 (6), 126 (7), 591 (4), 724 (9), 1004 (9); Jaramillo 926 (5).

Kalbreyer 715 (5); Killip 11952 (2), 15661 (5), 15705 (5), 17275 (5), 17406 (5), 17421 (5), 17597 (5), 17946 (5), 18538 (5); 19554 (5); Kirkbride 346 (2); Kubocz 80 (2).

Langenheim 3409 (5); 3683 (2); Linden 413 (8), 1394 (1); López 1627 (4), 1677 (4); López Figueras 9155 (9); Luteyn 5896 (5), 6025 (1, MO), 6025 (9, F, U), 6137 (4).

Maas 5307 (4); MacDougal 4322 (2); Maguire 39418 (4), 44037 (2); Mayor 46 (2); Melampy 1003 (5); Merxmüller 22874 (4); Molina 18S.407 (5); Moritz 1247 (4); Müller 1011 (4).

Oberwinkler 12799 (4).

Panchón 65 (1); Pennell 2058 (2), 4275 (5); Pipoly 12069 (1).

Rangel 13268 OR (1); Reed 76 (4); Renteria 568 (5); Romero Castañeda 1325 (5), 1831 (1); Ruiz Terán 11 (9), 198 (4).

Sánchez 2224 (2); Schlim 1129 (1); Schultes 22473 (2), 22501a (5); Schulz 44 (4), 119 (4), 439 (1); Smith 1101 (1); Soderstrom 1345 (2); Soejarto 61 (2), 257 (1); St. John 20754 (5); Stergios 636 (1), 763 (9), 772 (9), 773 (9), 815 (9), 2123 (4); Stergios & Zambrano 17694 (7); Steyermark 55345 (9), 56266 (9), 57374 (5), 57472 (9); 104856 (7), 101141 (5), 125382 (4), 125442 (9).

Triana 3754 (5), 6046 (2); Tryon 6043 (2).

Uribe 1810 (2), 1814 (1), 2466 (2), 4475 (1), 5522 (1), 5908 (1), 6787 (1), 7027 (1).

Vareschi 1416 (4), 1771 (4), 3048 (4), 5544 (9), 5565 (9), 979 (4).

Werff, van der 8863 (7); Wessels Boer 2121 (4); White 600 (3), 601 (3); Wood 3526 (2).

Yepes Agredo 3299 (5).