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REVISION OF GERANIUM SECTIONS AZORELLOIDA, NEOANDINA, AND PARAMENSIA (GERANIACEAE)

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SUMMARY

The sections *Azorelloida*, *Neoandina*, and *Paramensia* of *Geranium*, all of them from the Andes, are taxonomically revised. Fruits with the 'seed ejection-type' dispersal have been found in all species, which allows classifying them within subg. *Geranium*. The sections *Azorelloida* and *Paramensia* consist of one and two species respectively, while section *Neoandina* comprises 24 taxa. Prior to this revision, the stemless species of *Geranium* from the Andes have been considered to belong to sect. *Andina*. *Geranium sessiliflorum* (type of *Geranium* sect. *Andina*), however, should be included in sect. *Chilensia*. Therefore, recently a new sect. *Neoandina* has been described to include most of the sect. *Andina* species (Aedo, 2000). Diagnostic morphological features are analysed and compared within and between the sections. The parsimony analysis suggested an early separation of sect. *Paramensia* from the rest of the ingroup constituted by the sections *Azorelloida* and *Neoandina*. These sections would later on have become separated into two groups: one with paramo species, and the other with more xerophilous, cold-resistant puna species. The biogeographic analyses using Fitch parsimony, dispersal-vicariance optimisation, and Bremer analysis support a paramo origin for the entire group in the North Andes, followed by a colonisation of southernmost regions (puna) and vicariance. A key, species descriptions, a complete list of synonymy, a list of specimens examined, and distribution maps are provided. Most species are illustrated for the first time. Fifteen lectotypes and one neotype are designated.

Key words: Geraniaceae, *Geranium*, biogeography, distribution, phylogeny, systematics, S America.

RESUMEN

Se revisan los *Geranium* de tres secciones andinas: *Azorelloida*, *Neoandina* y *Paramensia* de desde un punto de vista taxonómico. Estas secciones tienen frutos del tipo de 'lanzamiento de semilla' lo que permite clasificarlas en el subg. *Geranium*. Las secciones *Azorelloida* y *Paramensia* están formadas por una y dos especies respectivamente, y la sect. *Neoandina* esta formada por 24 táxones. Los *Geranium* acaules de los Andes, que habían sido previamente incluidos en la sect. *Andina*, son en este trabajo considerados como pertenecientes a la sección *Neoandina* – ya que el tipo de la sect. *Andina* ha sido transferido a la sect. *Chilensia* – (Aedo, 2000). Se estudian los caracteres morfológicos y se comparan entre y dentro de cada sección. Un análisis de parsimonia sugirio una separación temprana de la sect. *Paramensia* de las otras dos secciones. Las sections *Azorelloida* and *Neoandina* se podrían haber separado más tarde en dos grupos: uno formado por las especies del páramo, y otro más xerófilo y resistente al frío, constituído por las especies de la puna. Los análisis biogeográficos basados en la parsimonia de Fitch, en la dispersión-vicarianza, y en la optimización de Bremer apoyan un origen en el páramo – en el norte de los Andes – para este grupo,

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seguido por una colonización hacia el sur – hacia la puna – y vicarianza. Se presenta una clave de identificación, descripción de especies, una lista completa de sinónimos y de ejemplares estudiados, y mapas de distribución. La mayoría de las especies es ilustrada por primera vez. Se designan quince lectotipos y un neotipo.

Key words: Geraniaceae, *Geranium*, biogeografía, distribución, filogenia, sistemática, Sudamérica.

INTRODUCTION

The genus *Geranium* L. (Geraniaceae) comprises about 430 species distributed throughout most of the world (Aedo et al., 1998b). A brief history of the generic delimitation and infrageneric classification, as well as a description of the genus, can be found in Aedo (1996). According to the currently accepted classification (Yeo, 1984), *Geranium* is divided into three subgenera: subg. *Geranium*, subg. *Erodioidea* (Picard) Yeo, and subg. *Robertium* (Picard) Rouy. *Geranium* subg. *Geranium* comprises over 380 species, grouped in at least 10 sections. Some of these sections have already been revised (Davis, 1970; Carlquist & Bissing, 1976), much more work, however, is necessary to attain a satisfactorily knowledge of subg. *Geranium*. According to Yeo's (1984) sectional classification, the subg. *Robertium* comprises 30 species in eight sections, some of which have also been revised (Yeo, 1973, 1992; Aedo et al., 1998a). The subg. *Erodioidea* which includes 22 species in four sections has recently been monographed (Aedo, 1996, 2001a).

For *Geranium*, S America is the richest area of the world with over 150 species. Most of these species belong to the subg. *Geranium*. The exceptions are sect. *Brasiliensia*, which belongs to subg. *Erodioidea* (Aedo, 2001a) and some non-native representatives of the subg. *Robertium* (Aedo et al., 1998b).

Knuth (1912) provided a treatment of the S American species as a part of a worldwide monograph of *Geranium*. This account was based on the limited material available at that time. After Knuth's (1912) work 58 species were briefly described from S America (Knuth 1915, 1922, 1930a, 1933, 1936, 1937, 1938; Standley, 1915, 1916; Blake, 1924; Killip, 1926; Johnston, 1928; Pittier, 1929; Baker, 1929; Sandwith, 1942; Moore, 1951, 1961, 1963; Halfdan-Nielsen, 1996; Halloy, 1998; Aedo, 2000).

Few recent taxonomic revisions for this area are available. The most noticeable are Barboza's (1996) account from Argentinean species, and Burger's (1991) study from Costa Rica species. Also remarkable is Macbride's (1949) work on Peruvian *Geranium*. Moore (1943) revised *Geranium* in Mexico and C America, but in his revision no species occurring south of Panama was studied. Additionally, some checklists have been compiled for several S American countries in which information on *Geraniums* is upgraded (Lasser, 1947; Foster, 1958; Marticorena & Quezada, 1985; Taylor, 1993; Jørgensen & León-Yánez, 1999). However, no study of supposed natural groups in *Geranium* subg. *Geranium* from S America has been performed yet.

Prior to this revision, all stemless *Geraniums* from the Andes were included in the sect. *Andina* (Knuth, 1912). We have transferred *G. sessiliflorum* (the type of the sect. *Andina*) to the sect. *Chilensia* (see discussion under *Geranium* sect. *Neoandina*), and described a new section *Neoandina* to shelter all these stemless species except *G. sessiliflorum*. Knuth (1912) recognised 17 species in the sect. *Andina*, 12 of which we accept and transfer to sect. *Neoandina*. The remaining five are synonymized or transferred to other sections. We have also included in sect. *Neoandina* three other species

described during our study, and seven more described after Knuth's monograph. The sections *Azorelloida* and *Paramensia* were described after Knuth's monograph, and have never been revised. *Geranium azorelloides* (of the monotypic sect. *Azorelloida*) is also stemless but has a distinctive leaf lamina, obtriangular, with three shallowly incised segments at the apex. Section *Paramensia* is quite different from sect. *Azorelloida*, since it has a shrubby habit and leaves with an abscission zone between lamina and petiole. *Geranium jahnii* (a species of sect. *Paramensia*), however, has a leaf outline similar to *G. azorelloides*. Consequently, a study of these three sections together seems wanted.

The large size of the genus in S America makes it unfeasible to study *Geranium* as a single unit. The three sections comprise a reasonable number of species (25) for investigation. Furthermore, the lack of any recent revision covering the entire group, makes a suitable starting point for the study of subgenus *Geranium* in S America. Thus, following recent revisions of selected *Geranium* groups (Aedo, 1996; Aedo et al., 1998a; Aedo, 2001a), and in pursuit of a comprehensive monograph of the genus, we present here a revision of the sections *Azorelloida*, *Neoandina*, and *Paramensia*.

MATERIALS AND METHODS

This revision is based on more than 700 herbarium specimens from the following herbaria: AAU, B, BC, BH, BM, BOLV, BP, BR, BRSL, C, CAS, COL, CONC, CTES, DUKE, E, F, FR, G, GH, GOET, H, HAL, HBG, JE, K, L, LD, LIL, LPB, M, MA, MICH, MO, MPU, NY, O, P, PORT, QCA, RSA, S, SI, TEX, U, UC, US, W, and Z. Additionally, we have studied one specimen from the private herbarium of Dr. Halloy (Mosgiel, New Zealand). A list of specimens is available at http://www.rjb.csic.es/Geranium/Index_geranium.html. Curators from BHUPM, CONN, MANCH, MIN, PAD, STU, and UPS kindly answered our petition, but they did not find any of the requested specimens in their herbaria.

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

Cladistic analyses based on 26 morphological characters were carried out using the PAUP 4.0 beta software package (Swofford, 1998). All characters were unweighted and unordered (Table 1 and 2). Heuristic searches were replicated 100 times using random taxon entries and acctran optimisation. All optimal trees were saved (MULPARS). A fast bootstrap analysis with 10,000 replicates was conducted. MacClade version 3.04 was used to edit the dataset analysed with PAUP (Maddison & Maddison, 1992). It was also used to map the distribution of particular character-state changes.

An area of endemism is usually defined as a geographic region to which one or more taxa are confined (Axelius, 1991; Morrone, 1994). Using current methods to identify areas of endemism, we have defined 11 areas: a) Páramos de Chirripó and Talamanca (Costa Rica and Panama); b) Sierra Nevada de Santa Marta (Colombia); c) Cordillera de Mérida (Venezuela); d) Cordillera Oriental (Colombia); e) Cordillera Occidental and Cordillera Central (Colombia); f) Cordillera Real (Ecuador); g) Cordillera de Cajas (Ecuador); h) Jalca Mts (Peru); i) Central Andine Cordillera (Peru);

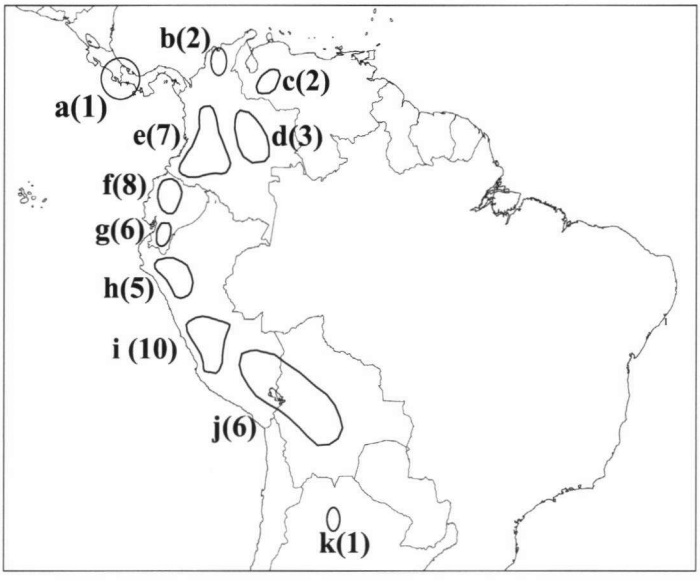
Table 1. Characters coded for phylogenetic analysis. Bistate characters were coded as either 0 or 1, respectively. The values used for multistate characters are given as bracketed values below. The slash (/) is used to separate different character states.

Character number	Character states
1	Rootstock vertical / rootstock horizontal
2	Caulescent / stemless
3	Vegetative stems absent / vegetative stems present
4	Xylem forming independent bundles separated by parenchyma, slightly developed (0) / xylem in bundles very rough or joined in a ring, with a parenchymatous central pith (1) / xylem developed in deep rays (2)
5	Parenchyma cortical cells rich in tannins absent / parenchyma cortical cells rich in tannins present
6	Herb / subshrub
7	Leaves palmatifid or palmatisect (0) / leaves digitate or tripartite (1) / leaves tridentate (2) / leaves entire (3)
8	Leaves cordate / leaves rounded or cuneate
9	Leaf lamina glabrous / leaf lamina hairy or sericeous
10	Leaf lamina not coriaceous / leaf lamina coriaceous
11	Leaf nerves not projected / leaf nerves projected
12	Abscission zone between lamina and petiole absent / abscission zone between lamina and petiole present
13	Petioles glabrous / petioles hairy
14	Old stipules absent on rootstock or aerial stem (0) / old stipules present on rootstock branches (1) / old stipules present on aerial stem branches (2)
15	Stipules without bristles / stipules with bristles
16	Stipules without a setaceous apex / stipules with a setaceous apex
17	Cymules 2-flowered / cymules 1-flowered
18	Peduncles present (0) / short peduncles present (1) / peduncles absent (2)
19	Sepals glabrous on the adaxial side / sepals hairy on the adaxial side
20	Sepals bristles absent / sepals bristles present
21	Petals glabrous on the abaxial side / petals hairy on the abaxial side
22	Petals purplish / petals white
23	Staminal filaments glabrous / staminal filaments hairy
24	Rostrum < 9 mm length / rostrum > 10 mm length
25	Rostrum without a narrowed apex / rostrum with a narrowed apex
26	Rostrum not sericeous / rostrum sericeous

j) Altiplano, Cordillera Real and Cordillera Central (Peru and Bolivia); and k) Tucuman Mts (Argentina) (Map 1). The paramo and puna areas were delimited according to Cuatrecasas (1979), Schnell (1987), and Luteyn (1999). The paramo extends from 11° N to 8° S in the northern Andes, from 3800 m to near 5000 m altitude. The plant communities are characterised by bunchgrasses (*Calamagrostis* and *Festuca*), dwarfed bamboos (*Chusquea*), shrubs of the Asteraceae, Ericaceae, Melastomataceae, and Hypericaceae, sedges (Cyperaceae), a dense mat of small plants at ground level including bryophytes, lichens, Ericaceae, cushion plant communities, and frequently in the northern Andes by giant rosette-plants like *Espeletia* (Asteraceae) and *Puya* (Bromeliaceae). The puna extends from 9° S to 27° S in C Andes, from 3200 to 4500 m altitude, and has an open grassy vegetation, corresponding to drier climates.

Table 2. Data matrix for phylogenetic analysis of *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*. Polymorphic data are coded as [01] and inapplicable or missing data are coded as '?'.

Taxa \ Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Outgroups																										
G. maculatum	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	[01]	1	1	1	0
G. santanderiense	0	0	0	0	?	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Section Azorelloida																										
G. azorelloides	1	1	1	0	1	0	2	1	0	[01]	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0
Section Neoandina																										
G. campii	1	1	1	1	0	0	1	1	1	1	0	0	1	1	1	0	1	0	0	1	0	[01]	0	0	0	0
G. costaricense	1	1	1	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	[01]	1	1	1	0
G. crassipes	1	1	0	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	0	0	0	[01]	1	0	0	1
G. digitatum	1	1	0	2	1	0	1	1	1	1	0	0	1	0	0	0	1	2	1	0	1	1	1	1	1	1
G. ecuadoriense	1	1	1	0	1	0	0	0	1	1	0	0	1	1	1	0	1	2	1	0	1	[01]	1	0	0	1
G. foreroi	1	1	1	0	1	0	0	0	0	1	0	0	1	1	1	0	1	2	0	0	0	1	1	0	0	0
G. humboldtii	0	1	1	0	0	0	0	0	1	1	0	0	[01]	1	1	0	1	2	1	0	0	0	0	0	0	0
G. jaekelae	1	1	0	2	1	0	0	0	0	1	0	0	1	0	0	0	1	2	0	0	0	1	0	0	0	0
G. macbridei	1	1	1	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	1	0	0	[01]	1	1	1	0
G. maniculatum	1	1	1	0	1	0	1	1	0	1	0	0	1	1	1	0	1	2	0	1	0	[01]	0	0	0	0
G. multipartitum	0	1	1	0	1	0	0	0	1	1	0	0	1	1	1	0	1	2	1	0	0	[01]	0	0	0	0
G. nivale	1	1	0	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	1	0	1	1	1	1	1	1
G. paludosum	1	1	0	2	1	0	0	0	0	1	0	0	1	1	1	0	1	2	0	0	1	0	1	[01]	0	0
G. pavonianum	1	1	0	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	0	0	0	0	0	0	0	0
G. planum	1	1	0	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	0	0	0	1	1	0	0	1
G. rhomboidale	1	1	1	0	1	0	1	1	0	[01]	0	0	1	1	1	1	1	2	0	0	0	0	0	0	0	0
G. ruizii	1	1	0	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	0	0	0	1	1	0	0	1
G. sericeum	1	1	0	2	1	0	0	0	2	1	0	0	1	0	0	0	1	2	1	0	1	0	1	1	0	1
G. sibbaldioides																										
subsp. *sibbaldioides*	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0
subsp. *beckianum*	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0
subsp. *elongatum*	1	1	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	2	0	1	0	[01]	0	0	0	0
G. stramineum	1	1	1	0	1	0	0	0	[01]	[01]	1	0	[01]	1	1	1	1	2	0	0	0	[01]	0	0	0	0
G. tovarii	1	1	0	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	1	0	0	[01]	0	0	0	0
G. weddellii	1	1	0	2	1	0	0	0	1	1	0	0	1	0	0	0	1	2	1	0	0	[01]	1	1	1	[01]
Section Paramensia																										
G. exallum	0	0	?	1	1	1	3	1	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	1	0	0
G. jahnii	0	0	?	1	1	1	2	1	0	0	1	1	1	2	0	1	1	0	0	0	1	0	0	?	?	?



Map 1. Areas for the biogeographic analysis of *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*: a. Páramos de Chirripó and Talamanca (Costa Rica and Panama); b. Sierra Nevada de Santa Marta (Colombia); c. Cordillera de Mérida (Venezuela); d. Cordillera Oriental (Colombia); e. Cordillera Occidental and Cordillera Central (Colombia); f. Cordillera Real (Ecuador); g. Cordillera de Cajas (Ecuador); h. Jalca Mts (Peru); i. Central Andine Cordillera (Peru); j. Altiplano, Cordillera Real and Cordillera Central (Peru and Bolivia); k. Tucuman Mts (Argentina). Taxa numbers per area are showed between brackets.

A historical biogeography was inferred from the phylogenetic estimate using three methods. The first one was to search possible succession of dispersion events through a Fitch parsimony character optimisation, in which polymorphic area states are proposed to terminal nodes. The data matrix was constructed by coding area as a single multistate character and the analysis carried up using MacClade (Maddison & Maddison, 1992). Ancestral states were conjectured by minimising the number of state changes in the tree (Maddison et al. 1992; Fritsch, 1999). Thus, present distribution is in this optimisation explained by the most parsimonious pattern of dispersions. The second method is Ancestral Areas Analysis (AA) (Bremer, 1992). The areas are optimised in the cladogram and number of gains (G), and losses (L) in each area are computed. This method uses onwards Camin-Sokal parsimony for gains and reverse Camin-Sokal for losses. Finally, the ratio between gains and losses in each area is estimated to find which individual area(s) had the highest G/L ratios, and therefore were part of the hypothetical ancestral area. The use of Camin-Sokal parsimony was criticised by Ronquist (1994), but AA uses Camin-Sokal only as a methodological tool. Therefore, it is not a strategy for optimising areas in the cladogram, and does not involve necessarily any further assumption. The third method is dispersal-vicariance analysis (DIVA version 1.1), which assumes that geographic distributions are the result of both vicariance and dispersal events. DIVA is an event-based method which uses a three-

dimensional cost matrix derived from a simple biogeographic model, to infer ancestral areas (Ronquist, 1996, 1997). As DIVA analysis require a fully resolved topology, one of the equally parsimonious trees was used.

MORPHOLOGY

Duration and habit

All species of *Geranium* sect. *Azorelloida* and sect. *Neoandina* are small perennial herbaceous plants. They usually have a vertical and branched rootstock, sometimes thickened although not turnip-shaped. The apical part of rootstock branches are not subterranean and are often covered by rests of stipules. Each branch ends in a leaf rosette from which one-flowered cymules arise directly. Thus, we have considered these species as stemless.

The leaf rosettes of sect. *Azorelloida* and some species of sect. *Neoandina* have a structure which probably represents the annual growth of this rosette, and we have described them as 'vegetative stems'. They are thin, covered by young stipules, and more or less horizontal (see drawing of *G. rhomboidale*, Fig. 28). This shape could be an adaptation to a habitat between mosses in bogs or in other wet paramo places.

The species belonging to sect. *Paramensia* have a shrubby habit with a horizontal rootstock. Their aerial stem is glabrous, densely clothed with old, imbricate persistent stipules and petioles, ligneous and erect, reaching 20 cm high.

To know the possible structural consequences of adaptation to Andine habitats, the anatomy of rootstock apex (in sections *Azorelloida* and *Neoandina*) and aerial stems (in sect. *Paramensia*) was explored. Both parts present a similar anatomical structure, and could have a common origin. The epidermis contains, in all species, a phellogen which produces layers of cork which easily peels off (Fig. 1d). Additionally, these parts are usually protected by remains of stipules and petioles of old leaves. Both cork and rests of leaves should protect them against wind and cold.

Three main internal structure types were found in transverse sections:

1) Twelve species have secondary xylem developed in deep rays not produced in a uniform manner around the circumference of the axis (Fig. 1b, 1e; Table 2). This type of structure seems adequate to form more wood on the side facing away from the wind (Dickison, 2000). Also the deep development of xylem produces a greater general wood production, while interfascicular secondary parenchymatous rays produce cells to accumulate water or reserves. The xylem rays have many lignified tracheary elements and fibers. This type of structure is common in species living in puna habitats.
2) Twelve taxa have bundles in an outer position among abundant parenchymatous cells (Fig. 1f; Table 2), showing a more herbaceous habit. The development of vascular bundles is quite variable, sometimes showing a greater secondary development of xylem (not forming a ring), which possibly aids to withstand better windy habitats.
3) The species of sect. *Paramensia* and *G. campii* (sect. *Neoandina*) have laterally developed bundles forming a lignified ring, with parenchymatous cells in the pith and cortex (Fig. 1a, 1c; Table 2). Both types 2 and 3 are common in species living in paramo habitats.

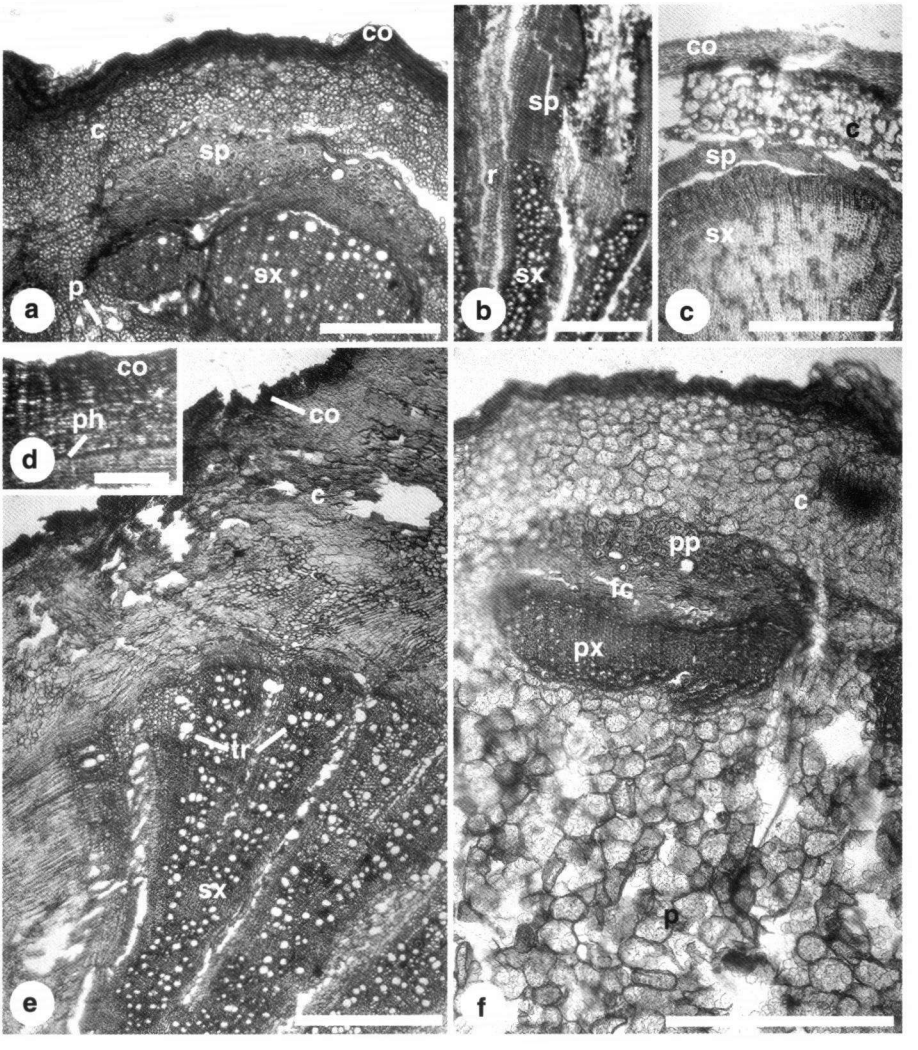


Fig. 1. Optical microscope photographs showing rootstock apex and stem anatomic features. a. *Geranium campii* (*Lewis & Lozano 2741*, MA); b. *G. planum* (*Halloy 3362*, Halloy herbarium); c. *G. jahnii* (*Duno & Riina 781*, MA); d. *G. crassipes* (*Weberbauer 2619*, G); e. *G. sericeum* (*Øllgaard & Balslev 8882*, AAU); f. *G. sibbaldioides* subsp. *beckianum* (*Jørgensen et al. 1237*, QCA). — Scale bars: a & f = 300 μm, b = 800 μm, c & e = 500 μm, d = 50 μm. c = cortex; co = cork; fc = fascicular cambium; p = pith; ph = phellogen; pp = primary phloem; px = primary xylem; r = interfascicular secondary parenchymatous ray; sp = secondary phloem; sx = secondary xylem; tr = tracheids.

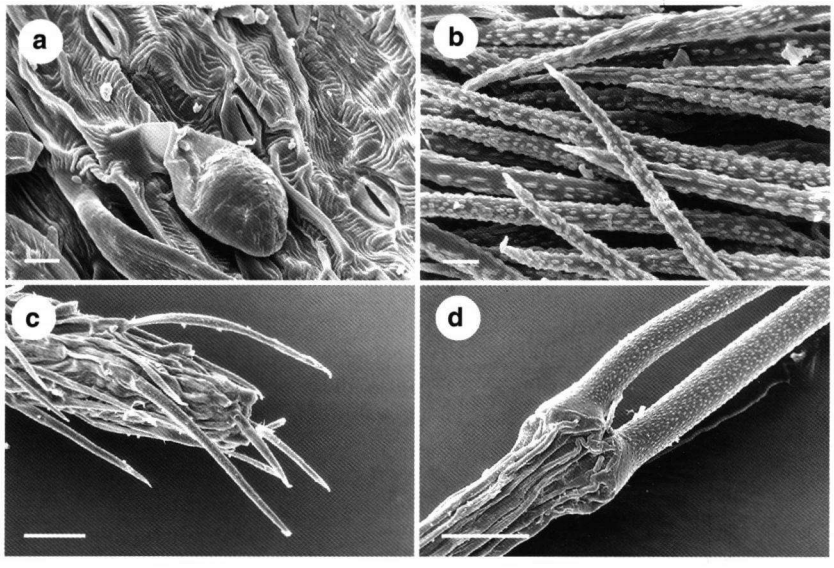


Fig. 2. SEM photographs showing stipule and hair features. a. Short glandular hair on leaf surface of *Geranium macbridei* (*Macbride 3269,* F); b. eglandular hairs on petiole of *G. planum* (*Halloy 3362,* Halloy herbarium); c. stipule apex of *G. tovarii* without bristles (*Hutchinson 4258,* UC); d. stipule apex of *G. rhomboidale* showing two bristles (*Idrobo et al. 3277,* P). — Scale bars: a & b = 10 μm, c & d = 50 μm.

Indumentum

In the species studied here three trichome types have been found, all of them simple and uniseriate (Theobald et al., 1979):

a) Eglandular, unicellular hairs of variable length (0.1–2 mm), usually with an ornamented surface (Fig. 2b). According to Payne (1978) they could be included in the 'subulate' type. They have been found in all species, widespread for all organs of the plant.
b) Long glandular hairs, with 3–5 cells, smooth, 0.4–0.7 mm long, restricted to pedicels and sepals of *G. janhii.*
c) Short glandular hairs (< 40 μm long), smooth, usually constituted by two cells, although they sometimes have a bicellular foot (Fig. 2a). They are present in all species here studied but they are not considered in the descriptions since they are only evident at high magnification.

Leaves

Section *Paramensia* shows some remarkable leaf features. *Geranium exallum* has a lanceolate entire leaf lamina, unique in *Geranium*, while *G. jahnii* has obtriangular, cuneate leaves, tridentate at the apex. Both species have alternate, coriaceous leaves, glabrous (or almost) with an abscission zone between lamina and petiole.

Geranium azorelloides has a leaf lamina similar to the lamina of *G. jahnii*, obtriangular, cuneate, tridentate at apex, coriaceous, and usually glabrous. It lacks, however, an abscission zone between lamina and petiole.

The leaves in most species of sect. *Neoandina* are polygonal in outline, cordate, palmatifid or palmatisect, usually with 5–7 segments. *Geranium multipartitum* has also palmatisect leaves always with 9 segments. A different leaf configuration is found in *G. rhomboidale*, *G. digitatum*, and *G. maniculatum*, which have a lamina that is rounded to cuneate at the base, polygonal to obtriangular in outline, and digitate with lateral segments upwards. These species have leaves with 3 to 5 segments. Finally, the leaves of *G. campii* are tripartite, rounded at the base, and triangular in outline. The middle segments are usually entire and lanceolate to broadly lanceolate in *G. campii*, *G. crassipes*, *G. digitatum*, *G. jaekelae*, *G. maniculatum*, *G. nivale*, *G. pavonianum*, *G. planum*, *G. sibbaldioides* subsp. *sibbaldioides*, and *G. sibbaldioides* subsp. *elongatum*. The remaining taxa of sect. *Neoandina* have 3-lobed, usually obtriangular middle segments, or more divided, generally rhombic middle segments such as *G. costaricense*, *G. humboldtii*, *G. multipartitum*, and *G. tovarii*.

A part of the species in *Geranium* sect. *Neoandina* have leaves that are sericeous on both sides: *G. crassipes*, *G. digitatum*, *G. ecuadoriense*, *G. nivale*, *G. planum*, *G. ruizii*, *G. sericeum*, *G. tovarii*, and *G. weddellii*. *Geranium pavonianum* and *G. campii* show densely hairy leaves, but not sericeous, while *G. humboldtii* has leaves that are sericeous above and glabrous beneath. The remaining species have glabrous to more or less pilose leaves.

The nine species with sericeous leaves on both sides mentioned above, have also sericeous petioles, usually with patent to retrorse hairs. Only *G. planum*, *G. ruizii*, *G. tovarii*, and *G. weddellii* have antrorse hairs. *Geranium exallum* has glabrous petioles, while *G. humboldtii* and *G. stramineum* occasionally show patents hairs. The remaining species show hairy petioles with patent to retrorse hairs.

The stipules are usually lanceolate, papery, and reddish. In *G. jahnii* and *G. rhomboidale* the stipules have a setaceous apex, which is also found in *G. stramineum*. In the last mentioned species, however, the stipules are obtuse, scarious, and stramineous. The stipules vary from glabrous on both sides (as in *G. azorelloides*) to sericeous on both sides (as in *G. planum*), although in most species they are hairy on the abaxial surface and glabrous adaxially. In a group of species including *G. azorelloides*, *G. campii*, *G. costaricense*, *G. ecuadoriense*, *G. foreroi*, *G. maniculatum*, *G. multipartitum*, *G. paludosum*, *G. rhomboidale*, *G. sibbaldioides*, and *G. stramineum*, the stipules end in a sheaf of bristles 0.2–0.8 mm long. Some of these species have such bristles also at the apex of sepals or leaf segments (Fig. 2c, 2d).

Inflorescence and branching

All species considered here share cymules that are 1-flowered, arising directly from basal rosettes (sect. *Azorelloida* and sect. *Neoandina*) or from aerial stems (sect. *Paramensia*). Although in subg. *Geranium* the cymules are usually 2-flowered, there are also unrelated species with 1-flowered cymules (i.e. *G. potentilloides* L'Hér. ex DC., *G. sanguineum* L., or *G. sibiricum* L.). In *Geranium* sect. *Azorelloida*, sect. *Paramensia*, and a few species of sect. *Neoandina* (*G. campii*, *G. costaricense*, *G. sibbaldioides* subsp. *sibbaldioides*, *G. sibbaldioides* subsp. *beckianum*) the cymules consist of a basal peduncle (short in the last two taxa), 2 bracteoles and a pedicel. In the remaining species of sect. *Neoandina*, the peduncles and bracteoles have disappeared, and the pedicels arise directly from rosettes. The indumentum of the pedicels

is usually as in the petiole. The most noticeable differences can be found in *G. tovarii* and *G. jahnii*. The former has glabrous (or almost) pedicels against sericeous petioles. The latter shows pedicels with glandular pluricellular hairs, a feature unique among the species here studied.

Calyx

The most taxonomically significant sepal feature is the mucro, which is lacking in *G. planum* and very short in *G. nivale*, *G. digitatum*, and *G. tovari*. In most species the indumentum varies from hairy to sericeous. Three taxa (*G. humboldtii*, *G. macbridei*, and *G. maniculatum*) are glabrous or almost on the abaxial side but they differ in adaxial indumentum: In *G. humboldtii* it is sericeous, *G. macbridei* has scattered, eglandular hairs, and in *G. maniculatum* it is glabrous. It is also remarkable that *G. jahnii* shows glandular and eglandular hairs on the sepal surface. A part of the species with bristles at the stipule apex also show bristles at the sepal apex (*G. azorelloides*, *G. campii*, *G. costaricense*, *G. maniculatum*, and *G. sibbaldioides*).

Corolla

The corolla is small in most species of the three sections. The petal size is correlated with reproductive success in *Geranium* and in other genera (Bell, 1985; Philip & Hansen, 2000), consequently longer petals are expected in xenogamous taxa; but the opposite trend was also reported (Bertin & Newman, 1993). In our case the petal length is significantly correlated with pollen-grain number per anther ($r = 0.6127$; $p < 0.0008$) (Fig. 3).

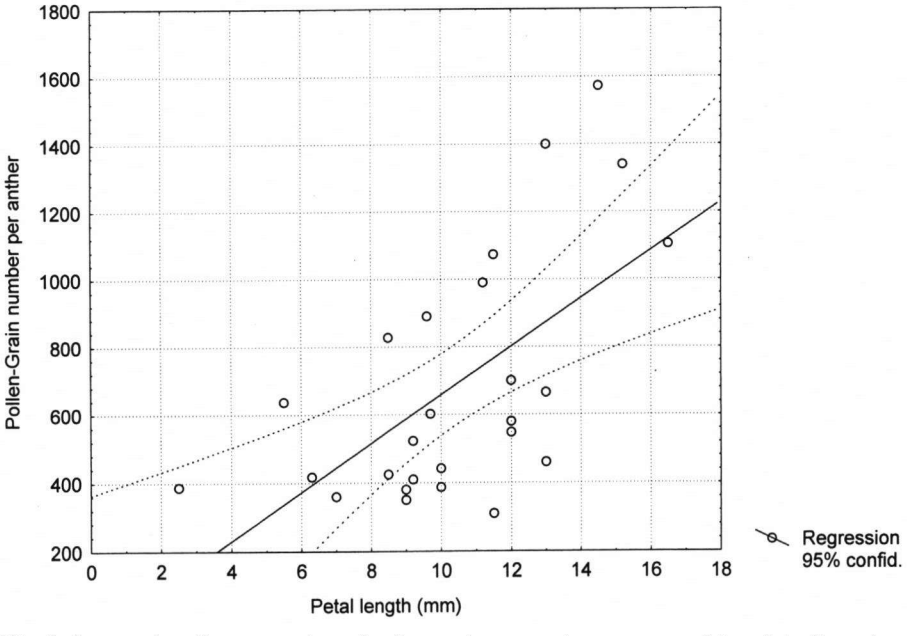


Fig. 3. Scatter plot of mean number of pollen grains per anther versus petal length in *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*. The correlation coefficient for these data is $r = 0.6127$.

The petals in the sections *Neoandina* and *Paramensia* have entire apices, while in *G. azorelloides* the petals are emarginate with a short notch 0.5 mm deep. In most of the species studied here the petals are tapered uniformly toward the base, without a claw, except in *G. jahnii* which possess a claw 2 mm long.

Fourteen species of *Geranium* sect. *Neoandina* and *G. azorelloides* have usually glabrous petals, even on the margin. The petals of *G. costaricense* and *G. exallum* are constantly glabrous except for a few marginal hairs at the base. The remaining species show hairy petals, on one or both sides.

White petals are exclusive or predominant in *G. costaricense*, *G. crassipes*, *G. digitatum*, *G. foreroi*, *G. jaekelae*, *G. nivale*, *G. pavonianum*, *G. planum*, *G. ruizii* (all from sect. *Neoandina*). In *Geranium* sect. *Azorelloida*, sect. *Paramensia* and in *G. humboldtii*, *G. paludosum*, *G. rhomboidale*, *G. sericeum*, *G. sibbaldioides* subsp. *sibbaldioides*, *G. sibbaldioides* subsp. *beckianum*, the petals are purplish, whereas they vary between purplish and white in the remaining taxa of sect. *Neoandina*.

Stamens and pollen

In *Geranium* the ten stamens are disposed in two whorls. The only exception is *G. pusillum* (from sect. *Batrachioidea*) in which the anthers of the external whorl are missing. The filaments are not exerted, lanceolate, sometimes with an abruptly narrowed apex. In sect. *Paramensia* the filaments are glabrous except for a few marginal

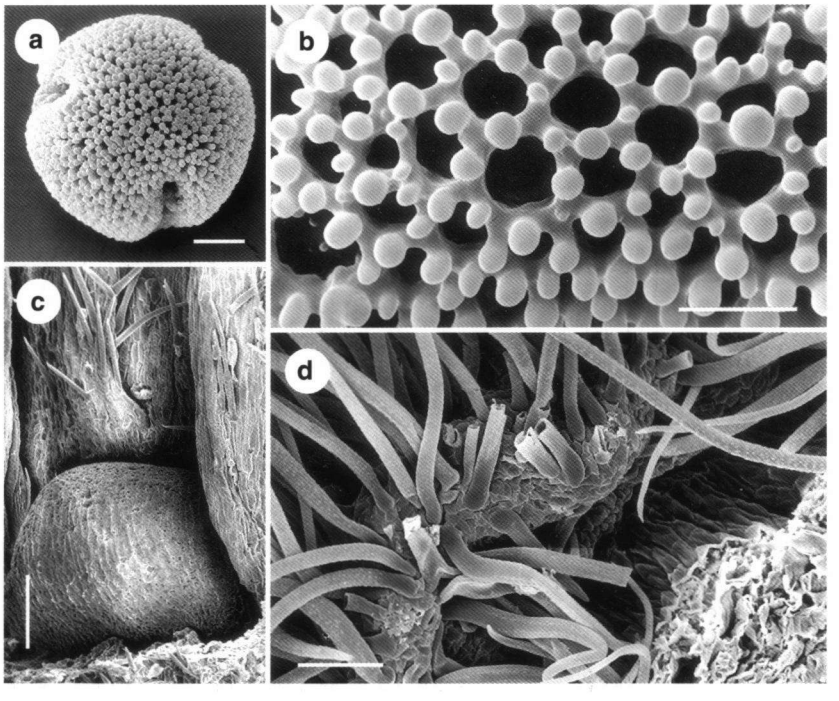


Fig. 4. SEM photographs showing pollen and nectaries features. a. Pollen grain of *Geranium macbridei* (*Macbride 3269*, F); b. Pollen ornamentation of *G. campii* (*Madsen 86766*, AAU); c. glabrous nectary of *G. paludosum* (*Cuatrecasas & Romero 24578*, MA); d. hairy nectary of *G. weddellii* (*Beck 22493*, MA). — Scale bars: a = 10 µm, b = 5 µm, c = 100 µm, d = 50 µm.

hairs, whereas in sect. *Azorelloida* they are usually glabrous. In sect. *Neoandina* the filament indumentum varies from fully glabrous (*G. tovarii*, *G. rhomboidale*) to hairy on the abaxial side and margin.

Pollen of all species studied here, as in almost the entire genus (Weber, 1996), is characterised by reticulate exine ornamentation with distinctly baculate, clavate, or gemmate supratectal elements (Fig. 4a, 4b).

According to Philipp (1985), most perennial species of *Geranium* produce large flowers with a pronounced protandry, avoiding selfing processes.

In other species a decrease in protandry is accompanied by a reduction of flower size, and at the same time increased chances for self-pollination. Cruden (1976, 1977) emphasised that the Log pollen-ovule ratios (Log P/O) are correlated with the breeding system. A substantial decrease in Log P/O suggests a pass from xenogamy to facultative xenogamy to autogamy. According to Cruden (2000) in autogamous species the mode is 2–2.5 Log P/O.

The species studied here show Log P/O ratios between 1.79 and 2.5 (Fig. 5; Table 3). The mode is 1.9–2.0 Log P/O suggesting a tendency to autogamy. This is congruent with adichogamy observed in herbarium specimens of these species. As in *G. sessiliflorum* (Philipp, 1985) autopollination could happen by inward movements of the stamens which come into contact with the stigma lobes. A few species (such as *G. digitatum*, *G. nivale*, and *G. weddellii*) show Log P/O ratios that are moderately higher, suggesting facultative xenogamy and have, in addition, longer petals. On the contrary, there is a moderate negative correlation between the petal size and the mean altitude of the species ($r = -0.275$, $p < 0.006$; measured in all species but *G. planum*). Alpine and arctic species show generally a greater incidence of self-compatibility and espontaneous autogamy (Henslow, 1888; Bertin & Newman, 1993). In tropical mountains the activity levels of pollinators have been shown to decrease significantly with altitude. Consequently the flowers are visited less frequently and are in some instances being compensated by autogamy.

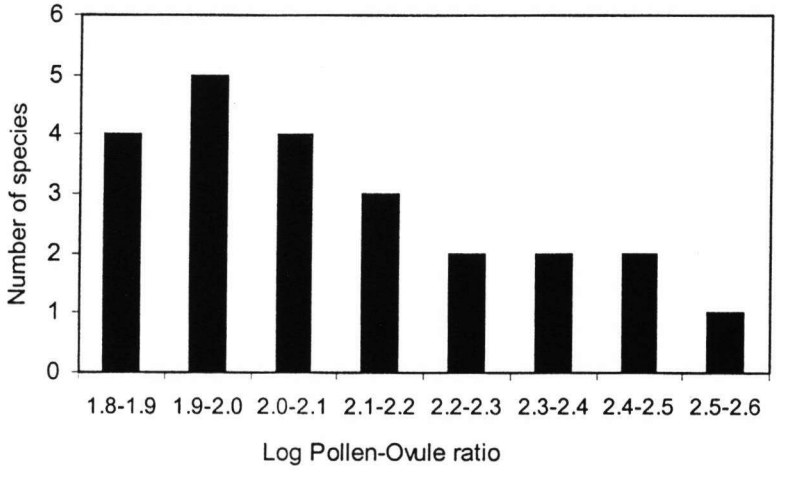


Fig. 5. Distribution of pollen-ovule ratios in *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*.

Table 3. Pollen-ovule ratio in *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia* (n.s.: not studied; sd: standard deviation).

Taxa	Pollen-ovule ratio	sd	Log pollen-ovule ratio
G. azorelloides	92	4.30	1.96
G. campii	85	9.00	1.93
G. costaricense	214.7	19.20	2.33
G. crassipes	104.5	13.20	2.02
G. digitatum	314.5	24.08	2.50
G. ecuadoriense	165.5	13.20	2.22
G. exallum	109.5	10.20	2.04
G. foreroi	221	24.50	2.34
G. humboldtii	120.4	9.20	2.08
G. jaekelae	n.s.		
G. jahnii	133	4.20	2.12
G. macbridei	198	19.50	2.30
G. maniculatum	88.4	14.52	1.95
G. multipartitum	83.5	3.70	1.92
G. nivale	268	16.60	2.43
G. paludosum	140	10.30	2.15
G. pavonianum	76	4.00	1.88
G. planum	n.s.		
G. rhomboidale	82	12.00	1.91
G. ruizii	116	16.00	2.06
G. sericeum	178	10.71	2.25
G. sibbaldioides			
subsp. *sibbaldioides*	70	12.25	1.85
subsp. *beckianum*	77.5	9.00	1.89
subsp. *elongatum*	72	7.20	1.86
G. stramineum	62	6.78	1.79
G. tovarii	127.5	9.98	2.11
G. weddellii	280	25.34	2.45

The ability to produce selfed seeds in high elevation species seems important when they colonise new areas or when suffering population bottlenecks. Other possible tendencies of high mountain species are: high levels of sympatry, attraction of generalist pollinators, meager rewards in flowers, and long anthesis periods (Berry & Calvo, 1989). Some of these tendencies were found by us in Andine *Geranium*, such as a long anthesis period, remarkable in both paramo and puna plants (see phenology under each taxon), and the presence of several sympatric species in an area (see Biogeography). However, many of these factors remain to be investigated.

Nectaries

The five hemispherical nectaries are arranged alternately to the external whorl of staminal filaments. In the sections *Azorelloida* and *Paramensia* they are glabrous, as in most of sect. *Neoandina* species. Only three species exhibit a tuff of hairs at the top of each nectary (*G. macbridei*, *G. digitatum*, and *G. weddellii*), and some exceptional specimens of *G. ruizii* (Fig. 4c, 4d).

Fruit

Geranium sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia* are assigned to subgenus *Geranium*, which exhibits the 'seed ejection-type' of fruit discharge (Yeo, 1984). The mericarps are smooth, with a basal callus, brownish in all cases (Fig. 6a, 6b). A sericeous indumentum is found in *G. nivale* and *G. sericeum* mericarps. The remaining species have hairy mericarps, or, as in *G. maniculatum* and *G. rhomboidale*, sometimes glabrous. A rostrum that tapers gradually to the remains of the stigmas is the most frequent condition in the species here considered. The alternative condition, a columnar rostrum abruptly narrowed at the apex, is only found in five species of sect. *Neoandina* (*G. costaricense*, *G. digitatum*, *G. macbridei*, *G. nivale*, *G. weddellii*). The rostrum is usually hairy except in eight species of sect. *Neoandina*, in which it is sericeous (*G. crassipes*, *G. digitatum*, *G. ecuadoriense*, *G. nivale*, *G. planum*, *G. ruizii*, *G. sericeum*, and *G. weddellii*).

According to Frantzen & Bouman (1989) the mode of dispersal in the Colombian Andes tends to shift with altitude from zoochory and autochory to anemochory, thus only a small number of autochorous taxa grow in the superparamo. However, the *Geranium* species here studied, all of them autochorous, grow in paramo, puna, and superparamo. The paramo species (see under Habitat and Distribution) have longer awns than those of higher habitats (puna or superparamo), and the dispersal distance would be greater there. The correlation between awn length and altitude is low but significantly negative ($r = -0.278$; $p < 0.006$). However, the seed size ($r = 0.029$, $p > 0.009$) and the mericarp body size ($r = 0.032$, $p > 0.02$) are not significantly correlated with altitude. Thus, a decrease of awn length with altitude seems not the result of a general reduction of plant organs.

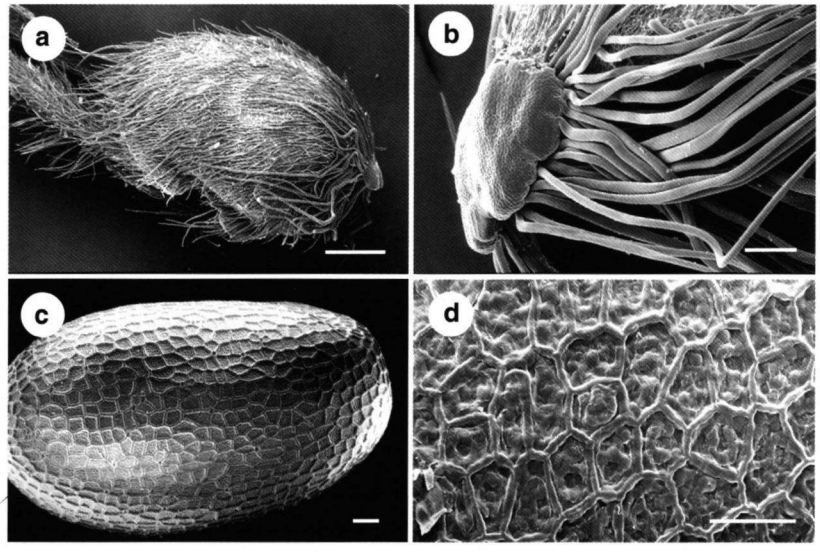


Fig. 6. SEM photographs showing fruit and seed features. a. Mericarp of *Geranium ecuadoriense* (*Penland & Summers 695*, P); b. basal mericarp callus of *G. weddellii* (*Beck 21990*, LPB); c. seed of *G. multipartitum* (*Iltis & Iltis 519*, MO); d. seed-coat ornamentation of *G. azorelloides* (*Torres 933*, COL). — Scale bars: a = 500 μm, b & c = 100 μm, d = 50 μm.

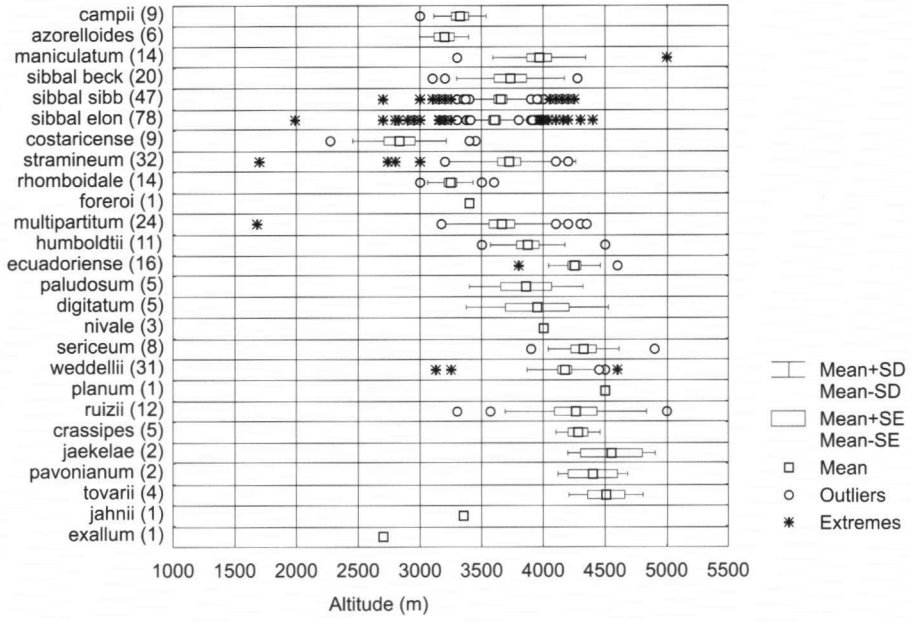


Fig. 7. Box plot showing altitude variation in species of *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*. The number of samples is indicated between brackets after the species epithet.

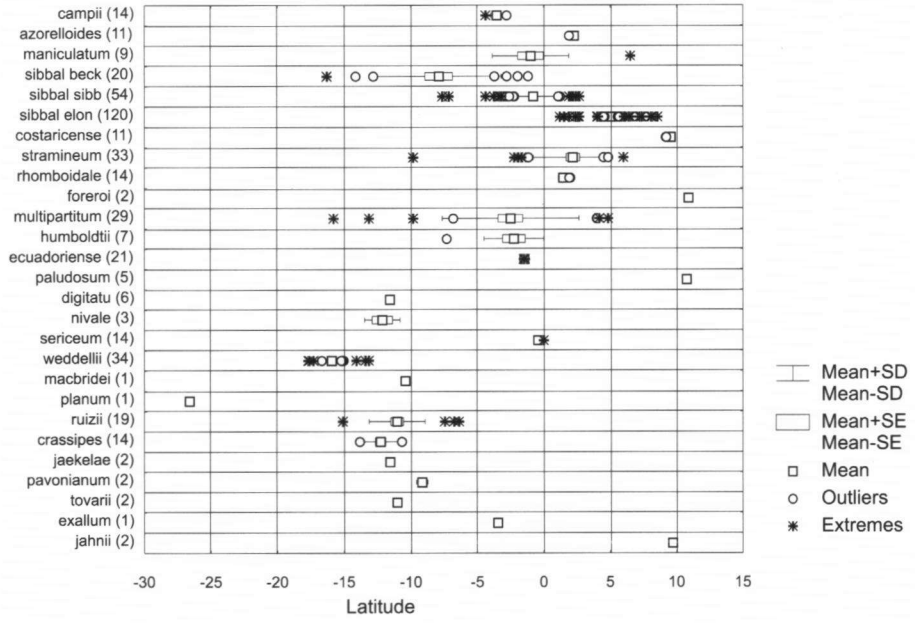


Fig. 8. Box plot showing latitude variation in species *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*. The number of samples is indicated between brackets after the species epithet.

The awn length is generally considered as correlated with dispersal distance, because the effectivity of ejection depends on the length and the strength of fibers located in the awn (Yeo, 1984). They are responsible of the explosive peeling away of the awn from the fruit columella. The higher slopes, the great ground irregularity, and common windy episodes occurring in higher altitude habitats probably aid during dispersal, and may partially substitute the awn development, saving resources and reaching similar distances with a shorter fruit.

Seeds

The seeds are more or less ellipsoid in the three sections. The seed-coat appears finely reticulate at a magnification of 30×, but SEM shows a reticulate surface due to the prominence of outer and middle layers of the outer integument (Fig. 6c, 6d). The outer layer has cells with thickened walls and collapsed lumina, forming a polygonal structure. The seed-coat is usually brownish and bears scattered stomata. The cotyledons have entire margins in all species examined.

HABITAT AND DISTRIBUTION

The genus *Geranium* is distributed throughout most of the world, although in tropical areas it only occurs in mountains. Section *Azorelloida* is restricted to a small area in S Colombia, whereas sect. *Paramensia* is distributed in two disjunct areas in W Venezuela and S Ecuador. *Geranium azorelloides*, the only species of sect. *Azorelloida*, grows in wet habitats of paramos. The precise habitat of species of sect. *Paramensia* is unknown; however, localities and altitudes of *G. jahnii* and *G. exallum* correspond to those of paramo and suggest a wet habitat. Section *Neoandina* occurs in two main areas: 1) the paramos of Costa Rica (mainly Chirripó and Talamanca), Venezuela (Cordillera de Mérida), Colombia (Sierra Nevada de Santa Marta, Cordillera Oriental, Cordillera Central, Cordillera Occidental), Ecuador (Cordillera Real, Cordillera de Cajas), and Peru (mainly Jalca Mts); 2) the punas of Peru (Central Andine Cordillera, Altiplano), Bolivia (Altiplano, Cordillera Real, Cordillera Central), and the North of Argentina (Tucuman Mts). The highest diversity area is the Central Andine Cordillera of Peru with 10 species. A second diversity centre is the Cordillera Real of Ecuador with 8 species.

In Fig. 7 the distribution of the altitudinal range for the species studied here is shown. The habitat preferences of each species appear to be associated with its distribution area: paramo species prefer wet habitats at lower altitudes, while puna species grow in dry and higher habitats. In Fig. 8 the distribution of the latitudinal range for the species studied here is shown.

In sect. *Neoandina* the paramo species are: *G. campii*, *G. costaricense*, *G. foreroi*, *G. ecuadoriense*, *G. humboldtii*, *G. maniculatum*, *G. paludosum*, *G. rhomboidale*, *G. sericeum*, and *G. stramineum*. They occur generally above the forest limit in wet habitats such as bogs or lake shores; although *G. sericeum* and *G. ecuadoriense* grow in dry places and *G. paludosum*, *G. campii* (and also *G. sibbaldioides* subsp. *sibbaldioides*) may occur also in open forest. The species of the puna are: *G. crassipes*, *G. digitatum*, *G. jaekelae*, *G. macbridei*, *G. nivale*, *G. pavonianum*, *G. planum*, *G. ruizii*, and *G. tovarii*. These taxa grow in dry places such as rocky or grassy areas. However,

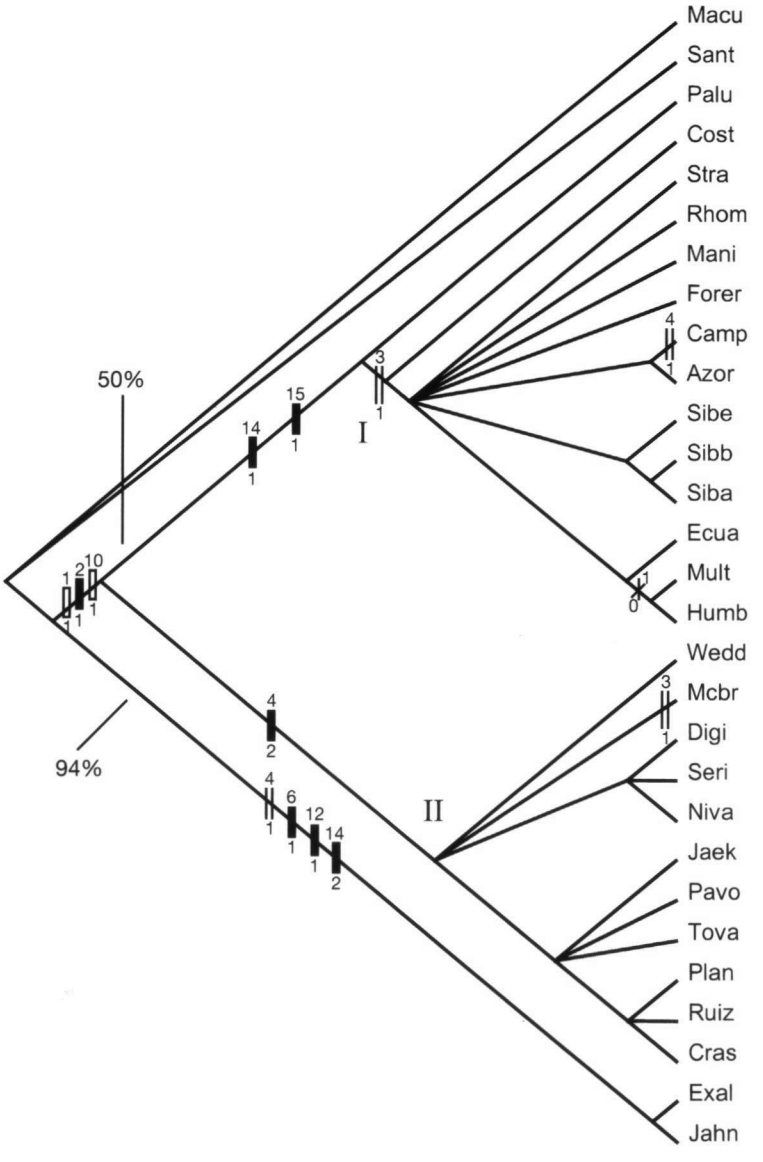


Fig. 9. The strict consensus tree of *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*. Acronyms: *G. azorelloides* (Azor), *G. campii* (Camp), *G. costaricense* (Cost), *G. crassipes* (Cras), *G. digitatum* (Digi), *G. ecuadoriense* (Ecua), *G. exallum* (Exal), *G. foreroi* (Forer), *G. humboldtii* (Humb), *G. jaekelae* (Jaek), *G. jahnii* (Jahn), *G. maniculatum* (Mani), *G. macbridei* (Mcbr), *G. multipartitum* (Mult), *G. nivale* (Niva), *G. paludosum* (Palu), *G. pavonianum* (Pavo), *G. planum* (Plan), *G. rhomboidale* (Rhom), *G. ruizii* (Ruiz), *G. sericeum* (Seri), *G. sibbaldioides* subsp. *sibbaldioides* (Siba), *G. sibbaldioides* subsp. *beckianum* (Sibb), *G. sibbaldioides* subsp. *elongatum* (Sibe), *G. stramineum* (Stra), *G. tovarii* (Tova), and *G. weddellii* (Wedd). Solid bars are synapomorphies, open bars are synapomorphies with reversals, double bars are parallelisms, and crosses are reversals. The numerals 'I' and 'II' denote branches defining clades addressed in the discussion. Bootstrap support greater than 50% is shown near the branches.

the only known specimen of *G. macbridei* was collected on wet grassy slopes and *G. nivale* grows in moist soils.

PHYLOGENETIC RELATIONSHIPS

A cladistic analysis of the species included in the sections *Azorelloida*, *Neoandina*, and *Paramensia* was carried out to explore their phylogenetic relationships. Two representatives of subg. *Geranium*: *Geranium maculatum* L. from N America (provisionally included in sect. *Geranium* (Aedo et al., 1998b)) and *G. santanderiense* R. Knuth from S America (sect. *Gracilia*) were chosen as outgroup, since they are related to the sections and have comparable features. The cladistic analysis gave 1742 minimal length cladograms of 92 steps, a consistency index (CI) of 0.5543, a homoplasy index (HI) of 0.663, a retention index (RI) of 0.7372, and a rescaled consistency index (RC) of 0.4087. The strict consensus tree is shown in Fig. 9, and one of the 1742 equally parsimonious trees is shown in Fig. 10. As it can be seen, the consensus tree is not fully resolved, and the CI shows considerable homoplasy. Moreover, most clades are not firmly supported by bootstrap values. Nevertheless, we consider that these results may aid to understand the relationships within the ingroup.

The group formed by caulescent plants included in sect. *Paramensia* is well supported (94% bootstrap) as sister group of the ensemble of the sections *Azorelloida* and *Neoandina*. The two species included in that section share three synapomorphies: shrub habit (character 6), abscission zone in the petiole (character 12), rests of old stipules which protect the aerial stems (character 14), and one parallelism: bundles forming a xylematic ring which includes a large pith (character 4). Surprisingly, character 12 relates sect. *Paramensia* with *Geranium* sect. *Neurophyllodes* of Hawaii, as was already suggested by Standley (1915). These relationships seem an exciting item to be investigated, preferably by molecular techniques.

In *Geranium* sect. *Paramensia* and sect. *Neurophyllodes* the petiole usually breaks in old leaves, and some rests remain, covering and protecting the stem. On the contrary, in sect. *Azorelloida* and sect. *Neoandina* this abscission zone is absent. In these sections, however, the plants are also protected by old stipules, suggesting close relationships.

The ensemble of *Geranium* sect. *Azorelloida* and sect. *Neoandina* is supported by very low bootstrap values (50%), and share acaule habit (character 2), lamina texture not coriaceous (character 10), and (with reversions) a vertical rootstock position (character 1). The two main clades in this group are I and II. Clade I is supported by two synapomorphies: old stipules present on rootstock branches (character 14) and stipules with bristles at the apex (character 15), while Clade II is supported by only one synapomorphy: xylem developed in deep rays (character 4). All species of Clade I but *G. paludosum* are also sustained by character 3: the presence of vegetative stems; however, this feature is also found in G. *macbridei*, a species belonging to Clade II.

The two clades seem related with two different geographical areas: Clade I mainly includes species distributed from Costa Rica to N Peru, while Clade II includes species from C Peru to Argentina. Furthermore, the species of Clade I grow in paramos, whereas the species of Clade II grow in punas. There are, however, some exceptions: *Geranium sibbaldioides* subsp. *beckianum* and *G. multipartitum* (both from Clade I) are widely distributed reaching Bolivian punas, and *G. sericeum* (belonging to Clade II) is found in paramos of volcano Antisana (C Ecuador).

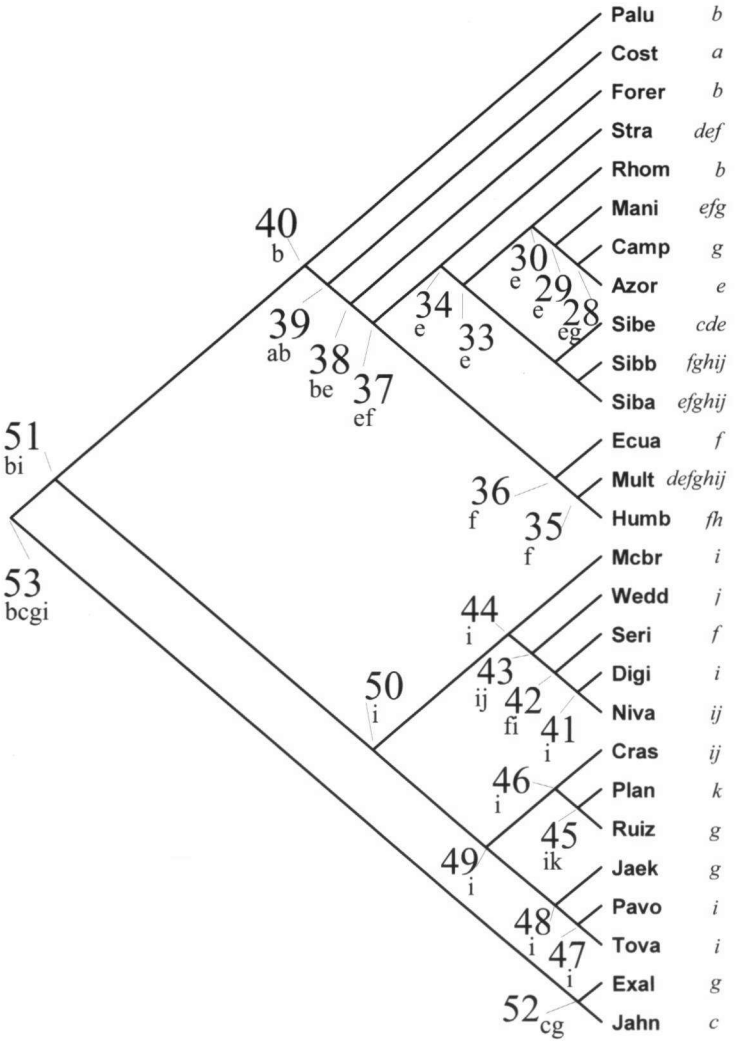


Fig. 10. Optimisation of ancestral state area assignments using dispersal-vicariance analysis (DIVA) on one of 1742 minimal length 92-step trees resulting from cladistic analysis of *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*. Numerals indicate nodes. The ancestral areas are indicated by letters on each node. The species are indicated by acronyms, and letters behind acronyms indicate the areas of endemism where the species are present. Acronyms of the taxa are indicated in Fig. 9. Areas of endemism are indicated in Map 1.

The polychotomies in both clades show the scarcity of useful characters to resolve this group adequately. Many other characters used in the analysis show a high homoplasy index, which suggests adaptive convergence possibly induced by sharing common habitats: mid-mountain mires, grassy slopes, or high-mountain gravel. An additional problem is the possible paraphyly of sect. *Azorelloida*. However, the weakness of the cladistic analysis does not permit any taxonomic rearrangement.

BIOGEOGRAPHY

The biogeographic analysis using Fitch parsimony resulted in a single most parsimonious tree of 35 steps, while DIVA resulted in a single optimal reconstruction requiring 30 dispersal events (Fig. 10, for DIVA results see letters in nodes). The biogeographic analyses were elaborated from a poorly supported cladogram. Thus the results should be carefully interpreted. Moreover, none of the methods used

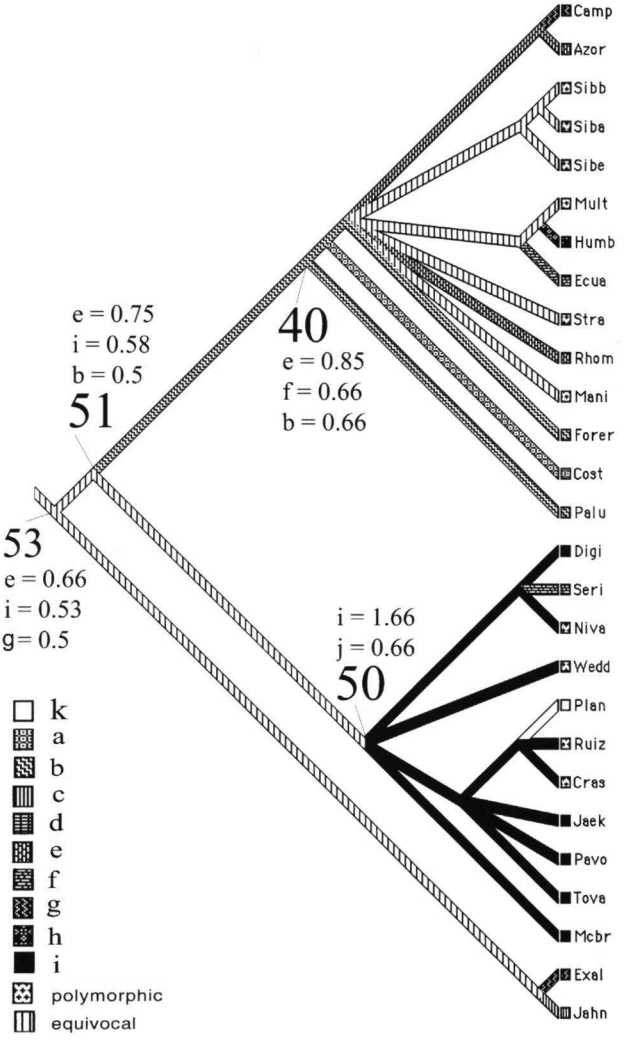


Fig. 11. Optimisation of ancestral state area assignments using Fitch parsimony analysis on the strict consensus tree resulting from cladistic analysis of *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia*. Numerals indicate nodes. Values below nodes are G/L quotients for each area resulting from Bremer analysis. The ancestral area obtained in Fitch optimisation is indicated by shading within the branches. Acronyms of the taxa are indicated in Fig. 9. Areas of endemism are indicated in Map 1.

Table 4. Estimation of ancestral area for *Geranium* sect. *Azorelloida*, sect. *Neoandina*, and sect. *Paramensia* based on Fig. 11. G = number of necessary gains under forward Camin-Sokal parsimony (Bremer analysis). L = number of necessary losses under reverse Camin-Sokal parsimony. RQ = quotients rescaled to a maximum value of 1 by dividing with the largest G/L value.

Area	node 53				node 51				node 50				node 40			
	G	L	G/L	RQ	G	L	G/L	RQ	G	L	G/L	RQ	G	L	G/L	RQ
a) Páramos de Chirripó and Talamanca (Costa Rica and Panama)	1	7	0.14	0.21	1	6	0.16	0.21	0	1	0	0	1	5	0.2	0.23
b) Sierra Nevada de Santa Marta (Colombia)	2	5	0.4	0.6	2	4	0.5	0.66	0	1	0	0	2	3	0.66	0.77
c) Cordillera de Mérida (Venezuela)	2	9	0.22	0.33	1	8	0.12	0.16	0	1	0	0	1	7	0.14	0.16
d) Cordillera Oriental (Colombia)	3	10	0.3	0.45	3	9	0.33	0.44	0	1	0	0	3	8	0.37	0.43
e) Cordillera Occidental and Cordillera Central (Colombia)	6	9	0.66	1	6	8	0.75	1	0	1	0	0	6	7	0.85	1
f) Cordillera Real (Ecuador)	5	11	0.45	0.68	5	10	0.5	0.66	1	4	0.25	0.15	4	6	0.66	0.77
g) Cordillera de Cajas (Ecuador)	5	10	0.5	0.75	4	9	0.44	0.58	0	0	0	0	4	8	0.5	0.58
h) Jalca Mts (Peru)	3	12	0.25	0.37	3	11	0.27	0.36	1	4	0.25	0.15	2	7	0.28	0.32
i) Central Andine Cordillera (Peru)	7	13	0.53	0.80	7	12	0.58	0.77	5	3	1.66	1	2	9	0.22	0.25
j) Altiplano, Cordillera Real and Cordillera Central (Peru and Bolivia)	6	16	0.37	0.56	6	15	0.4	0.53	4	6	0.66	0.39	2	9	0.22	0.25
k) Tucuman Mts (Argentina)	1	6	0.16	0.24	1	5	0.2	0.26	1	4	0.25	0.15	0	1	0	0

provided any concluding evidence about the ancestral area of the whole group. However, information about Clade I and II ancestral areas seem of interest. According to the DIVA results, the inferred ancestral distribution for the basal node of the tree (53) is disjunct (Sierra Nevada de Santa Marta (b) + Cordillera de Mérida (c) + Cordillera de Cajas (g) + Central Andine Cordillera of Peru (i)), suggesting extinctions in the intermediate areas. Thus, the ancestral area could cover nearly all northern Andes. The Ancestral Area Analysis (AA) indicates that the Cordillera Occidental and Cordillera Central of Colombia (e) could be part of the ancestral geographic range of our group, considering its relatively high G/L value of 0.66 (Fig. 11; Table 4). Subsequent values are those of the Central Andine Cordillera of Peru (i) with 0.538 and the Cordillera de Cajas (g) with 0.5. Thus, the only coincidence between AA and DIVA results was that they selected as ancestral areas different parts from N Andes.

In a similar way, the ancestors of *Geranium* sect. *Paramensia* (node 52) and sections *Azorelloida* and *Neoandina* (node 51) are not satisfactorily solved, neither by DIVA nor by Fitch optimisations.

The ancestor of the paramo group (node 40) was assigned to the Sierra Nevada de Santa Marta (b), while the ancestor of the puna group (node 50) was assigned to the Central Andine Cordillera of Peru (i), both by DIVA and Fitch analyses. The AA, in contrast, assigned the ancestor of the paramo group (node 40) to the Cordilleras Occidental and Central of Colombia (e). The following step (node 39) is assigned by DIVA to the Sierra Nevada de Santa Marta plus Costa Rica, which suggests a dispersal event followed by vicariance of *G. costaricense*. This might have occurred after the formation and uplift of the Panama isthmus (c. 3.5–2.4 Ma), which was later fragmented and its parts isolated during the Quaternary, due to cyclic sea level changes (Graham, 1997).

As DIVA 1.1 can only handle fully bifurcate trees, all individual trees should be tested, while Fitch analysis was carried out using the consensus tree. The main polytomy involves nodes 33–34 and 37–38, and they were assigned by DIVA to several combinations of areas 'b', 'e', and 'f'. These results do not provide a single hypothesis about dispersion and vicariance events order, during the diversification of the paramo group core.

One of these alternatives is shown in Fig. 10 (nodes 37 and 38): a first dispersion to the Cordillera Occidental and the Cordillera Central of Colombia (e), followed by vicariance between *G. foreroi* growing in the Sierra Nevada de Santa Marta (b) and the ancestor of the remaining paramo species in the Cordillera Occidental and the Cordillera Central of Colombia (e) plus the Cordillera Real of Ecuador (f). The second event could take place if the ancestor of *G. ecuadoriense*, *G. multipartitum*, and *G. humboldtii*, was isolated in the Cordillera Real of Ecuador (f), separate of the ancestor of *G. stramineum*, *G. rhomboidale*, *G. maniculatum*, *G. campii*, *G. azorelloides*, and *G. sibbaldioides*, in the Cordillera Occidental and the Cordillera Central of Colombia (e) (nodes 34 and 36).

The nodes 35 and 36 are assigned both by Fitch and DIVA to the Cordillera Real of Ecuador (f), suggesting a sympatric speciation for *G. ecuadoriense*, *G. multipartitum*, and *G. humboldtii*; there exist, however, some differences: *G. ecuadoriense* grows in drier and higher habitats than the other two species. Finally, node 32 shows three subspecies of *G. sibbaldioides* growing in extensive and fairly different areas.

The most intermediate steps of the puna group (nodes 41, 43–44, 46–50) were assigned to the Central Andine Cordillera of Peru (i), both by DIVA and Fitch analyses. In node 42 the results of both analyses indicate a dispersal event from the Central Andine Cordillera of Peru (i) to the Cordillera Real of Ecuador (f) followed by vicariance. The results of node 45 also suggest a vicariance event of *G. planum* in the Tucuman Mts (Argentina).

The origin of the paramo flora has been largely discussed by biogeographers, concluding that many of the taxa are related to lowland Neotropical ones. The paramo is generally considered having originated in the Pliocene (Wijninja, 1996); but the existence of an early-Pliocene, mid-altitude, transitional 'protoparamo' was proposed to explain the origin of many paramo species (Van der Hammen, 1989). Hills up to approximately 1000 m may have existed already during the lower Tertiary (Van der Hammen, 1989). Then, progressively colder, drier and more windy habitats appeared, and plants would have been forced to progressively adapt to these new conditions such as severe night freezing episodes (Cleef, 1981).

This hypothesis is consistent with the proposal of a very high level 'in situ' speciation in paramos (Simpson, 1975; Simpson & Todzia, 1990; Taylor, 1995; Sklenář & Jørgensen, 1999). It is well known that the Colombian area remained moist and tropical during long periods of the Andes uplift. The autochthonous speciation was probably lower in puna (Simpson & Todzia, 1990), whose species are the result of more recent, random colonisation from several parts, such as C and N America, Holartic or S America-Antartic regions (Cleef, 1981; Simpson & Todzia, 1990). Only a small portion of this puna colonisation was derived from the paramo (Simpson & Todzia, 1990), which seems to have been the case in our group.

In this scenario, a paramo origin is conceivable for old ancestors of sect. *Paramensia*, probably followed by a long-distance dispersion to Hawaii. The first paramo *Geranium* pollen was reported from early Pleistocene sediments, i.e. the Tilata formation, Sabana de Bogotá (Hooghiemstra, 1984; Van der Hammen & Cleef, 1986). Subsequent phases of Andes uplift induced the appearance of new taxa, better adapted to progressively colder, higher paramos, and among these taxa the ancestors of *Geranium* sect. *Azorelloida* and sect. *Neoandina* may have been included.

The basal separation of taxa chiefly adapted to night freezing (paramo species) from other also adapted to windy, cold and soil unstable habitats (puna species) can be deduced from Fig. 10 and 11. Characters as sericeous leaves and deep well-developed xylem occur mainly in puna species, while old stipules on rootstock branches are only noticeable in most paramo species. However, some cases of adaptation of the latter taxa to subsnowy habitat are also apparent and might be related to vicariance (*G. ecuadoriense*) or dispersal events (*G. humboldtii*, *G. multipartitum*). The expansion and contraction of the paramo surface during Pleistocene cycles may have fragmented ancestral populations and promoted allopatric speciation (Simpson & Todzia, 1990). Later on, some of them can have been able to colonise higher and cooler habitats in more southern latitudes, thus becoming better adapted to puna conditions.

TAXONOMY

KEY AND DESCRIPTIONS

1a. Leaves with an abscission zone between lamina and petiole; small shrubs .. 2
b. Leaves without an abscission zone between lamina and petiole; stemless herbs 3
2a. Lamina lanceolate, entire, with marginal cilia; pedicels without glandular hairs ..... **24. G. exallum**
b. Lamina obtriangular, tridentate at the apex, glabrous; pedicels with glandular hairs ..... **25. G. jahnii**
3a. Lamina white-sericeous at least above 4
b. Lamina glabrous to densely hairy, never sericeous 13
4a. Lamina sericeous above, glabrous beneath ..... **8. G. humboldtii**
b. Lamina sericeous on both sides 5
5a. Lamina digitate, with 3–5 segments; lateral segments upward **5. G. digitatum**
b. Lamina palmatifid to palmatisect; lateral segments patent or downward 6
6a. Lamina palmatisect 7
b. Lamina palmatifid 10
7a. Petiole sericeous, with antrorse hairs 8
b. Petiole sericeous, with patent or retrorse hairs 9
8a. Petals 4–7 mm; nectaries glabrous; fruit rostrum without a narrowed apex ... . **22. G. tovarii**
b. Petals 11–15 mm; nectaries hairy; fruit rostrum with a narrowed apex 1–1.5 mm long ..... **23. G. weddellii**
9a. Lamina 0.45–0.82 cm long; petioles with retrorse, ± appressed hairs 0.2–0.3 mm long; sepals 4.5–7.2 mm long with a mucro 0.5–0.9 mm long .... **6. G. ecuadoriense**
b. Lamina 0.9–1.7 cm long; petioles with patent to retrorse (not appressed) hairs 0.8–1.6 mm long; sepals 7–9 mm long with a mucro c. 0.3 mm long .... **19. G. sericeum**
10a. Middle and usually lateral leaf segments 3-lobed ..... **18. G. ruizii**
b. Middle and lateral leaf segments entire 11
11a. Lamina 0.2–0.5(–0.6) cm long, with 5 segments; sepals without mucro .... **16. G. planum**
b. Not as above 12
12a. Petals 7–10.5 mm long; fruit rostrum without a narrowed apex; lamina 0.42–0.7 cm long ..... **4. G. crassipes**
b. Petals 13–18 mm long; fruit rostrum with a narrowed apex; lamina 0.9–1.2 cm long ..... **13. G. nivale**
13a. Lamina tridentate at the apex, with entire or rarely dentate teeth; petals emarginate ..... **1. G. azorelloides**
b. Not as above 14
14a. Lamina tripartite ..... **2. G. campii**
b. Lamina digitate, palmatifid or palmatisect 15
15a. Lamina digitate, with 3–5 segments; lateral segments upward 16
b. Lamina palmatifid or palmatisect; lateral segments patent or downward ... 17

16a. Lamina glabrous or with antrorse cilia on the margin; middle leaf segment entire ..... **11. G. maniculatum**
b. Lamina with patent cilia on the margin; middle leaf segment 3-lobed ..... **17. G. rhomboidale**
17a. Lamina palmatisect 18
b. Lamina palmatifid 19
18a. Petiole with retrorse, appressed hairs; nectaries hairy; fruit rostrum with a narrowed apex 1 mm long ..... **10. G. macbridei**
b. Petiole with patent hairs (sometimes glabrous); nectaries glabrous; fruit rostrum without a narrowed apex ..... **12. G. multipartitum**
19a. Stipules scarious, stramineous, obtuse, with a setaceous apex 3–6 mm long ..... **21. G. stramineum**
b. Stipules papery, reddish, lanceolate, without a setaceous apex 20
20a. Petiole with antrorse hairs ..... **9. G. jaekelae**
b. Petiole with patent to retrorse hairs 21
21a. Lamina hairy on one or both sides 22
b. Lamina glabrous except on the margins 23
22a. Stipules not ending in bristles; fruit 11–12 mm long .... **15. G. pavonianum**
b. Stipules ending in 1–3 bristles 0.2–0.3 mm long; fruit 8.5–10.5 mm long ... **20c. G. sibbaldioides** subsp. **elongatum**
23a. Middle segment of the lamina entire, sometimes with a lateral tooth ..... **20a. G. sibbaldioides** subsp. **sibbaldioides**
b. Middle segment of the lamina 3–9-lobed at the apex 24
24a. Petiole with patent, eglandular hairs 0.2–0.7 mm long; petals 15–18 mm long ..... **7. G. foreroi**
b. Petiole with retrorse, appressed, eglandular hairs 0.1–0.4 mm long; petals 9–15.5 mm long 25
25a. Lamina (1.7–)1.9–2.8 cm wide, deeply divided (middle segment 3–9-lobed at the apex; ratio main-sinus length of the middle segment/middle-segment length = 0.35–0.53); rostrum 9–9.5 mm long, with a narrowed apex 0.5–1 mm long ..... **3. G. costaricense**
b. Lamina 0.8–1.85 cm wide, shallowly divided (middle segment 3-lobed at the apex; ratio main-sinus length of the middle segment/middle-segment length = 0.1–0.35); rostrum 5–9 mm long, without a narrowed apex 26
26a. Sepals with a mucro 0.3–0.7 mm long; petals 10.5–15.5 mm long, hairy on both sides, mainly on the base of adaxial side ..... **14. G. paludosum**
b. Sepals with a mucro 0.7–1.2 mm long; petals 9–11.5 mm long, usually glabrous ..... **20b. G. sibbaldioides** subsp. **beckianum**

GERANIUM section AZORELLOIDA

Geranium sect. *Azorelloida* Aedo, Muñoz Garm. & Pando (1998b) 243. — Type: *Geranium azorelloides* Sandwith.
Geranium sect. *Petraea* R. Knuth (1936) 220, nom. illeg., non Bubani 1901. — Type: *Geranium guanacosense* R. Knuth.

Perennial herbs with rootstock vertical, not tuberculate, not turnip-shaped, without fusiform-swollen roots; aerial stem absent; with vegetative stems. *Leaf* lamina ob-

triangular in outline, cuneate, without abscission zone, tridentate, usually glabrous, ± coriaceous, nerves not projected; segments 3, lanceolate, 1(–3)-lobed at the apex; cauline leaves absent; stipules lanceolate, free, papery, reddish, glabrous. *Inflorescence* in 1-flowered cymules, solitary; peduncles and pedicels with eglandular hairs; bracteoles lanceolate, glabrous; pedicel and peduncle together often not overtopping the subtending leaf. *Sepals* smooth, not accrescent, 3-nerved, mucronate, with scarious margins, glabrous except on the margin. *Petals* erect-patent, ± obovate, emarginate, without claw, glabrous, purplish. *Stamens* 10, both whorls bearing anthers; filaments not exserted, lanceolate, yellowish, glabrous, or with few eglandular hairs on the margin. Nectaries hemispherical, glabrous. *Fruit* of the seed-ejection type; mericarps smooth, without longitudinal rib, without basal beak, with a basal callus, without a basal prong, with eglandular hairs, brownish; rostrum without a narrowed apex; stigmatic remains with 5 glabrous lobes. *Seeds* ellipsoid, finely reticulate, brownish; hilum 1/4 as long as the perimeter. Cotyledons entire.

Note — This section comprises one species, *G. azorelloides*, known from S Colombia. This species is stemless as sect. *Neoandina*. It also has bristles at the apex of the stipules and sepals, and vegetative stems as some species of sect. *Neoandina*. Its obtriangular leaves, however, that are tridentate at apex, strongly resemble those of *G. jahnii* from sect. *Paramensia*, from which it differs in the absence of an abscission zone in the petiole. The petals in *G. azorelloides* are emarginate with a short notch, while in both sections *Neoandina* and *Paramensia* the petals have entire apices.

1. Geranium azorelloides Sandwith — Fig. 12, Map 2

Geranium azorelloides Sandwith (1929) 121. — Type: *Lehmann 2139* (lectotype, here designated, K; iso BH, BM, US-938458), Colombia, Cauca, Páramo de Guanacas, Nov. 1882.
Geranium guanacosense R. Knuth (1936) 219. — Type: *Lehmann 2139* (holo US-938458; iso BH, BM, K), Colombia, Cauca, Páramo de Guanacas, Nov. 1882.

Herbs 5–7 cm tall. *Rootstock* 2–3 mm diam., ± vertical; with short vegetative stems. *Leaf* lamina 0.9–1.6 by 0.3–0.5 cm, obtriangular in outline, cuneate, tridentate, divided for 0.25–0.3 of its length, usually glabrous, sometimes with erect-patent, eglandular cilia 0.2–0.5 mm long on the margin, each segment ending in 1 or 2 bristles 0.5–1.2 mm long, ± coriaceous, nerves not projected; segments 3, 1(–3)-lobed at the apex, lanceolate, 1.5–2 mm wide at the base; petioles to 2.5 cm long, with retrorse, appressed, eglandular hairs 0.3–0.5 mm long; stipules 8–10 by 3–4 mm, lanceolate, papery, reddish, glabrous on both sides, ending in 1 or 2 bristles 0.4–0.7 mm long. Peduncles 0.4–0.9 cm long, with retrorse, appressed, eglandular hairs 0.3–0.5 mm long; bracteoles 9–10 by 1.8–2 mm, lanceolate, glabrous on both sides, with eglandular hairs on the margin, ending in 1 or 2 bristles 0.4–0.7 mm long; pedicels 1–1.7 cm long, with retrorse, appressed, eglandular hairs 0.3–0.5 mm long; pedicel and peduncle together often not overtopping the subtending leaf. *Sepals* 6.5–7.5 by 1.7–2.2 mm (ratio pedicel length/sepal length = 1.5–2.3), 3-nerved, mucronate (with mucro 0.5–0.7 mm long), with scarious margins 0.1 mm wide, with erect-patent, eglandular hairs 0.3–0.5 mm long on the margin, glabrous on both sides, ending in 1 or 2 bristles 0.4–0.6 mm long. *Petals* 12–14 by 4–4.5 mm (ratio petal length/petal width = 3–3.1), emarginate (notch 0.5 mm deep), glabrous, purplish. Filaments 3.5–4 mm long, lan-

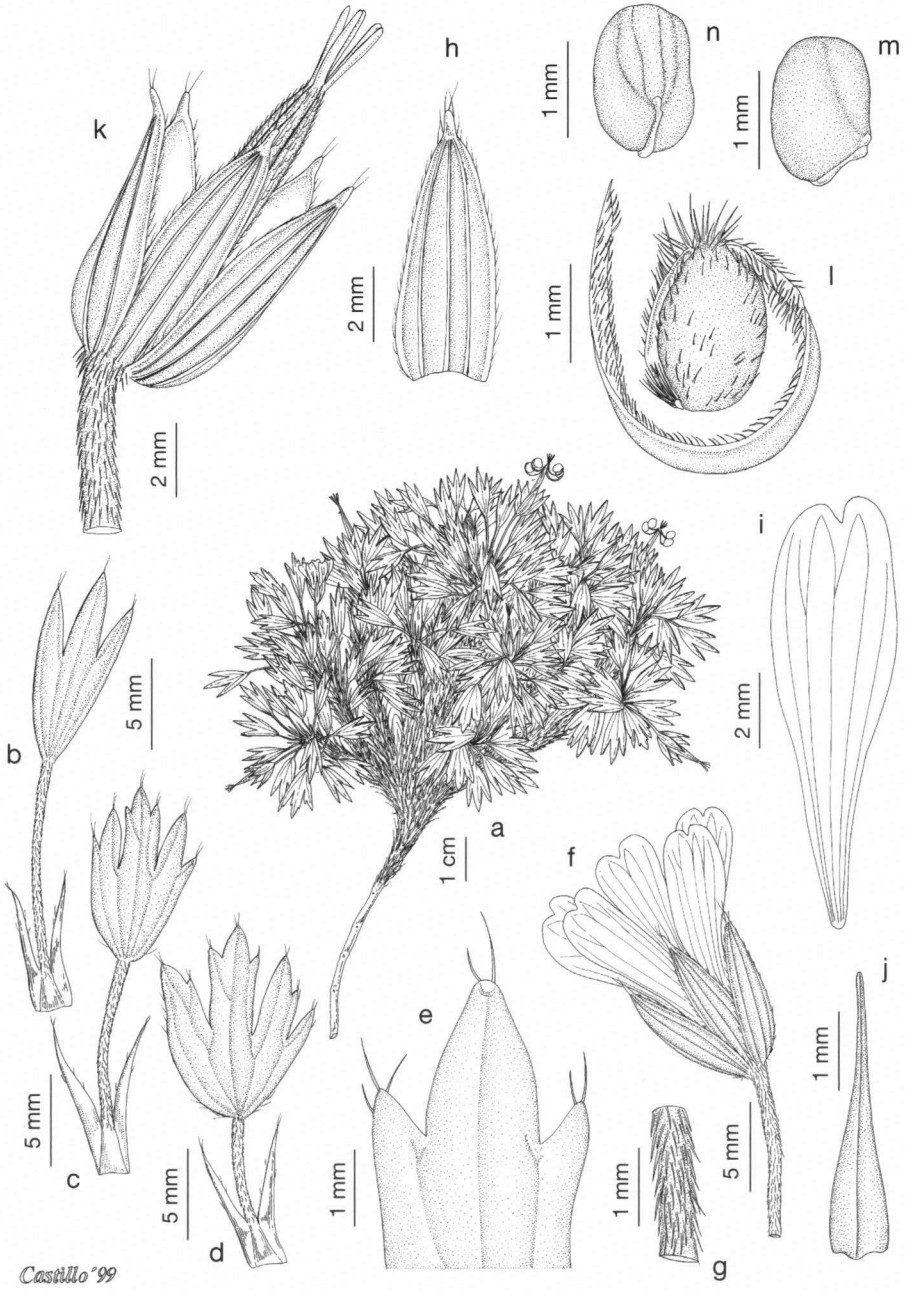
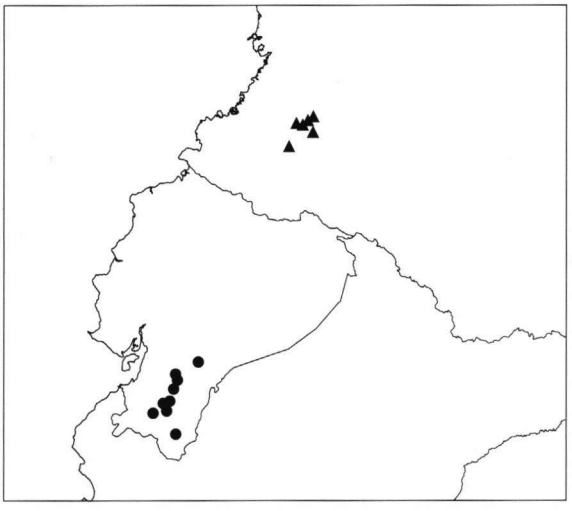


Fig. 12. *Geranium azorelloides* Sandwith. a. Habit; b–d. leaves; e. apex of the middle segment; f. flower; g. peduncle; h. sepal; i. petal; j. stamen; k. fruit; l. mericarp; m & n. seeds (all *Barclay & Juajibioy 5983*, MO).



Map 2. Distribution of *Geranium azorelloides* Sandwith (▲) and *G. campii* H.E. Moore (●).

ceolate, glabrous, or with few eglandular hairs 0.1–0.2 mm long on the margin; anthers 0.7 by 0.6 mm, purplish. Nectaries glabrous. Gynoecium 4 mm long, purplish. *Fruit* 10–10.5 mm long; mericarps 1.7–2 by 1.1 mm, with antrorse, ± appressed, eglandular hairs 0.1–0.2 mm long on the surface and eglandular hairs 0.5–0.8 mm long on the margin; rostrum 6.5–7 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1–0.2 mm long; stigmatic remains 1.5 mm long (ratio fruit length/stigmatic remains length = 6.6), with 5 glabrous lobes. *Seeds* 1.5 by 1 mm; hilum 1/4 as long as the perimeter. Cotyledons entire.

Distribution — S Colombia.

Habitat & Phenology — In wet paramo and on lake shores. Altitude 3000–3450 m. Flowering: September to April.

Notes — *Geranium azorelloides* is a species with a striking leaf lamina, obtriangular in outline, with three shallowly incised segments at the apex. No *Geranium* has such a leaf lamina, except some representatives of sect. *Neurophyllodes* (endemic from Hawaii) and *G. jahnii* (from Venezuela). However, in those groups the petiole is articulated with the lamina or the stipules, whereas *G. azorelloides* lacks this feature.

Geranium azorelloides usually has a glabrous leaf lamina. However, in some cases it is possible to find patent cilia on the margin (*Beck 13065*, LPB; *Cuatrecasas & Willard 26343*, COL). Most of the specimens examined have entire segments at the apex of the leaf lamina, but occasionally these segments could have 1 or 2 lateral teeth (*Barclay & Juajibioy 5983*, MO).

GERANIUM section NEOANDINA

Geranium sect. *Neoandina* Aedo (2000) 183. — Type: *Geranium sibbaldioides* Benth.

Perennial herbs with rootstock usually vertical, not tuberculate, not turnip-shaped, without fusiform-swollen roots; aerial stem absent; with or without vegetative stems.

Leaf lamina orbicular to polygonal obtriangular in outline, usually cordate, sometimes rounded to cuneate, without abscission zone, tripartite, palmatifid, palmatisect, or digitate (with lateral segments upward), glabrous to sericeous, usually not coriaceous, and with nerves not projected; segments 3–9, lanceolate, obtriangular or rhombic, 1–9-lobed in the distal half or at the apex; cauline leaves absent; stipules lanceolate, free, papery or scarious, reddish or stramineous, glabrous to sericeous. *Inflorescence* in 1-flowered cymules, solitary; peduncles (when present) and pedicels glabrous to sericeous; bracteoles lanceolate to linear-lanceolate, glabrous to hairy; pedicel and peduncle together usually not overtopping the subtending leaf. *Sepals* ovate, smooth, not accrescent, 3–5-nerved, usually mucronate, with scarious margins, glabrous (except on the margin) to sericeous. *Petals* erect-patent, ± obovate, entire, without claw, glabrous to hairy, purplish to white. *Stamens* 10, both whorls bearing anthers; filaments not exserted, lanceolate with an abruptly narrowed apex, yellowish, glabrous to hairy. Nectaries hemispherical, glabrous or with a tuft of hairs at the top. *Fruit* of the seed-ejection type; mericarps smooth, without longitudinal rib, without basal beak, with a basal callus, without a basal prong, usually with eglandular hairs, brownish; rostrum with or without a narrowed apex; stigmatic remains with 5 hairy or glabrous lobes. *Seeds* ellipsoid, finely reticulate, brownish; hilum 1/4–1/6 as long as the perimeter. Cotyledons entire.

Notes — The section *Neoandina* contains 22 species, occurring from Costa Rica to N Argentina. It can be distinguished by the stemless habit and the palmatifid to palmatisect leaves (rarely digitate). Morphological similarities between sect. *Neoandina* and sect. *Azorelloida* are discussed under sect. *Azorelloida*.

Knuth (1912) characterised sect. *Chilensia* by its 'caules ± elati', 'root' turnip-shaped, and peduncles usually 2-flowered, and sect. *Andina* by its 'caules abbreviati et sub foliis occulti', 'root' not turnip-shaped, and peduncles 1-flowered. *Geranium sessiliflorum* was selected by Knuth (1912: 45) as type of his section *Andina*. However, *G. sessiliflorum* has a turnip-shaped rhizome with a constriction at the apex. Usually this species is stemless but some specimens can be found with short but evident aerial stems. Thus it seems more suitable to transfer this species to sect. *Chilensia*, and as a result of it to synonymise sect. *Chilensia* to sect. *Andina*. Consequently a new section has been described to include species that until recently were comprehended in sect. *Andina*, except *G. sessiliflorum* (Aedo, 2000: 183).

2. Geranium campii H.E. Moore — Fig. 13, Map 2

Geranium campii H.E. Moore (1963) 92, 93 f. 1. — Type: *Camp E-5138* (holo NY; iso BH), Ecuador, Azuay, Páramo del Castillo, 31 Aug. 1945.

Herbs 2–9 cm tall. *Rootstock* 2–4 mm diam., vertical; with short vegetative stems. *Leaf* lamina 0.35–1 by 0.62–1.6 cm, triangular in outline, rounded, tripartite (divided for 0.7–0.9 of its length), densely hairy on both sides, not coriaceous, nerves not projected; segments 3(–5), entire, broadly lanceolate, 0.5–1.4 mm wide at the base; petioles to 4 cm long, with patent (sometimes retrorse, appressed), eglandular hairs 0.2–0.5 mm long; stipules 6–10 by 1.2–2 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.2–0.4 mm long. Peduncles 0.4–1.1 cm long, with patent, eglandular hairs 0.3–0.4

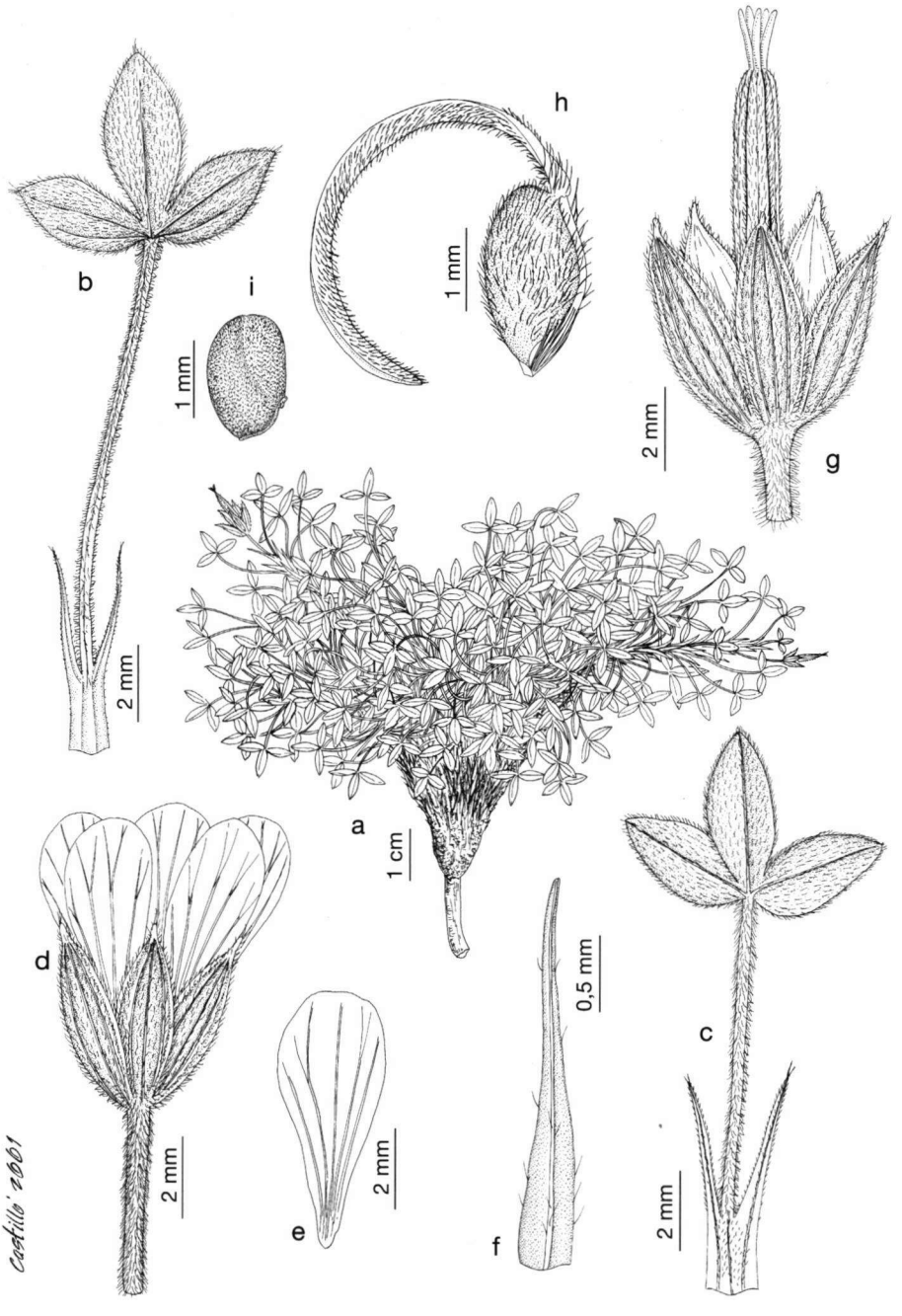


Fig. 13. *Geranium campii* H.E. Moore. a. Habit; b. leaf (adaxial side); c. leaf (abaxial side); d. flower; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a–f: *Øllgaard et al. 90971*, MO; g–i: *André 4455*, GH).

mm long; bracteoles 4–7 by 0.5–1 mm, linear-lanceolate, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.3–0.4 mm long; pedicels 1.2–3 cm long, with patent, eglandular hairs 0.3–0.4 mm long; pedicel and peduncle together often overtopping the subtending leaf. *Sepals* 4.3–5.6 by 1.8–2.8 mm (ratio pedicel length/sepal length = 2.7–5.3), 3-nerved, mucronate (with mucro 0.4–0.8 mm long), with scarious margins 0.1 mm wide, with erect-patent, eglandular hairs 0.2–0.4 mm long on the base of the abaxial side and margin, glabrous adaxially, ending in 1–3 bristles 0.3–0.4 mm long. *Petals* 8–9 by 3–3.3 mm (ratio petal length/petal width = 2.6–3), entire, glabrous on both sides and margin, purplish, sometimes white. Filaments 3–3.5 mm long, lanceolate, glabrous, or with few eglandular hairs 0.1 mm long on the abaxial side and margin; anthers 0.7 by 0.6 mm, yellowish. Nectaries glabrous. Gynoecium 3.5–4 mm long, yellowish. *Fruit* 8.5–10 mm long; mericarps 2.2–2.5 by 1–1.2 mm, with antrorse, ± appressed, eglandular hairs 0.1–0.2 mm long; rostrum 5.5–7 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 0.8–1 mm long (ratio fruit length/stigmatic remains length = 10–11), with 5 glabrous lobes. *Seeds* 1.7–1.8 by 0.9–1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — S Ecuador.

Habitat & Phenology — Moss cushions, bogs or grassy areas in paramo, subparamo and upper montane forest. Altitude 3000–3840 m. Flowering: August to February.

Notes — As Moore (1963: 92) pointed out, *G. campii* is quite similar to *G. sibbaldioides*. It differs, however, in the tripartite leaf-blades hairy on both faces, in the usually patent hairs on petioles and peduncles, and in the hairy sepals.

Geranium campii is endemic to S Ecuador where *G. sibbaldioides* also occurs, and they share similar wet habitats in 'paramos'. In this area some intermediate specimens have been collected with a variable combination of characters, including leaves with 5 segments, hairy only on the adaxial surface, petioles and peduncles with retrorse hairs, and sepals almost glabrous. Additional collections and a detailed field study may help to understand this variability, which could be produced by hybridisation.

3. **Geranium costaricense** H.E. Moore — Fig. 14, Map 3

Geranium costaricense H.E. Moore (1951) 253. — *Geranium cucullatum* var. *multifidum* Suess. (1942) 276. — Type: *Kupper 1298* (lectotype, designated by Moore, 1951: 253, M), Costa Rica, Chirripó Grande, 27 April 1932.

Herbs 4–10 cm tall. *Rootstock* 4–6 mm diam., ± vertical; with long vegetative stems. *Leaf* lamina (1.5–)1.9–2.8 by (1.7–)1.9–2.8 cm, polygonal in outline, cordate, palmatifid (divided for 0.75–0.88 of its length), glabrous on both sides, with antrorse, eglandular cilia 0.1–0.2 mm long on the margin, each segment ending in 1–3 bristles 0.3–0.5 mm long, not coriaceous, nerves not projected; segments 7, obtriangular to rhombic with linear-lanceolate lobes, 1.5–2 mm wide at the base, 3–9-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.35–0.53); petioles to 9 cm long, with retrorse, appressed, eglandular hairs 0.1–0.4 mm long; stipules 13–19 by 2–3 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.3–0.6 mm long. Peduncles 0.8–5.3 cm long, with retrorse, appressed, eglandular hairs 0.2–0.4

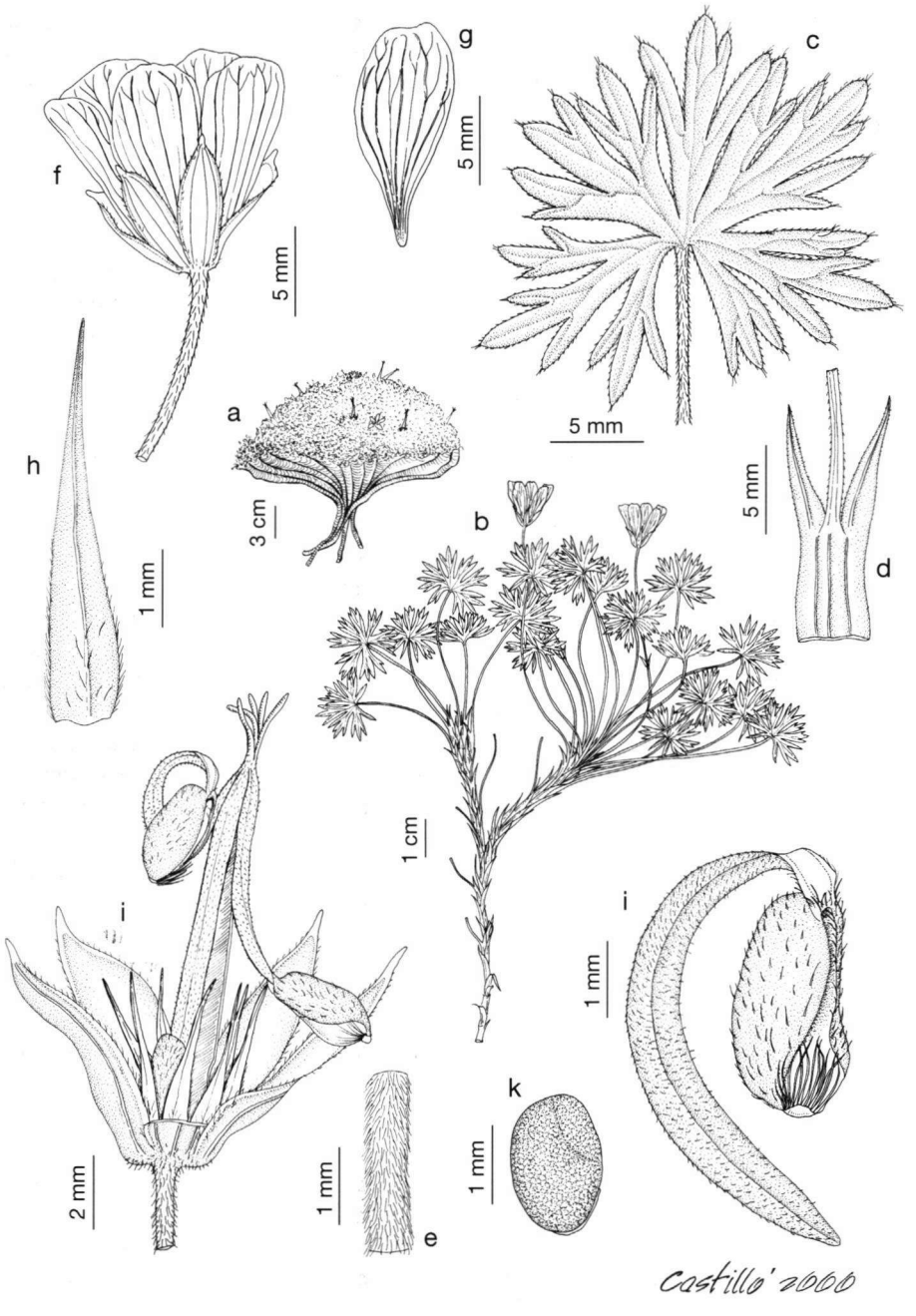
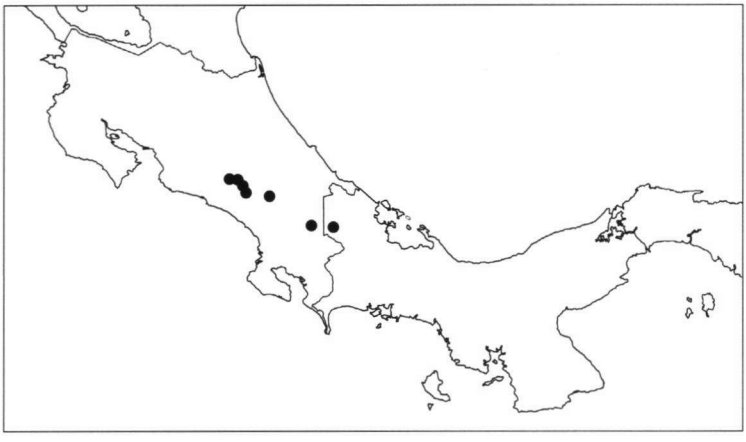


Fig. 14. *Geranium costaricense* H.E. Moore. a. Habit; b. flowering branch; c. leaf; d. stipule; e. peduncle; f. flower; g. petal; h. stamen; i. fruit; j. mericarp; k. seed (a, b, f–h: *Almeda & Nakai 4763*, CAL; c–e, i–k: *Wilbur 20321*, DUKE).



Map 3. Distribution of *Geranium costaricense* H.E. Moore.

mm long; bracteoles 5.5–9 by 1–1.5 mm, lanceolate, usually glabrous on both sides, with eglandular hairs on the margin, ending in 1–3 bristles 0.4–0.7 mm long; pedicels 2.6–6.4 cm long, with retrorse, appressed, eglandular hairs 0.2–0.4 mm long; pedicel and peduncle together often overtopping the subtending leaf. *Sepals* 5.5–7.2 by 2–2.7 mm (ratio pedicel length/sepal length = 4.4–8.8), 3–5-nerved, mucronate (with mucro 0.8–1.3 mm long), with scarious margins 0.1–0.2 mm wide, with scattered erect-patent, eglandular hairs 0.2–0.3 mm long on the base of the abaxial side and margin, glabrous adaxially, ending in 1–3 bristles 0.4–0.6 mm long. *Petals* 9–14 by 4–5 mm (ratio petal length/petal width = 2.25–2.87), entire, glabrous on both sides, ciliate on the basal margin, white, sometimes purplish. Filaments 4.5–5 mm long, not exserted, lanceolate, with eglandular hairs 0.2–0.3 mm long on the abaxial side and margin; anthers 1.2 by 0.6 mm, yellowish. Nectaries glabrous. Gynoecium 6.5 mm long, purplish. *Fruit* 12–14.5 mm long; mericarps 2.5–3 by 1.2–1.3 mm, with antrorse, ± appressed, eglandular hairs 0.2–0.4 mm long; rostrum 9–9.5 mm long, with a narrowed apex 0.5–1 mm long, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 1.5–2 mm long (ratio fruit length/stigmatic remains length = 6.8–8), with 5 glabrous lobes. *Seeds* 1.9–2.1 by 0.9–1.2 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — S Costa Rica and N Panama.

Habitat & Phenology — In low boggy depressions with *Blechnum*, *Isoetes*, and *Sphagnum*, and in *Puya* bogs in open forest. Altitude 2275–3450 m. Flowering: February to August.

Notes — *Geranium costaricense* is recognised by its leaves that are much larger and more deeply divided than in *G. foreroi* and *G. paludosum*. This species also has a distinctive fruit feature: a rostrum with a narrowed apex 0.5–1 mm long, lacking in both *G. foreroi* and *G. paludosum*. It has usually been considered as closely related to *G. sibbaldioides* (Moore 1951: 253; Burger, 1991: 18). However, *G. sibbaldioides* has leaf laminas 0.5–1.3 cm long (1.5–2.8 cm long in *G. costaricense*), with a middle segment 1–3-lobed at apex (3–9-lobed in *G. costaricense*). The nearest populations

of *G. sibbaldioides* are more than 800 km far in N Colombia. In this area *G. sibbaldioides* is represented by subsp. *elongatum*, which has hairy leaves (at least adaxially), while *G. costaricense* has glabrous leaves except on the margins.

Geranium costaricense is the only known representative of sect. *Neoandina* in C America.

4. Geranium crassipes Hook. ex A. Gray — Fig. 15, Map 4

Geranium crassipes Hook. ex A. Gray (1854) 309. — Type: *Matthews 683* (lectotype, here designated, K; isolectotype W), Peru, Pasco, Cerro Pasco.

Geranium sericeum var. *microphyllum* Wedd. (1861) 285, '*microphylla*'. — *Geranium lechleri* R. Knuth (1912) 80. — Type: *Lechler 1985* (lectotype, here designated, G; isolectotypes GOET, HAL-84323, K, P, W), Peru, Puno, Agapata, June 1854.

Geranium muscoideum R. Knuth (1906) 567. — Type: *Weberbauer 2619* (lectotype, here designated, G; isolectotypes BRSL, F), Peru, Junín, Tarma, La Oroya.

Herbs 1–2.2 cm tall. *Rootstock* 6–16 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.42–0.7 by 0.52–0.9 cm, polygonal in outline, cordate, palmatifid (divided for 0.69–0.78 of its length), sericeous on both sides, not coriaceous, nerves not projected; segments 7, entire, lanceolate, 0.5–1 mm wide at the base; petioles to 1.7 cm long, sericeous, with patent to retrorse (sometimes antrorse), eglandular hairs 0.2–0.5 mm long; stipules 5–8 by 0.6–1 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.2–1 cm long, sericeous, with patent to retrorse, eglandular hairs 0.3–0.5 mm long; pedicel not overtopping the subtending leaf. *Sepals* 4.2–6 by 1.3–2 mm (ratio pedicel length/sepal length = 0.4–1.8), 3-nerved, mucronate (with mucro 0.2–0.4 mm long), with scarious margins 0.1 mm wide, sericeous with erect-patent, eglandular hairs 0.2–0.5 mm long on the abaxial side and patent, eglandular hairs 1–1.3 mm long on the margin, glabrous adaxially. *Petals* 7–10.5 by 2.8–4.5 mm (ratio petal length/petal width = 2.3–3), entire, glabrous, white. Filaments 3.6–4.5 mm long, lanceolate, with eglandular hairs 0.2–0.5 mm long on the abaxial side and margin; anthers 0.7–0.8 by 0.5 mm, yellowish. Nectaries glabrous. Gynoecium 4–4.5 mm long, yellowish. *Fruit* 6.5–10 mm long; mericarps 2.5–2.7 by 1.4 mm, with antrorse, ± appressed, eglandular hairs 0.2–0.4 mm long; rostrum 4–7 mm long, without a narrowed apex, sericeous, with antrorse, appressed, eglandular hairs 0.2–0.5 mm long; stigmatic remains 0.5 mm long (ratio fruit length/stigmatic remains length = 13–20), with 5 hairy lobes. *Seeds* 1.5–2.1 by 0.7–1.1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — C and S Peru.

Habitat & Phenology — Rocky outcrops in puna. Altitude 4000–4500 m. Flowering: April.

Notes — *Geranium crassipes* is easily distinguished from most of the sericeous species of sect. *Neoandina* by its palmatifid leaves, sericeous on both sides and with entire segments. It is quite similar to *G. planum*, from which it differs principally by its leaves with 7 segments, and its sepals with mucro and long, patent, hairs on the margin. *Geranium crassipes* might at first be mistaken for *G. nivale*, but it has fruit without a narrowed apex, shorter lamina and petals.

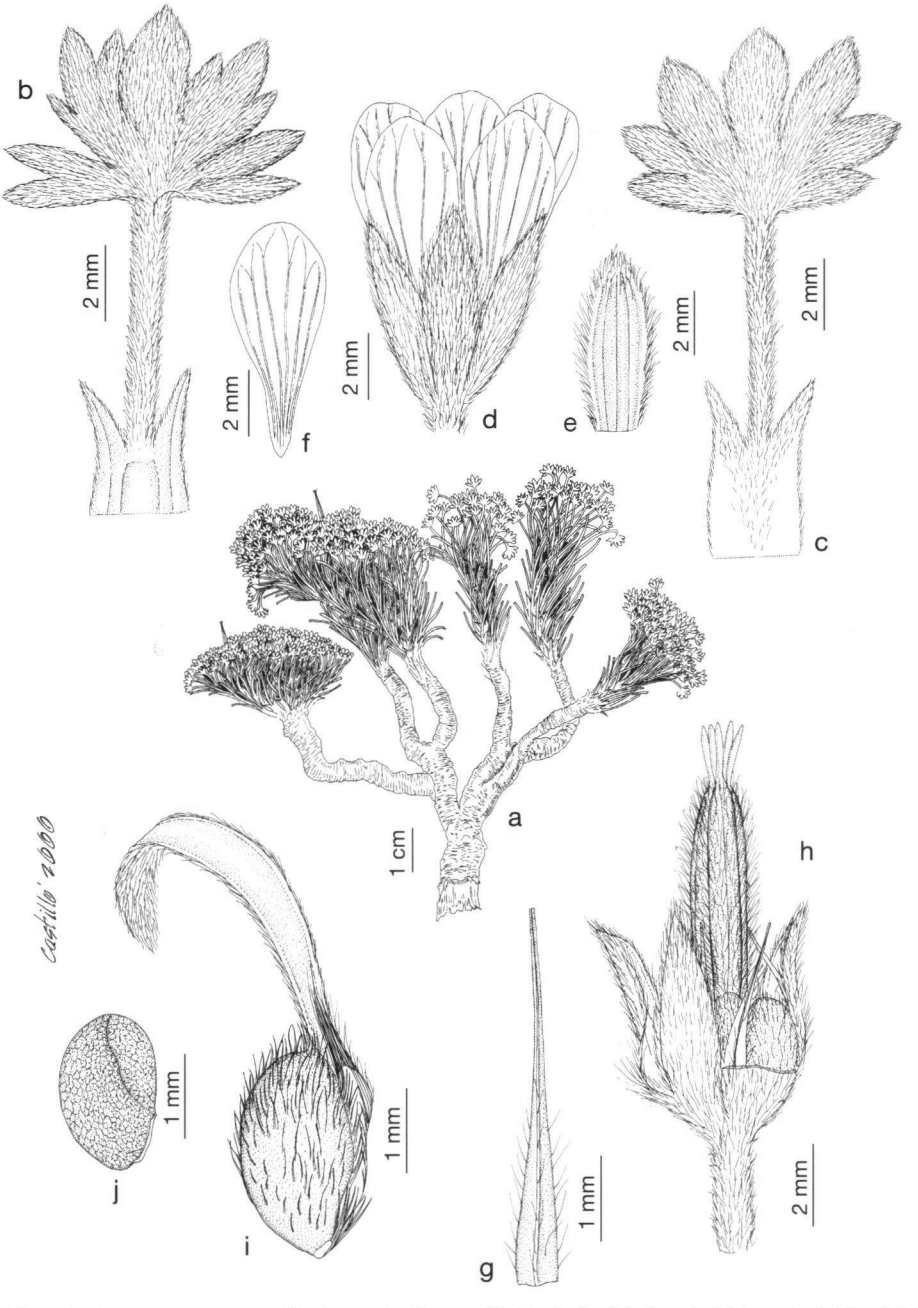
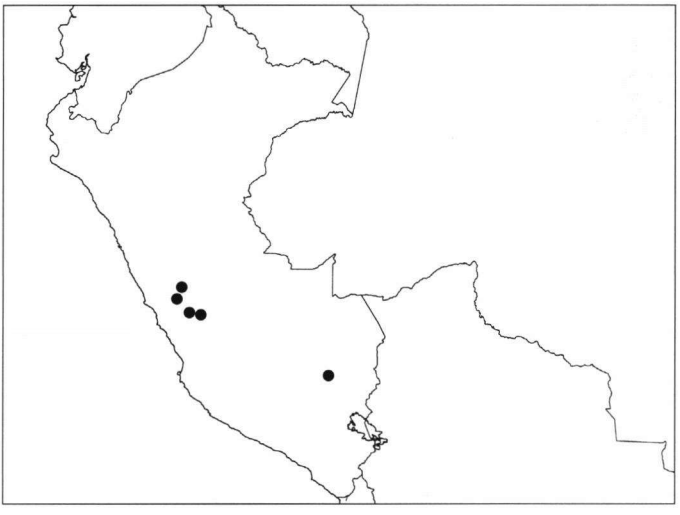


Fig. 15. *Geranium crassipes* Hook. ex A. Gray. a. Habit; b. leaf (adaxial side); c. leaf (abaxial side); d. flower; e. sepal; f. petal; g. stamen; h. fruit; i. mericarp; j. seed (a, g–j: *Moore et al. 8319*, BH; b: *Humbert 30852*, P; c–f: *Killip & Smith 21968*, US).



Map 4. Distribution of *Geranium crassipes* Hook. ex A. Gray.

Knuth (1912: 83) considered *G. crassipes* as synonym of *G. sessiliflorum*, although he could not examine any type material. In my view *G. sessiliflorum* is a representative of sect. *Andina*, it is easily distinguished from *G. crassipes* by its turnip-shaped rhizome with a constriction at the apex, its middle leaf-segment 3–13-lobed in distal half, and its indumentum (not sericeous). In addition, Knuth (1912: 87) recognised the taxonomic entity here described as *G. muscoideum*. He also described *G. lechleri* as an independent species. Knuth (1912: 78) distinguished both taxa on the basis of the length of the leaf indumentum, this being "brevi subsericeo" in *G. muscoideum* and "satis longa argenteo-lanato-sericea" in *G. lechleri*. Macbride (1949: 513) considered *G. muscoideum* as synonym of *G. crassipes*, and distinguished *G. lechleri* by its "leaves often less deeply 5-parted". I have found, however, a continuous variation of the length of the leaf indumentum. On the contrary the number of leaf segments seems to be constantly 7, even in the type material of *G. lechleri*. All these data suggest that there is no basis for recognising *G. lechleri*, which I have subsumed under *G. crassipes*.

5. Geranium digitatum R. Knuth — Fig. 16, Map 5

Geranium digitatum R. Knuth (1930a) 1. — Type: *Macbride & Featherstone 940* (holo F-517468; iso G, W), Peru, La Oroya, 27 May–7 June 1922.

Herbs 1.5–7 cm tall. *Rootstock* 4–9 mm diam., vertical; sometimes with short vegetative stems. *Leaf* lamina 0.5–1.5 by 0.45–1.45 cm, polygonal to obtriangular in outline, cuneate, digitate with lateral segments upward (divided for 0.52–0.73 of its length), sericeous on both sides, not coriaceous, nerves not projected; segments 3–5, entire, lanceolate, 1.4–2 mm wide at the base; petioles to 6.5 cm long, sericeous, with patent to retrorse, eglandular hairs 0.3–0.5 mm long; stipules 8.5–12 by 1.5–2 mm, lanceolate, papery, reddish, sericeous on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 1–6.7 cm long, sericeous, with patent to retrorse, eglandular

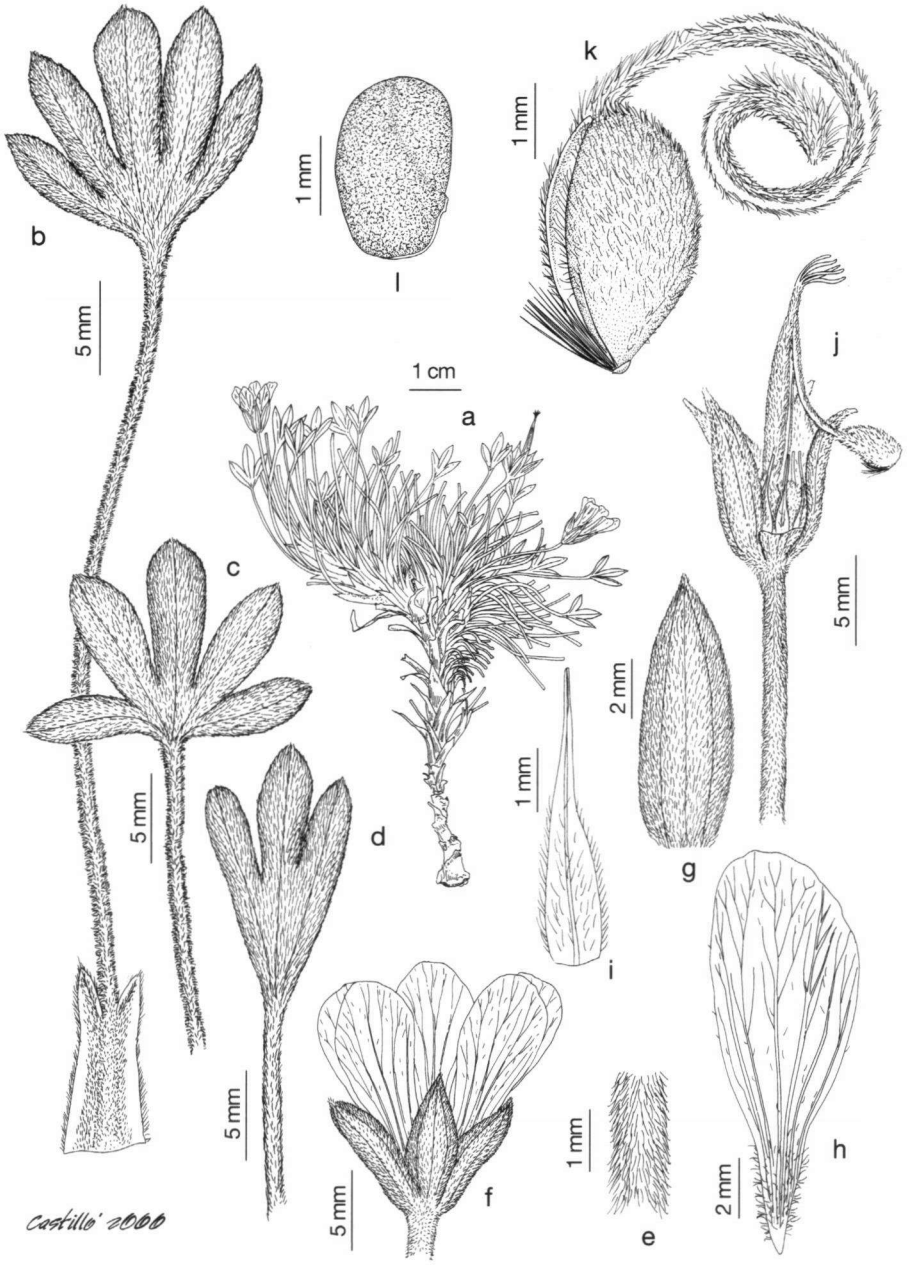


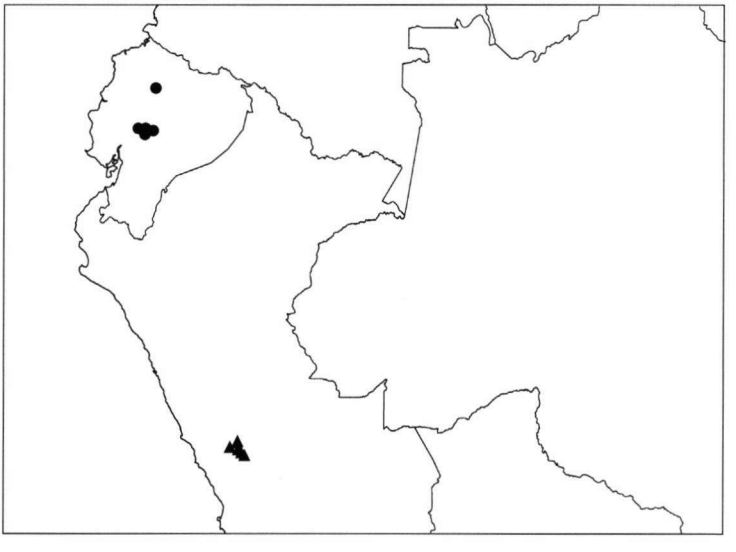
Fig. 16. *Geranium digitatum* R. Knuth. a. Fruiting branch; b–d. leaves; e. peduncle; f. flower; g. sepal; h. petal (abaxial side); i. stamen; j. fruit; k. mericarp; l. seed (a, d, g, i–l: *Iltis et al. 107*, MO; b, c: *Macbride & Featherstone 940*, W; e, f, h: *Saunders 710*, K).

hairs 0.3–0.5 mm long; pedicel not overtopping the subtending leaf. *Sepals* 6.5–9.8 by 2.2–2.8 mm (ratio pedicel length/sepal length = 1.4–7), 3-nerved, mucronate (with mucro 0.1–0.2 mm long), with scarious margins 0.2 mm wide, sericeous with erect-patent, eglandular hairs 0.3–0.5 mm long. *Petals* 12–17 by 5–8 mm (ratio petal length/petal width = 2.1–2.4), entire, hairy on the base of abaxial side and margin, glabrous adaxially, white. Filaments 4.5–5.2 mm long, not exserted, lanceolate, with eglandular hairs 0.3–0.5 mm long on the abaxial side and margin; anthers 1 by 0.6 mm, yellowish. Nectaries with a tuft of hairs at the top, dorsally glabrous. Gynoecium 5.2–6 mm long, yellowish. *Fruit* 14–18.5 mm long; mericarps 3–3.2 by 1.5–2 mm, with antrorse, ± appressed, eglandular hairs 0.2–0.3 mm long; rostrum 10–12 mm long, with a narrowed apex 1.6–2 mm long, sericeous, with erect-patent, eglandular hairs 0.2–0.4 mm long; stigmatic remains 2.5–3 mm long (ratio fruit length/stigmatic remains length = 4.6–7.4), with 5 hairy lobes. *Seeds* 2.5–2.9 by 1.4–1.7 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — C Peru.

Habitat & Phenology — In arid natural or grazed grassland on limestone or in open moorland. Altitude 3000–4500 m. Flowering: November to May.

Note — *Geranium digitatum* is easily distinguished from other sericeous species of sect. *Neoandina* by its digitate leaves with entire segments. In the type material leaves with 5 segments are predominant (Fig. 16c) while in remaining collections almost all leaves have 3 segments. Some variation has also been found in indumentum of the nectaries: most of the specimens have a tuft of hairs at the top of each nectary but *Smith 5687* (MO, NY, TEX) has only scattered hairs there. *Geranium digitatum* shares with *G. weddellii* hairy nectaries and a rostrum with a narrowed apex. However, deeply divided, short leaves, petiole antrorsely hairy and glabrous petals are consistently reliable characters that distinguish *G. weddellii* from *G. digitatum*.



Map 5. Distribution of *Geranium digitatum* R. Knuth (▲) and *G. ecuadoriense* Hieron. (●).

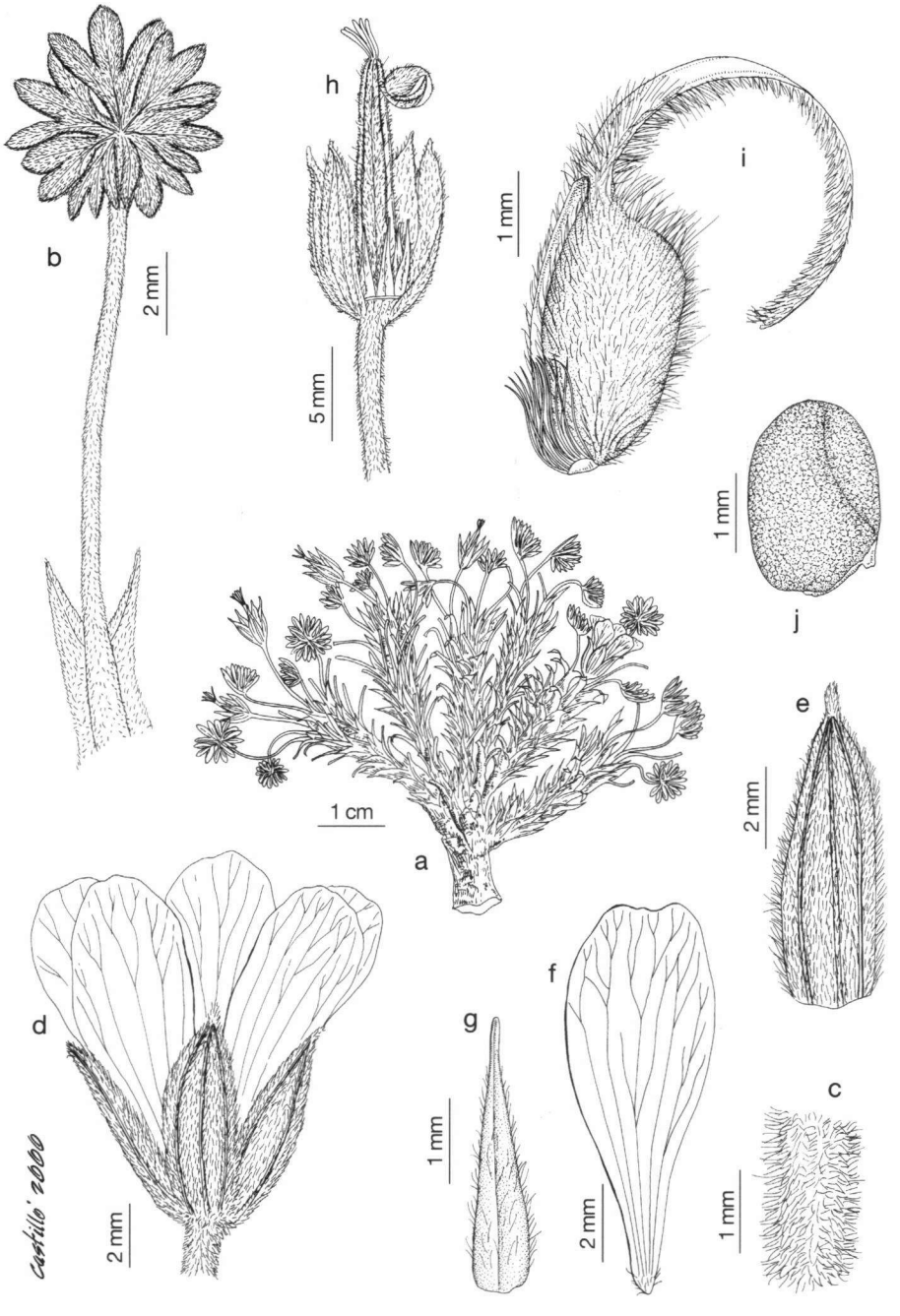


Fig. 17. *Geranium ecuadoriense* Hieron. a. Flowering and fruiting branch: b. leaf; c. peduncle; d. flower; e. sepal; f. petal; g. stamen; h. fruit; i. mericarp; j. seed (a: *Penland & Summers 695*, GH; b–j: *Asplund 8378*, S).

6. Geranium ecuadoriense Hieron. — Fig. 17, Map 5

Geranium ecuadoriense Hieron. (1895a) 30. — Type: *Lehmann 6642* (lectotype, here designated, K; iso BH-418691), Ecuador, Mt Chimborazo.

Herbs 2–5 cm tall. *Rootstock* 3–6 mm diam., vertical; with short vegetative stems. *Leaf* lamina 0.45–0.82 by 0.68–1.18 cm, polygonal in outline, cordate, palmatisect, sericeous on both sides, not coriaceous, nerves not projected; segments 7, obtriangular with lanceolate lobes, 0.4–0.6 mm wide at the base, 3-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.53–0.76); petioles to 3 cm long, sericeous, with retrorse, ± appressed, eglandular hairs 0.2–0.3 mm long; stipules 5–12 by 1–2 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.3–0.6 mm long. Peduncles absent; pedicels 0.6–1.1 cm long, sericeous, with retrorse, ± appressed, eglandular hairs 0.2–0.3 mm long; pedicel not overtopping the subtending leaf. *Sepals* 4.5–7.2 by 1.5–2.5 mm (ratio pedicel length/sepal length = 1.38–1.7), 3-nerved, mucronate (with mucro 0.5–0.9 mm long), with scarious margins 0.1 mm wide, sericeous with erect-patent, eglandular hairs 0.2–0.5 mm long on both sides, and patent, eglandular hairs 0.6–1.5 mm long on the margin. *Petals* 7–10 by 2.2–3.9 mm (ratio petal length/petal width = 2.5–3.3), entire, glabrous on the adaxial side and margin, hairy on the base of the abaxial side, purplish, sometimes white. Filaments 3–3.5 mm long, not exserted, lanceolate, with eglandular hairs 0.2–0.3 mm long on the abaxial side and margin; anthers 0.7–0.9 by 0.4–0.6 mm, yellowish. Nectaries glabrous. Gynoecium 4–4.5 mm long, yellowish. *Fruit* 10–12 mm long; mericarps 3 by 1.5 mm, with antrorse, ± appressed, eglandular hairs 0.2–0.5 mm long; rostrum 7–8 mm long, without a narrowed apex, sericeous, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 1–1.2 mm long (ratio fruit length/stigmatic remains length = 9.5–11), with 5 hairy lobes. *Seeds* 2.1 by 1.2 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — C Ecuador.

Habitat & Phenology — In sand or gravel paramo, with occasional cushions of plants and scattered *Loricaria* shrubs. Altitude 3800–4600 m. Flowering: throughout the year.

Notes — *Geranium ecuadoriense* is an endemic to Ecuador, restricted to a small area around Volcano Chimborazo. Additionally, one Jameson's collection from Volcano Pichincha has been found at G. From this locality there are no new collections since 1850, which is a bit surprising since Pichincha Mt (near Quito) is one of the best collected sites in Ecuador. Thus, it can not be excluded to be a labelling mistake and the Jameson's plant originating from another locality.

Among the *Geranium* sect. *Neoandina* species, *G. ecuadoriense* resembles shallowly to *G. weddellii* and *G. tovarii*, considering its deeply divided, short, sericeous leaves. However, *G. ecuadoriense* has petioles and pedicels with retrorse hairs and hairy petals on the base of the abaxial side versus antrorse hairs and glabrous petals in *G. tovarii* and *G. weddellii*. In addition, *G. ecuadoriense* shares sepals with long, patent, hairs on the margin and glabrous nectaries with *G. tovarii*, and leaves with a 3-lobed middle segment with *G. weddellii*.

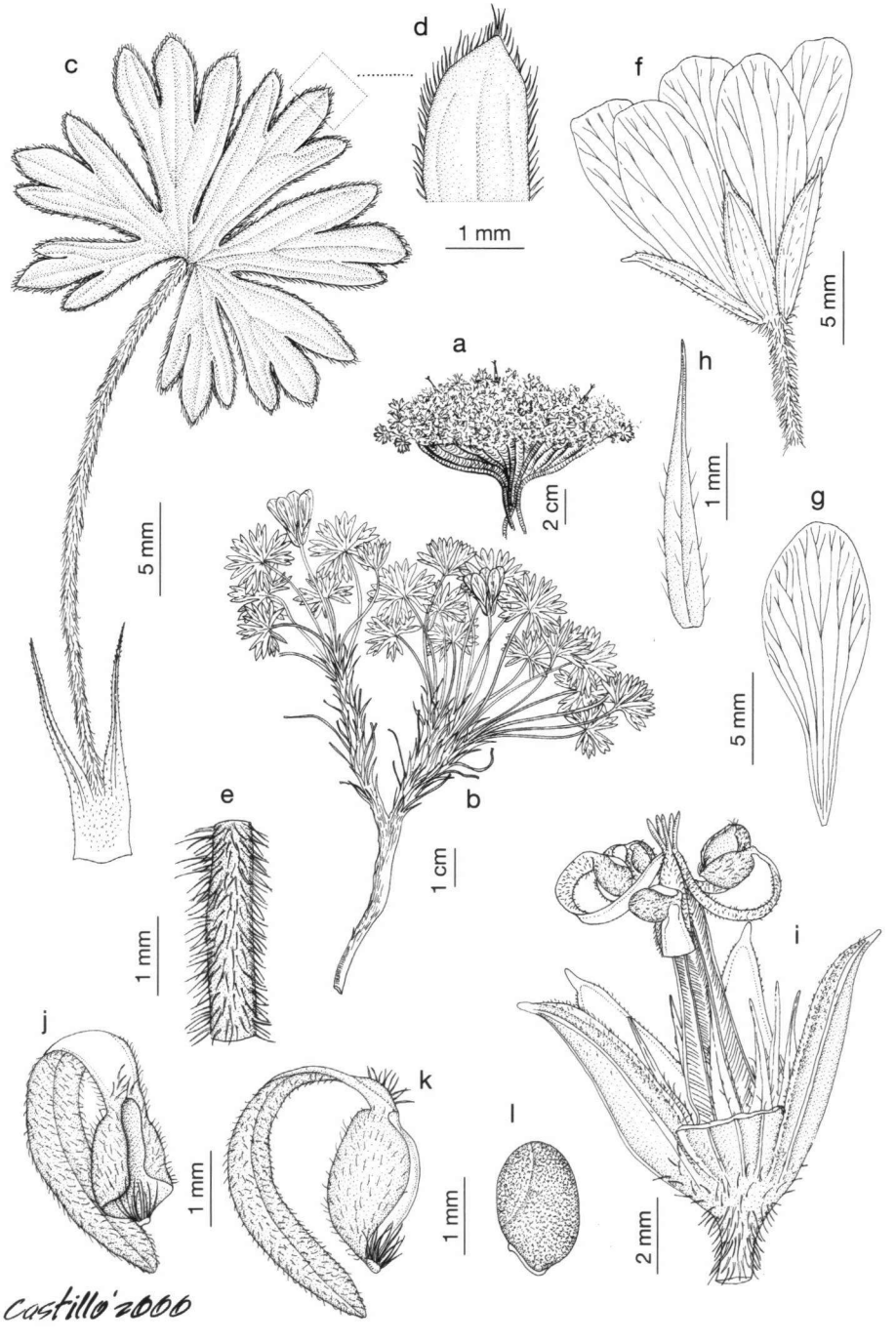


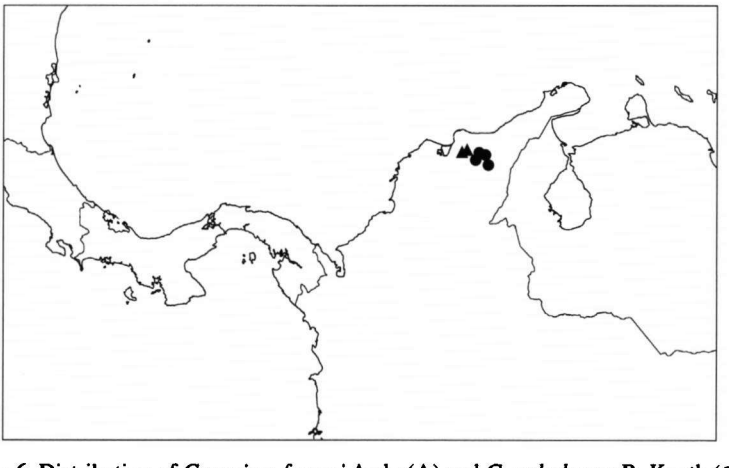
Fig. 18. *Geranium foreroi* Aedo. a. Habit; b. flowering branch; c. leaf; d. leaf lobe; e. peduncle; f. flower; g. petal; h. stamen; i. fruit; j & k. mericarps; l. seed (all *Forero & Kirkbride 635*, COL).

7. **Geranium foreroi** Aedo — Fig. 18, Map 6

Geranium foreroi Aedo (2000) 183. — Type: *Forero & Kirkbride 635* (holo COL-191289), Colombia, Magdalena, Sierra Nevada de Santa Marta, 1 km al NW de la quebrada de la laguna Río Frío, en dirección al pico José Hilario, 31 July 1972.

Herbs 2–3.5 cm tall. *Rootstock* 3–4 mm diam., ± vertical; with short vegetative stems. *Leaf* lamina 0.95–1.95 by 1.5–2.2 cm, polygonal in outline, cordate, palmatifid (divided for 0.7–0.81 of its length), glabrous on both sides, with antrorse, eglandular cilia 0.1–0.4 mm long on the margin, usually each segment ending in 1–3 bristles 0.2–0.4 mm long, not coriaceous, nerves not projected; segments 7, obtriangular with linear-lanceolate lobes, 1.2–1.7 mm wide at the base, 3-lobed at the apex (ratio main-sinus length of the middle segment/middle-segment length = 0.26–0.34); petioles to 2.5 cm long, with patent, eglandular hairs 0.2–0.7 mm long; stipules 6–8 by 1.5–2 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.2–0.4 mm long. Peduncles absent; pedicels 2.5–3.1 cm long, with patent, eglandular hairs 0.2–0.7 mm long; pedicel not overtopping the subtending leaf. *Sepals* 6.5–8 by 2 mm (ratio pedicel length/sepal length = 3.6–3.9), 5-nerved, mucronate (with mucro 0.4–0.7 mm long), with scarious margins 0.1–0.2 mm wide, with erect-patent, eglandular hairs 0.2–0.7 mm long on the abaxial side and margin, glabrous adaxially. *Petals* 15–18 by 6.5–7 mm (ratio petal length/petal width = 2.5–2.6), entire, hairy on the base of the adaxial side and margin, glabrous abaxially, white. Filaments 5–5.5 mm long, not exserted, lanceolate, with eglandular hairs 0.2–0.3 mm long on the abaxial side and margin; anthers 1.1 by 0.7 mm, yellowish. Nectaries glabrous. Gynoecium 5 mm long, colour unknown. *Fruit* 9–11 mm long; mericarps 2.3 by 1 mm, with antrorse, ± appressed, eglandular hairs 0.1–0.2 mm long; rostrum 7 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 1 mm long (ratio fruit length/stigmatic remains length = 9), with 5 glabrous lobes. *Seeds* 1.6 by 0.9 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — N Colombia (Sierra Nevada de Santa Marta).



Map 6. Distribution of *Geranium foreroi* Aedo (▲) and *G. paludosum* R. Knuth (●).

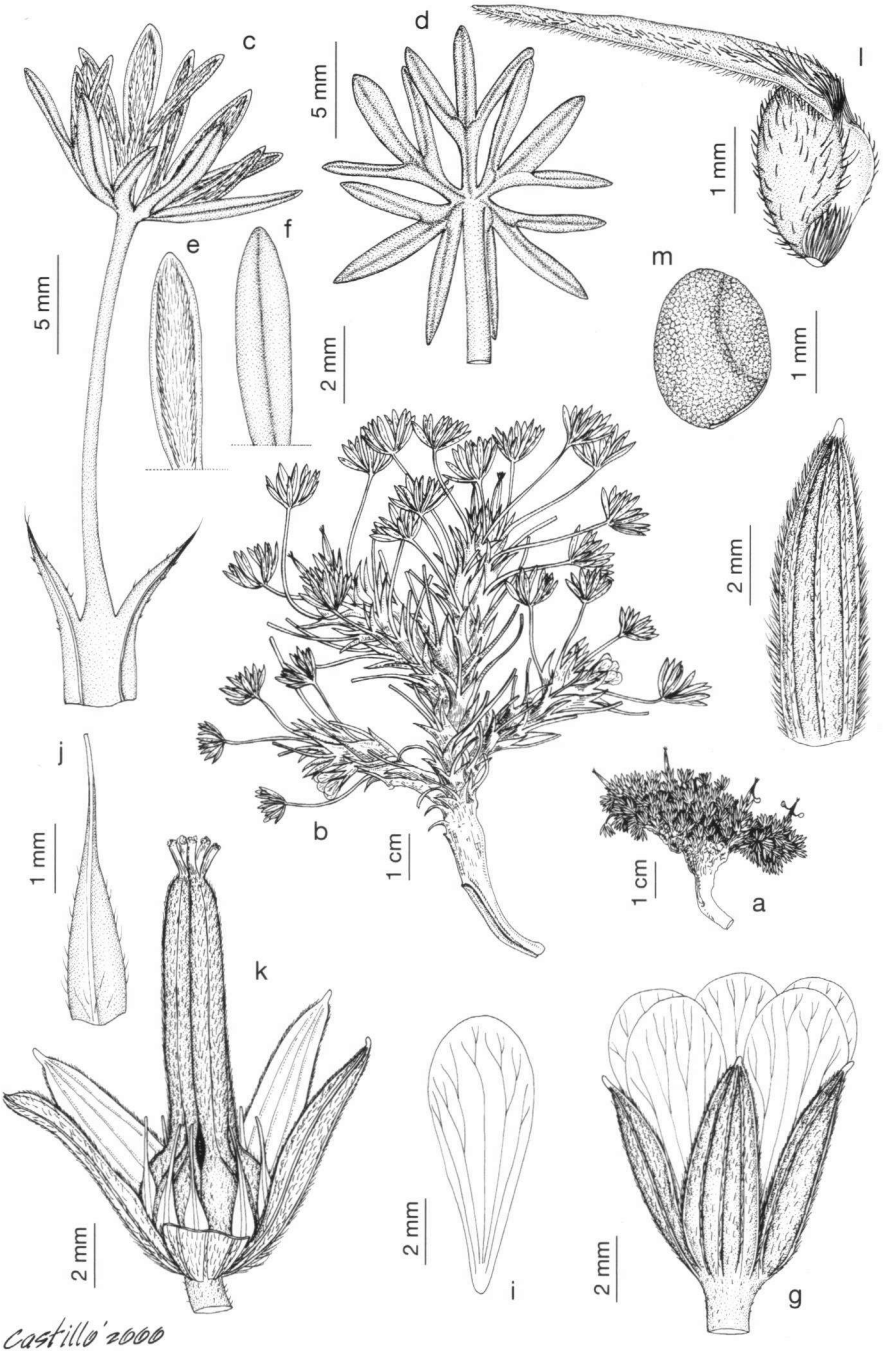


Fig. 19. *Geranium humboldtii* Spreng. a. Habit; b. fruiting branch; c & d. leaves; e. leaf lobe in abaxial view; f. leaf lobe in adaxial view; g. flower; h. sepal; i. petal; j. stamen; k. fruit; l. mericarp; m. seed (a, l & m: *Bonpland 2240*, P; b–k: *Cazalet & Pennington 5758*, B).

Habitat & Phenology — Unknown habitat. Altitude 3300–3400 m. Flowering: July.

Notes — *Geranium foreroi* has petioles and pedicels with patent, eglandular hairs 0.2–0.7 mm long and petals 15–18 mm long. This species could be confused with *G. paludosum*, which has retrorse short hairs (0.1–0.2 mm long) on the petioles and pedicels, and shorter petals (10.5–15.5 mm long). Both species share petals with hairs on the base of the adaxial side and margin, a quite unusual feature in *Geranium* sect. *Neoandina*. For differences between *G. foreroi* and *G. costaricense*, see the latter species.

The only two known collections are from Sierra Nevada de Santa Marta, where *G. paludosum* grows as well. However, both species are apparently allopatric, since the first has been found in the NW part of this mountain while *G. paludosum* was collected on C and E slopes of the Sierra Nevada.

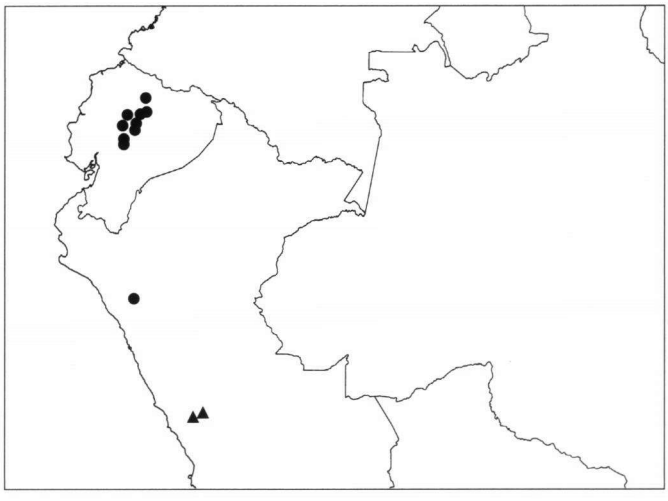
8. Geranium humboldtii Spreng. — Fig. 19, Map 7

Geranium humboldtii Spreng. (1826) 70. — Type: *Humboldt s.n.* (lectotype, here designated, B-Willd.-12533), Ecuador, in monte Antisana et Pichincha.

Geranium acaule Willd. ex Kunth (1822) 230, nom. illeg., non L. (1759). — *Geranium sessiliflorum* var. *acaule* (Willd. ex Kunth) Reiche (1895) 573. — Type: *Humboldt & Bonpland 2240* (lectotype, designated by Knuth, 1912: 87, B†; isolectotype BH-418693, P), Ecuador, Antisana.

Geranium hypoleucum Benth. (1845) 166. — Type: *Hartweg s.n.* (lectotype, here designated, K; isolectotype BH-418694), Ecuador, Hacienda de Antisana, 1851.

Herbs 2–8 cm tall. *Rootstock* 2–7 mm diam., ± horizontal; with short vegetative stems. *Leaf* lamina 1.1–1.5 by 0.9–1.6 cm, polygonal in outline, cordate, palmatisect, sericeous above, with antrorse, appressed, eglandular hairs, and glabrous beneath, not coriaceous, nerves not projected; segments 7, rhombic with linear-lanceolate lobes, 0.6–1 mm wide at the base, 3- or 4-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.53–0.66); petioles to 7 cm long, usually glabrous, sometimes with scattered, patent, eglandular hairs 0.8–1.2 mm long; stipules 12–14 by 2–3 mm, lanceolate, papery, reddish, glabrous on both sides, with patent, eglandular ciliae 0.2–0.3 mm, ending in 1 or 2 bristles 0.5–0.8 mm long. Peduncles absent; pedicels 0.5–0.6 cm long, glabrous; pedicel not overtopping the subtending leaf. *Sepals* 6.5–7.5 by 1.9–2 mm (ratio pedicel length/sepal length = 0.7–0.85), 3-nerved, mucronate (with mucro 0.5 mm long), with scarious margins 0.1 mm wide, glabrous or with scattered eglandular hairs abaxially, erect-patent, eglandular hairs 0.5–1 mm long on the margin, and ± sericeous adaxially. *Petals* 8.5–11 by 2.5–4 mm (ratio petal length/petal width = 2.7–3.4), entire, usually glabrous, sometimes hairy on the lower 1/4 of their adaxial surface, ciliate on the basal margin and glabrous abaxially, purplish. Filaments 3–4 mm long, not exserted, lanceolate or lanceolate with an abruptly narrowed apex, glabrous, or with eglandular hairs 0.2–0.4 mm long on the abaxial side and margin; anthers 0.8–1 by 0.5–0.6 mm, yellowish. Nectaries glabrous. Gynoecium 4–5 mm long, yellowish. *Fruit* 11–12 mm long; mericarps 2.2 by 1.3 mm, with antrorse, ± appressed, eglandular hairs 0.2–0.3 mm long; rostrum 6.5–7 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1–0.2 mm long; stigmatic remains 1.2 mm long (ratio fruit length/stigmatic remains length = 9.1), with 5 glabrous lobes. *Seeds* 1.9 by 1.1 mm; hilum 1/4 as long as the perimeter. Cotyledons unknown.



Map 7. Distribution of *Geranium humboldtii* Spreng. (●) and *G. jaekelae* J.F. Macbr. (▲).

Distribution — Ecuador and N Peru.

Habitat & Phenology — Grassy and rocky slopes, or open wet boggy depressions in paramo. Altitude 3500–5000 m. Flowering: throughout the year.

Notes — *Geranium humboldtii* can be distinguished from all other species treated here in that the palmatisect leaves are white-sericeous above and glabrous beneath. All other 'sericeous' species belonging to sect. *Neoandina* have leaves with dense indumentum on both sides. *Geranium humboldtii* has sometimes been confused with *G. multipartitum* since both share deeply divided leaves. However, *G. multipartitum* differs from *G. humboldtii* in its leaves with ± scattered, subpatent hairs on both sides (sometimes glabrous).

The description of the seeds of *G. humboldtii* is preliminary since the available material is scarce and not well developed.

A sheet from Peru (Cajamarca, *Sánchez & Castillo 6449*) shows petals hairy on the adaxial surface (not glabrous) and staminal filaments lanceolate (not subulate). Otherwise, it is similar to other specimens of *G. humboldtii*.

9. Geranium jaekelae J.F. Macbr. — Fig. 20, Map 7

Geranium jaekelae J.F. Macbr. (1934) 7. — *Geranium minimum* R. Knuth (1906) 567, nom. illeg., non Cav. (1787). — Type: *Weberbauer 2623* (lectotype, here designated, G; isolectotype BRSL), Peru, Junín, La Oroya.

Herbs 0.8–1.3 cm tall. *Rootstock* 4–11 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.35–0.9 by 0.5–0.95 cm, polygonal in outline, cordate, palmatifid (divided for 0.63–0.71 of its length), glabrous or scattered hairy on both sides, with antrorse, eglandular cilia 0.2–0.3 mm long on the margin, not coriaceous, nerves not projected; segments 7, broadly lanceolate, 0.9–2 mm wide at the base, 1- (or 2-)lobed at the apex (ratio main-sinus length of the middle segment/middle-segment length = 0.18); petioles to 1.3 cm long, with antrorse, appressed, eglandular hairs 0.2–0.4 mm long; stipules

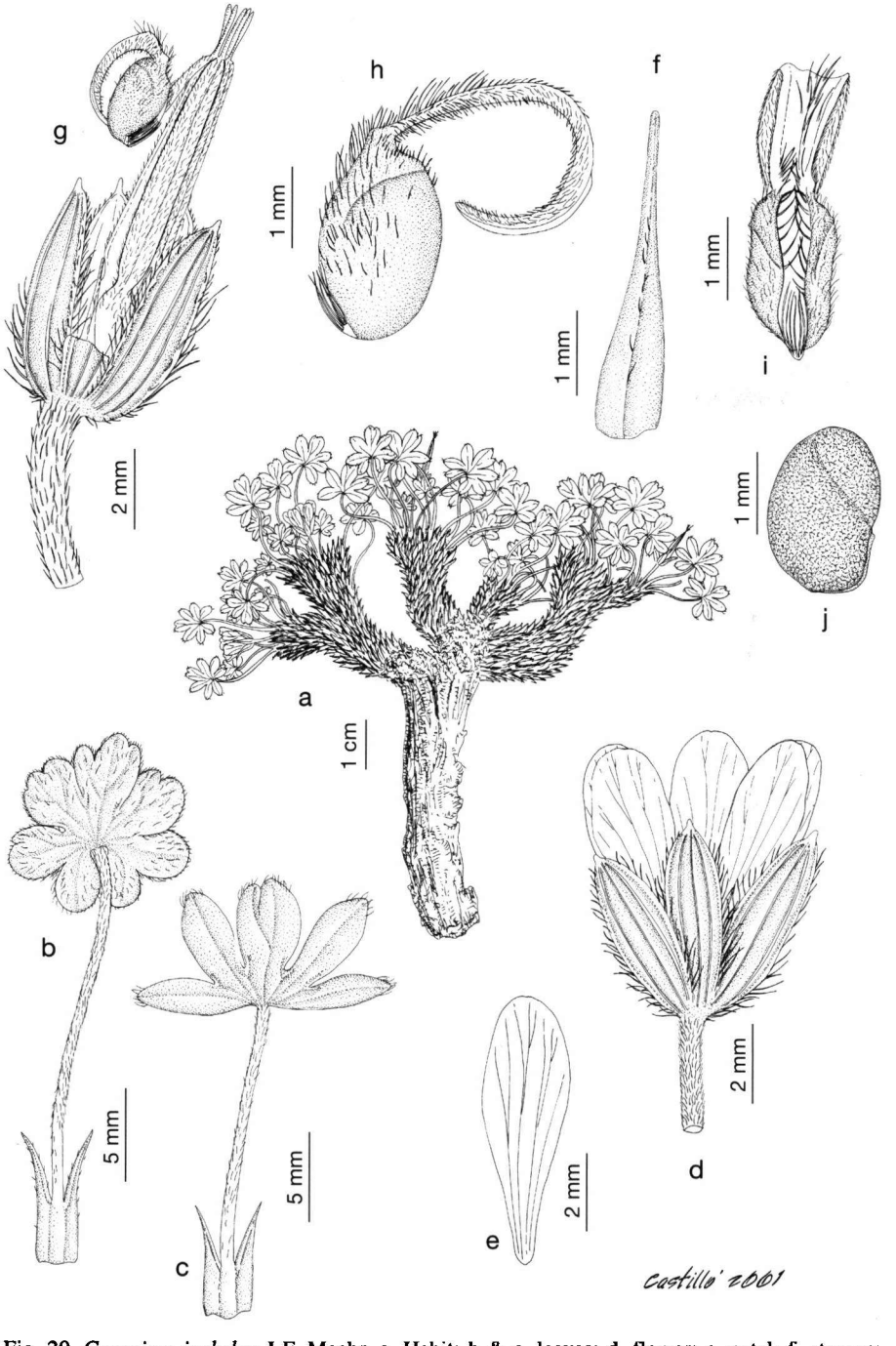


Fig. 20. *Geranium jaekelae* J.F. Macbr. a. Habit; b & c. leaves; d. flower; e. petal; f. stamen; g. fruit; h & i. mericarp; j. seed (a, c: *Weberbauer 2623*, G; b, d–j: *Asplund 11643*, S).

3–6 by 0.8–1 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.2–0.6 cm long, with antrorse, appressed, eglandular hairs 0.2–0.4 mm long; pedicel not overtopping the subtending leaf. *Sepals* 4–4.5 by 1.5 mm (ratio pedicel length/sepal length = 0.8), 3-nerved, mucronate (with mucro 0.3–0.4 mm long), with scarious margins 0.1 mm wide, with erect-patent, eglandular hairs 0.2–0.4 mm long on the abaxial side (patent hairs 0.8–1.2 mm long on the margin), glabrous adaxially. *Petals* 5 by 1.5–1.8 mm (ratio petal length/petal width = 2.7–3.3), entire, glabrous on both sides and margin, white. Filaments 2–2.2 mm long, not exserted, lanceolate, glabrous, or with few eglandular hairs 0.2–0.3 mm long on the abaxial side and margin; anthers 0.5–0.6 by 0.3 mm, purplish. Nectaries glabrous. Gynoecium 2 mm long, yellowish. *Fruit* 9–10 mm long; mericarps 2.2 by 1.3 mm, with antrorse, ± appressed, eglandular hairs 0.5–0.8 mm long; rostrum 7–8 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 0.9 mm long (ratio fruit length/stigmatic remains length = 10), with 5 hairy lobes. *Seeds* 1.6 by 1.1 mm; hilum 1/6 as long as the perimeter. Cotyledons unknown.

Distribution — C Peru.

Habitat & Phenology — On hard gravely grounds. Altitude 4300–4800 m. Flowering: June.

Note — *Geranium jaekelae* is a rare endemic to C Peru. It is distinguished from sympatric species by its small leaves, with usually entire segments, and a retrorsely hairy petiole. The original material (*Weberbauer 2623*) has glabrous leaves except for some antrorse cilia on the margin. The only other collection known (*Asplund 11643*) shows sparsely hairs on both sides, but matches it otherwise. More collections would help to clarify the degree of character variation within this species.

10. Geranium macbridei Aedo — Fig. 21, Map 8

Geranium macbridei Aedo (2001b) 358. — Type: *Macbride 3296* (holo F; iso G, US, W), Peru, Pasco, Chasqui.

Herbs 2.5–7 cm tall. *Rootstock* 5–8 mm diam., ± vertical; with short vegetative stems. *Leaf* lamina 1–2.1 by 1.1–2.1 cm, polygonal in outline, cordate, palmatisect, pilose, with ± scattered antrorse, appressed eglandular hairs (on margin and nerves) on both sides, not coriaceous, nerves not projected; segments 7, obtriangular with linear-lanceolate lobes, 1–1.2 mm wide at the base, 3-lobed in distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.54–0.65); petioles to 5 cm long, with retrorse, appressed, eglandular hairs 0.2–0.4 mm long; stipules 9–12 by 1–1.5 mm, lanceolate, papery, reddish, glabrous or with scattered eglandular hairs. Peduncles absent; pedicels 0.9–2.1 cm long, with retrorse, appressed, eglandular hairs 0.2–0.4 mm long; pedicel not overtopping the subtending leaf. *Sepals* 6.5–6.7 by 2–2.2 mm (ratio pedicel length/sepal length = 1.3–3.1), 3-nerved, mucronate (with mucro 0.4–0.6 mm long), with scarious margins 0.2 mm wide, glabrous on the abaxial side, with scattered eglandular hairs 0.2–0.4 mm long on the adaxial side, and erect-patent, eglandular hairs 0.4–0.6 mm long on the margin. *Petals* 9.5–13 by 4 mm (ratio petal length/petal width = 2.3–3.25), entire, glabrous, purplish, sometimes white. Filaments 4 mm long, not exserted, lanceolate with an abruptly narrowed apex, with eglandular hairs 0.2–0.5 mm long on the abaxial side and margin; anthers 1 by 0.7 mm, purplish.

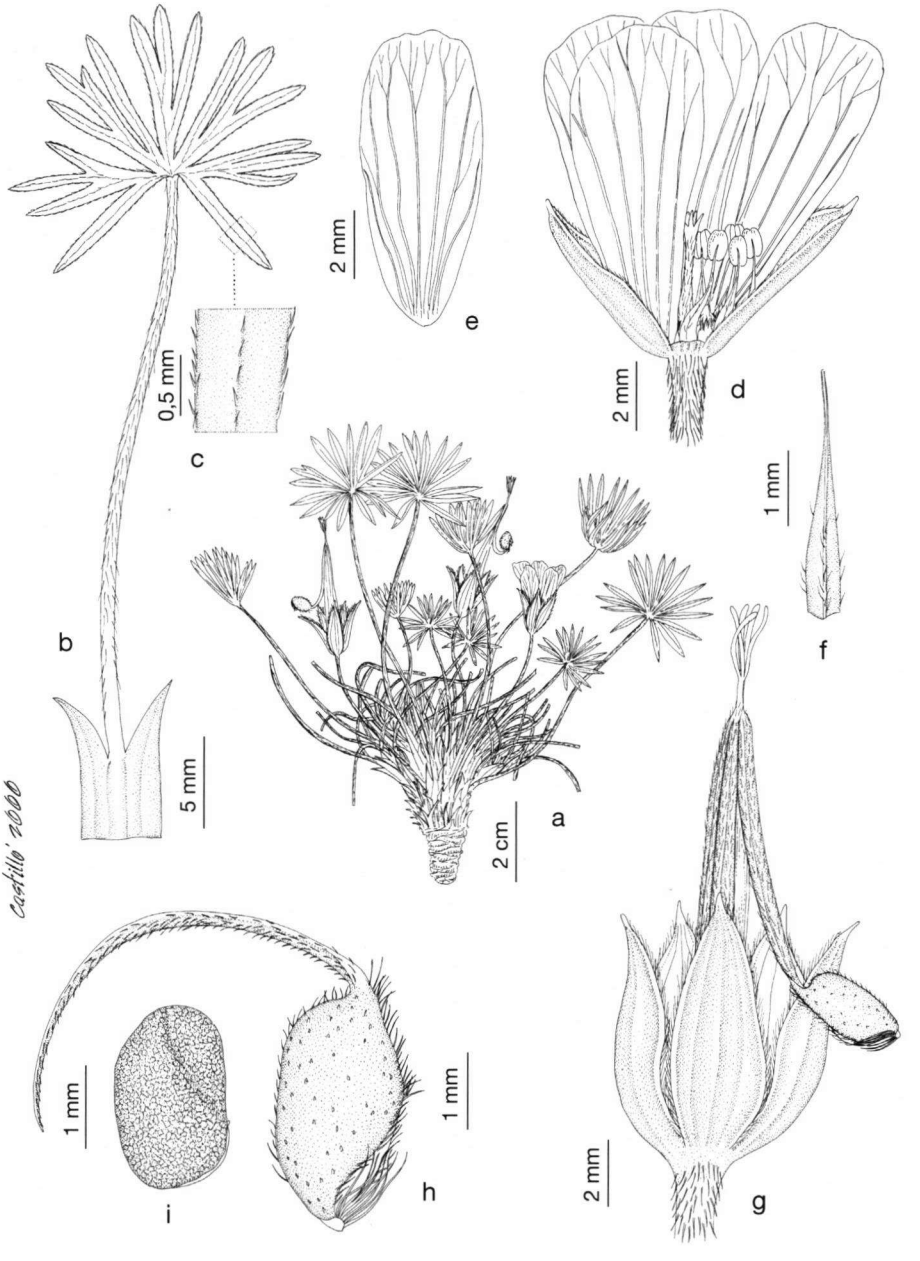
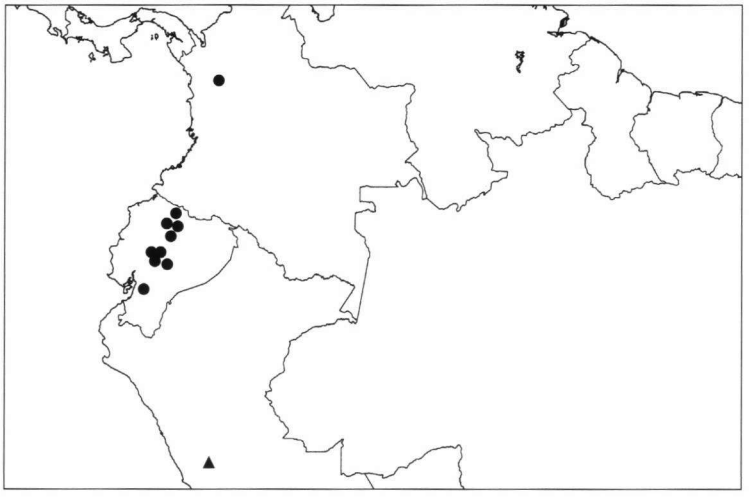


Fig. 21. *Geranium macbridei* Aedo. a. Fruiting branch; b. leaf; c. leaf detail; d. flower; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a–c: *Macbride 3296*, F; d–f: *Macbride 3296*, US; g–i: *Macbride 3296*, W).



Map 8. Distribution of *Geranium macbridei* Aedo (▲) and *G. maniculatum* H.E. Moore (●).

Nectaries with a tuft of hairs at the top, dorsally glabrous. Gynoecium 4–4.5 mm long, purplish. *Fruit* 12–13 mm long; mericarps 2.4 by 1.2 mm, with scattered antrorse, eglandular hairs 0.2–0.5 mm long on the margins and on the dorsal nerve; rostrum 11 mm long, with a narrowed apex 1 mm long, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 2–2.5 mm long (ratio fruit length/stigmatic remains length = 5.2–6.25), with 5 glabrous lobes. *Seeds* 1.7 by 1.3 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — C Peru.

Habitat & Phenology — In wet grassy stream slopes. Altitude unknown. Flowering unknown.

Note — *Geranium macbridei* is only known from the type, a flowering and fruiting collection from Peru, and is most similar to *G. multipartitum*. These two differ from all other species in sect. *Neoandina* by their palmatisect and not sericeous leaves. In *G. macbridei* the laminas have scattered antrorse, appressed hairs (on margin and nerves) on both sides, whereas in *G. multipartitum* they have scattered subpatent hairs on both sides (rarely the leaves are glabrous). In *G. macbridei* the petioles and pedicels have retrorse appressed hairs, 0.2–0.4 mm long, whereas in *G. multipartitum* they have patent hairs 0.2–1 mm long (rarely glabrous). *Geranium macbridei* is also easily distinguished from *G. multipartitum* by its much longer petals, hairy nectaries, and fruit with a narrowed apex.

11. **Geranium maniculatum** H.E. Moore — Fig. 22, Map 8

Geranium maniculatum H.E. Moore (1951) 254, f. 102. — Type: *Steyermark 53159* (holo BH; iso F, NY), Ecuador, Azuay, páramos in the vicinity of Toreador, between Molleturo and Quinoas, 15 June 1943.

Herbs 2–4 cm tall. *Rootstock* 2–4 mm diam., vertical; with short vegetative stems. *Leaf* lamina 0.6–1.28 by 0.62–1.6 cm, polygonal to obtriangular in outline, rounded

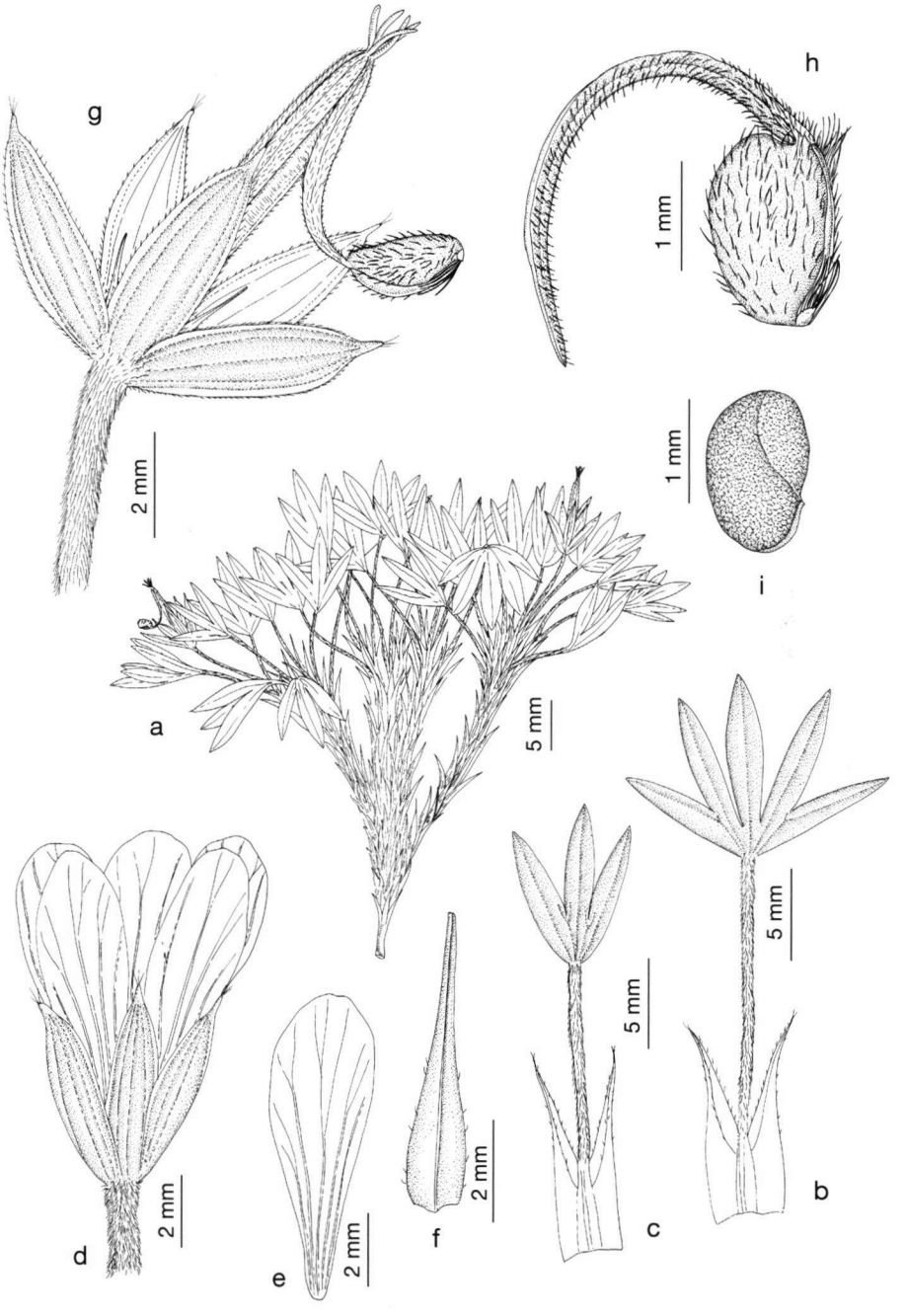


Fig. 22. *Geranium maniculatum* H.E. Moore. a. Habit; b & c. leaves; d. flower; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a–f: *Harling 4393*, S; g–i: *Weber & Gradstein s.n.*, U).

to cuneate, digitate with lateral segments upward (divided for 0.66–0.8 of its length), glabrous on both sides, sometimes with antrorse, eglandular cilia 0.1–0.2 mm long on the margin, each segment ending in 1–3 bristles 0.3–0.6 mm long, not coriaceous, nerves not projected; segments (3–)5, entire, lanceolate, 1–1.7 mm wide at the base; petioles to 2.4 cm long, with retrorse, appressed, eglandular hairs 0.2–0.4 mm long; stipules 6–10 by 0.8–1.1 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.2–0.7 mm long. Peduncles absent; pedicels 0.5–1.3 cm long, with retrorse, appressed, eglandular hairs 0.3–0.4 mm long; pedicel not overtopping the subtending leaf. *Sepals* 5–7 by 1.7–2.3 mm (ratio pedicel length/sepal length = 0.8–1.8), 3-nerved, mucronate (with mucro 0.2–0.5 mm long), with scarious margins 0.1 mm wide, glabrous or with scattered erect-patent, eglandular hairs 0.2–0.3 mm long on the base of the abaxial side and margin, glabrous adaxially, ending in 1–3 bristles 0.4–0.7 mm long. *Petals* 8.1–12 by 2.5–3.5 mm (ratio petal length/petal width = 2.7–3.4), entire, glabrous on both sides and margin (sometimes ciliate on the basal margin), purplish, sometimes white. Filaments 3–4 mm long, not exserted, lanceolate, glabrous, or with few eglandular hairs 0.2–0.3 mm long on the abaxial side and margin; anthers 0.6 by 0.5 mm, yellowish. Nectaries glabrous. Gynoecium 4 mm long, yellowish. *Fruit* 7.2–9.2 mm long; mericarps 2–2.2 by 1–1.1 mm, glabrous or with antrorse, ± appressed, eglandular hairs 0.2 mm long; rostrum 4.3–5.6 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 1–1.2 mm long (ratio fruit length/stigmatic remains length = 7.2–8), with 5 glabrous lobes. *Seeds* 1.6 by 0.8 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — Colombia and Ecuador.

Habitat & Phenology — Boggy depressions in bunch grass paramo or margins of small lakes. Altitude 3300–5000 m. Flowering: throughout the year.

Note — *Geranium maniculatum* is characterised by the digitate leaf blade with usually five segments. The lateral segments are directed upward and the central segment is entire, lanceolate. The leaves are usually glabrous but some specimens have short antrorse hairs on the margin. *Geranium sibbaldioides* and *G. rhomboidale* are two species morphologically alike to *G. maniculatum*. From *G. sibbaldioides* subsp. *sibbaldioides* it may be discriminated by some leaf features: a) lateral segment directed upward; b) middle segment narrowly lanceolate; and c) margin usually glabrous. *Geranium sibbaldioides* subsp. *elongatum* is easily recognisable by its hairy leaves, while *G. sibbaldioides* subsp. *beckianum* has a middle segment that is 3-lobed at the apex. In *G. maniculatum* the fruit and the sepal mucro are shorter than in *G. rhomboidale*. Other leaf features to distinguish them are reported in the notes of *G. rhomboidale*.

12. Geranium multipartitum Benth. — Fig. 23, Map 9

Geranium multipartitum Benth. (1845) 166. — Type: *Hartweg s.n.* (lectotype, designated by Knuth 1912: 86, K), Ecuador, near the hacienda de Antisana.

Geranium multipartitum var. *glabrescens* Hieron. ex R. Knuth (1906) 566. — Type: *Stuebel 185i* (holo B†), Ecuador, Antisana, Estancia.

Geranium multipartitum var. *velutinum* R. Knuth (1906) 566. — Type: *Weberbauer 3990* (no original material located), Peru, Cajamarca, am passe Coymolache oberhalb Hualgayoc.

Geranium heinrichsae R. Knuth (1936) 216. — Type: *Heinrichs s.n.* (holo B†), Ecuador, Páramo del Angel, La Parada, 1934.

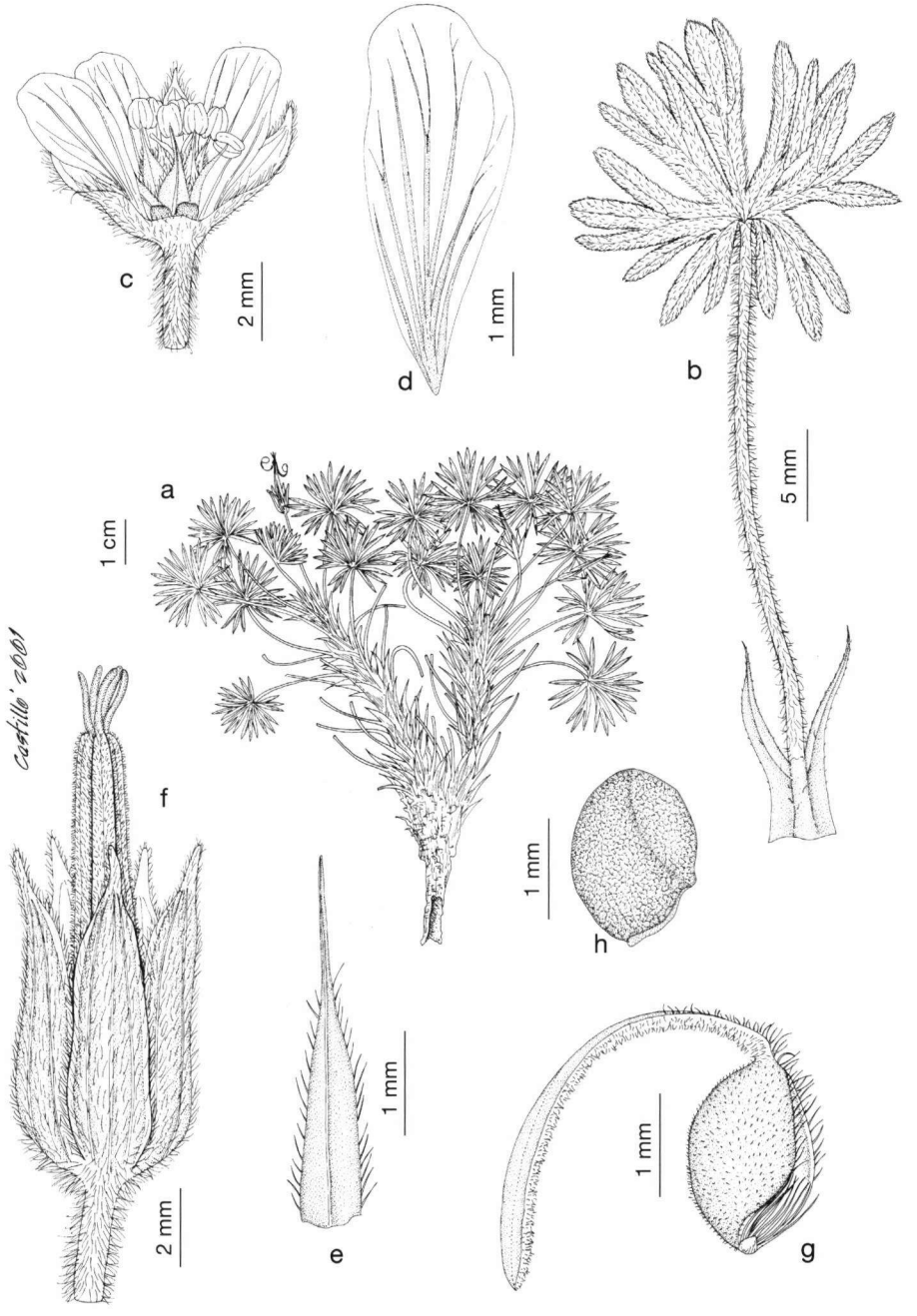
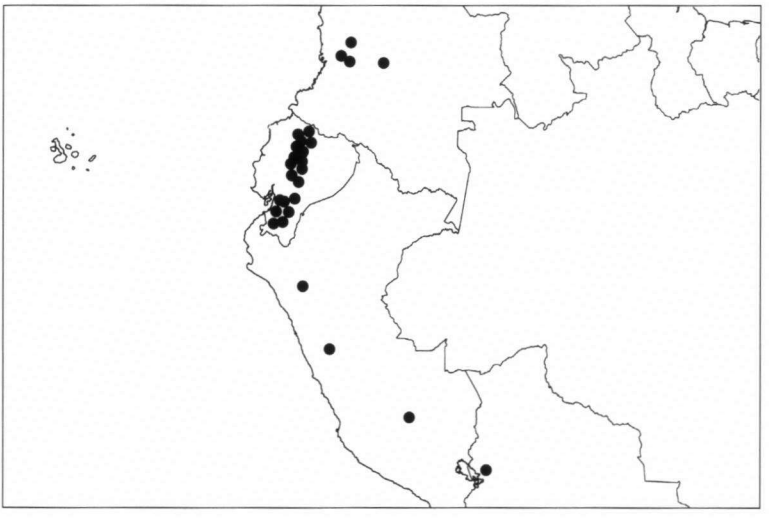


Fig. 23. *Geranium multipartitum* Benth. a. Fruiting branch; b. leaf; c. flower; d. petal; e. stamen; f. fruit; g. mericarp; h. seed (a & b: *Øllgaard et al. 34087*, LD; c & d: *Holm-Nielsen & León 65*, C; e–h: *Barclay & Juajibioy 8008*, COL).

Herbs 2–7(–16) cm tall. *Rootstock* 4–8 mm diam., ± horizontal; sometimes with short vegetative stems. *Leaf* lamina 0.7–1.7(–2.7) by 0.8–1.8(–3) cm, polygonal in outline, cordate, palmatisect, pilose, with ± scattered subpatent, eglandular hairs on both sides (rarely glabrous), each segment usually ending in 1–3 bristles 0.5 mm long, not coriaceous, nerves not projected; segments 9, rhombic with linear-lanceolate lobes, 0.5–1 mm wide at the base, 3–5-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.5–0.68); petioles to 8 cm long, with patent, eglandular hairs 0.2–1 mm long, sometimes glabrous; stipules 6–8 by 1–1.5 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.5 mm long. Peduncles absent; pedicels 0.5–1.4 cm long, with patent, eglandular hairs 0.2–0.6 mm long; pedicel not overtopping the subtending leaf. *Sepals* 5–8 by 1.2–1.7 mm (ratio pedicel length/sepal length = 1–1.75), 3-nerved, mucronate (with mucro 0.5–0.9 mm long), with scarious margins 0.2 mm wide, with ± patent, eglandular hairs 0.2–1.5 mm long on both sides, sometimes patent, eglandular hairs 1–2.2 mm long on the margin. *Petals* 5.2–7.4 by 2.2–2.9 mm (ratio petal length/petal width = 2.3–2.5), entire, glabrous, purplish, sometimes white. Filaments 2.5 mm long, not exserted, lanceolate with an abruptly narrowed apex, glabrous on both sides, ciliate on the proximal half, with hairs 0.2–0.3 mm long; anthers 0.6 by 0.5 mm, yellowish. Nectaries glabrous. Gynoecium 3–3.5 mm long, yellowish. *Fruit* 10–11 mm long; mericarps 2.2–2.5 by 1.2 mm, with ± patent, eglandular hairs 0.1–0.2 mm long on the surface and eglandular hairs 0.4–0.6 mm long on the margin; rostrum 6–6.5 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 1.5–2 mm long (ratio fruit length/stigmatic remains length = 5.25–6.6), with 5 glabrous lobes. *Seeds* 1.7–2 by 1.1–1.3 mm; hilum 1/4 as long as the perimeter. Cotyledons entire.

Distribution — Colombia, Ecuador, Peru and Bolivia.



Map 9. Distribution of *Geranium multipartitum* Benth.

Habitat & Phenology — In upper montane forest or in semihumid grass paramo dominated by cushion plants. Altitude 1680–4700 m. Flowering: throughout the year.

Notes — *Geranium multipartitum* can be distinguished from all other species treated here by its palmatisect leaves with 9 segments and with ± scattered eglandular, subpatent hairs on both sides (sometimes glabrous). It also has petioles and pedicels with patent, eglandular hairs. It has been frequently confused with *G. humboldtii*, a species characterised by its glabrous pedicels, and by its palmatisect leaves with 7 segments, sericeous above and glabrous beneath.

Two sheets from Colombia (Dep. del Valle, *Cuatrecasas 20083, 20550*) have glabrous pedicels. Otherwise they are similar to other specimens of *G. multipartitum*. A specimen from Ecuador (Prov. Pichinca, *Barclay & Juajibioy 8894*) shows leaves densely hairy above somewhat as *G. humboldtii*. However it has laminas with 9 segments that fit with *G. multipartitum*.

Geranium heinrichsae was described from *Heinrichs s.n.* (B), which was destroyed during the Second World War. Unfortunately, no duplicate of this collection has been found. Jørgensen & León-Yánez (1999: 492) considered it as synonym of *G. multipartitum*. This view seems suitable after examining the original description (Knuth, 1936: 216).

13. **Geranium nivale** R. Knuth — Fig. 24, Map 10

Geranium nivale R. Knuth (1906) 563. — Type: *Weberbauer 2533* (lectotype, here designated, BRSL), Peru, Junín, Tarma, La Oroya.

Herbs 1–3 cm tall. *Rootstock* 5–7 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.9–1.2 by 1.1–1.4 cm, polygonal in outline, cordate, palmatifid (divided for 0.8–0.86 of its length), sericeous on both sides, not coriaceous, nerves not projected; segments 5(–7), entire, broadly obovate, 0.7–1.5 mm wide at the base; petioles to 1.8 cm long, sericeous, with patent to retrorse, eglandular hairs 0.2–0.7 mm long; stipules 8–12 by 2 mm, lanceolate, papery, reddish, sericeous on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.7–2.2 cm long, sericeous, with patent, eglandular hairs 0.4–0.7 mm long; pedicel not overtopping the subtending leaf. *Sepals* 6.7–8.2 by 2–3 mm (ratio pedicel length/sepal length = 1–2.7), 3-nerved, mucronate (with mucro 0.2 mm long), with scarious margins 0.2 mm wide, sericeous with erect-patent, eglandular hairs 0.3–0.7 mm long on the abaxial side and margin, sparsely hairy adaxially. *Petals* 13–18 by 5–5.5 mm (ratio petal length/petal width = 2.3–3.6), entire, hairy on the base of the abaxial side and margin, glabrous adaxially, white. Filaments 6–6.5 mm long, not exserted, lanceolate, with eglandular hairs 0.2–0.5 mm long on the abaxial side and margin; anthers 1.1 by 0.6 mm, yellowish. Nectaries glabrous. Gynoecium 7 mm long, yellowish. *Fruit* 12–13 mm long; mericarps 2.5 by 1.5 mm, sericeous, with erect-patent, eglandular hairs 0.4–0.6 mm long; rostrum 9.5–10 mm long, with a narrowed apex 1.2–1.5 mm long, sericeous, with erect-patent, eglandular hairs 0.4–0.6 mm long; stigmatic remains 1 mm long (ratio fruit length/stigmatic remains length = 12–13), with 5 hairy lobes. *Seeds* unknown. Cotyledons unknown.

Distribution — C and S Peru.

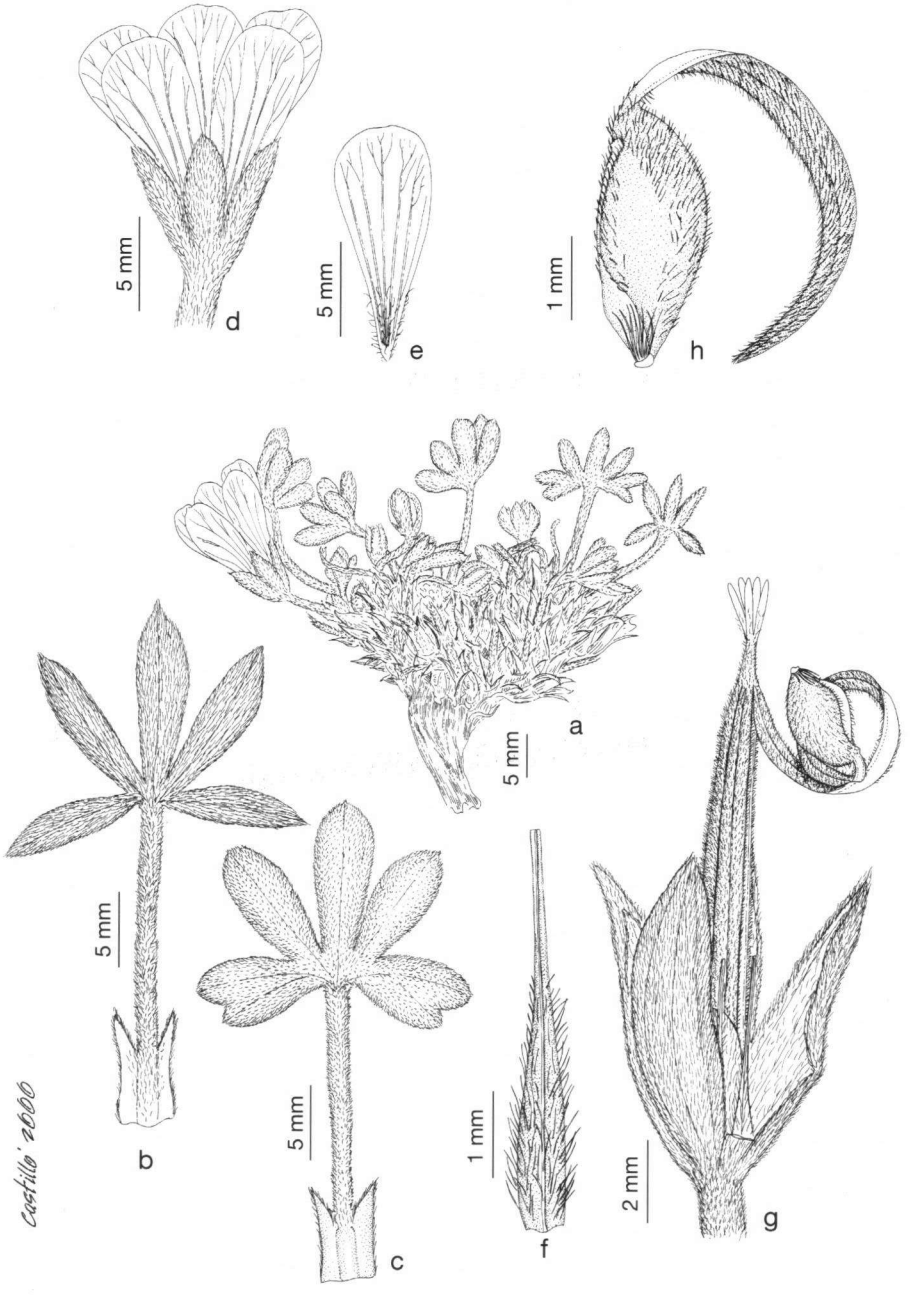
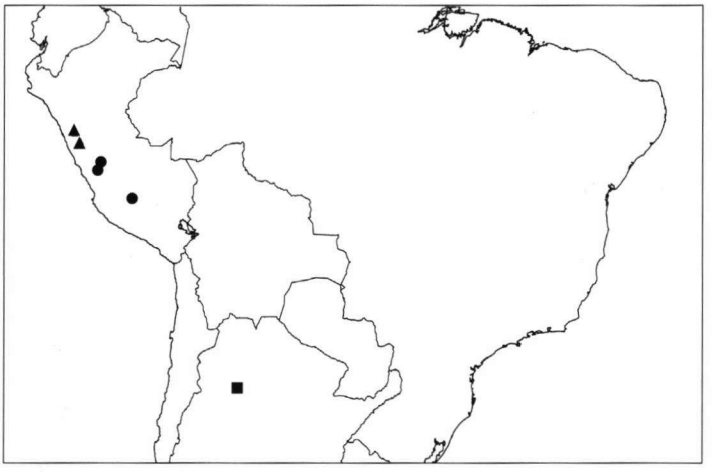


Fig. 24. *Geranium nivale* R. Knuth. a. Habit; b. leaf (abaxial side); c. leaf (adaxial side); d. flower; e. petal; f. stamen; g. fruit; h. mericarp (a, d–h: *Isern 569*, F; b: *Weberbauer 2533*, BRSL; c: *Kalenborn & Kalenborn 88*, CAS).



Map 10. Distribution of *Geranium nivale* R. Knuth (●), *G. pavonianum* Briq. (▲), and *G. planum* Halloy (■).

Habitat & Phenology — At moist grounds in puna. Altitude 4000 m. Flowering: September to February.

Notes — *Geranium nivale* shares palmatifid sericeous leaves with *G. ruizii*, *G. planum*, and *G. crassipes*. However, *G. nivale* exhibits two unique features among these species: a rostrum with a narrowed apex and longer petals. *Geranium nivale* has longer leaves than *G. ruizii*, but in the former they are with lanceolate entire segments whereas the leaves of the latter are with obtriangular segments, 3-lobed at the apex. *Geranium planum* and *G. crassipes* are also species with entire segments, but they have short leaf laminas (to 0.7 cm long) versus long leaf laminas of *G. nivale* (0.9–1.2 cm long).

Among the scarcely available material of *G. nivale*, no collection had mature seeds useful for description.

14. Geranium paludosum R. Knuth — Fig. 25, Map 6

Geranium paludosum R. Knuth (1930a) 2. — Type: *Cuatrecasas & Romero 24578* (neotype, here designated, COL), Colombia, Magdalena, Sierra Nevada de Santa Marta, Siminchuená-Adurimeira, valley descending southwestern from Picos Reina and Ojeda, around laguna Naboba, Laguna Mamito and Laguna Mamo, 3 October 1959.

Herbs 2–6 cm tall. *Rootstock* 3–5 mm diam., ± vertical; sometimes with short vegetative stems. *Leaf* lamina 0.8–1.2 by 0.9–1.85 cm, polygonal in outline, cordate, palmatifid (divided for 0.7–0.81 of its length), glabrous on both sides, with antrorse, eglandular cilia 0.1–0.2 mm long on the margin, not coriaceous, nerves not projected; segments 7, obtriangular, with linear-lanceolate lobe, 0.8–1.7 mm wide at the base, 3-lobed at the apex (ratio main-sinus length of the middle segment/middle-segment length = 0.16–0.27); petioles to 3 cm long, with retrorse, appressed, eglandular hairs 0.1 mm long; stipules 5–8.5 by 1–2 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.2–0.3

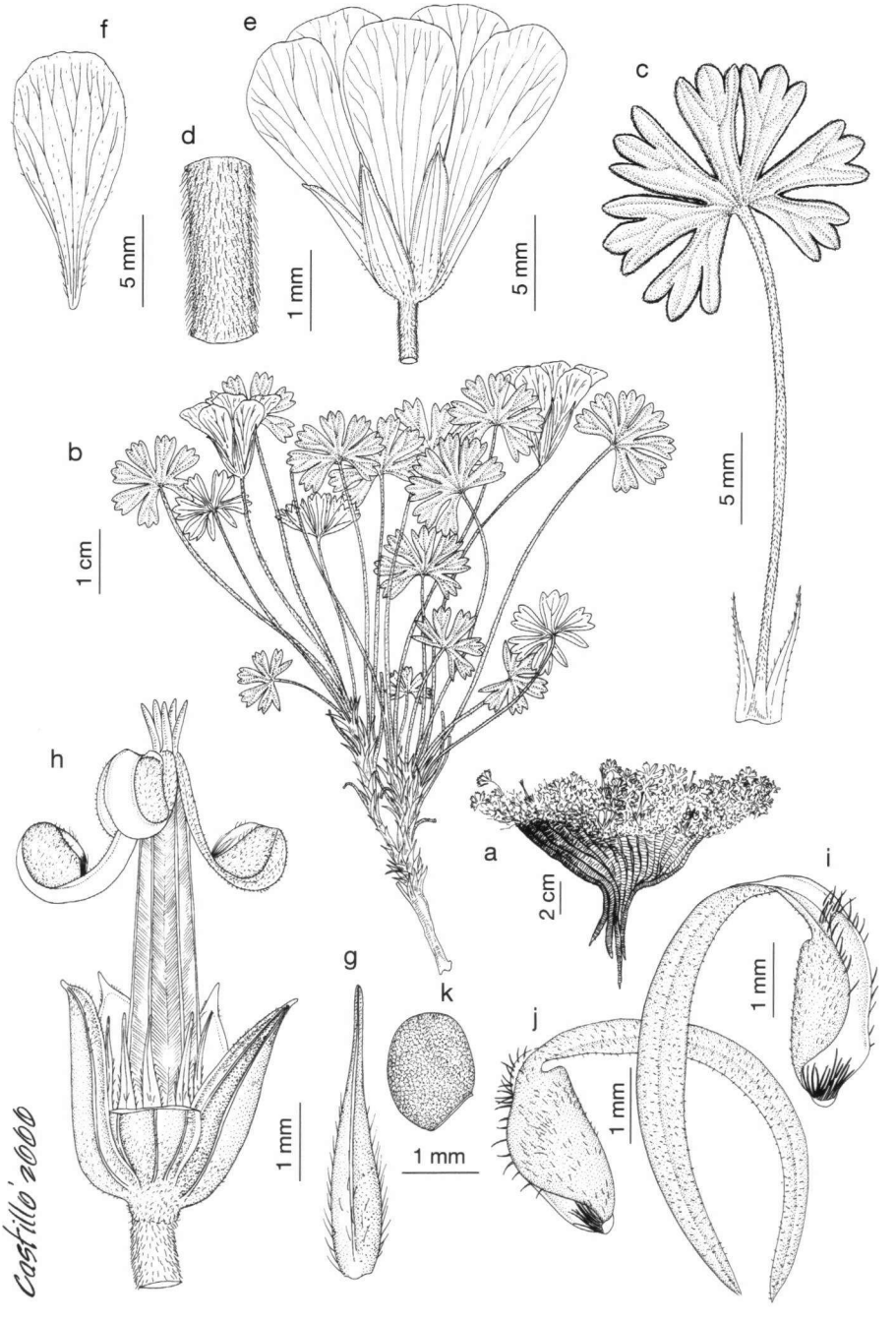


Fig. 25. *Geranium paludosum* R. Knuth. a. Habit; b. flowering branch; c. leaf; d. peduncle e. flower; f. petal; g. stamen; h. fruit; i & j. mericarps (a, d, g–k: *Cuatrecasas 24578*, COL; b, c e, f: *Rangel 1881*, COL).

mm long. Peduncles absent; pedicels 0.8–3.6 cm long, with retrorse, appressed, eglandular hairs 0.1–0.2 mm long; pedicel usually overtopping the subtending leaf. *Sepals* 5.5–7.5 by 1.5–2.2 mm (ratio pedicel length/sepal length = 1.1–4.8), 3-nerved, mucronate (with mucro 0.3–0.7 mm long), with scarious margins 0.1–0.2 mm wide, with erect-patent, eglandular hairs 0.2–0.4 mm long on the abaxial side and margin, glabrous adaxially. *Petals* 10.5–15.5 by 4.2–7 mm (ratio petal length/petal width = 2–3), entire, hairy on both sides (mainly on the base of the adaxial side), ciliate on the margin, purplish. Filaments 3.5–4 mm long, not exserted, lanceolate, with eglandular hairs 0.2 mm long on the abaxial side and margin; anthers 0.8–1 by 0.6–0.7 mm, yellowish. Nectaries glabrous. Gynoecium 3.5 mm long, yellowish. *Fruit* 11–12 mm long; mericarps 2 by 0.7–1 mm, with antrorse, ± appressed, eglandular hairs 0.1 mm long; rostrum 8.5–9 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 0.9–1 mm long (ratio fruit length/stigmatic remains length = 12–13), with 5 glabrous lobes. *Seeds* 2 by 1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — Colombia (Sierra Nevada de Santa Marta).

Habitat & Phenology — In paramo or in upper montane forest. Altitude 3200–4500 m. Flowering: May to December.

Notes — *Geranium paludosum* is an endemic of Sierra Nevada de Santa Marta (N Colombia) readily recognised by its small and shallowly divided leaf laminas. It also has sepals with a short mucro and long petals that are hairy on the base. It is interesting to note that on herbarium specimens the leaves become almost black.

Knuth (1930a: 2) designated as type of this species name a collection from Sierra Nevada de Santa Marta (*Schultze 1314*) kept at the Berlin herbarium. Since this collection was destroyed during the Second World War and no duplicate has been located, a neotype should be selected. Thus I have neotypified this name with a specimen collected by *Cuatrecasas & Romero* in these mountains.

15. Geranium pavonianum Briq. — Fig. 26, Map 10

Geranium pavonianum Briq. (1908) 183. — Type: *Pavon 110* (lectotype, designated by Knuth 1912: 83, G; isolectotype MA), Peru, without locality.

Herbs 1–2 cm tall. *Rootstock* 4–10 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.5–1.1 by 0.7–1.2 cm, polygonal in outline, cordate, palmatifid (divided for 0.5–0.78 of its length), densely hairy on both sides, not coriaceous, nerves not projected; segments 7, broadly obovate, 1.3–2.2 mm wide at the base, 1(–3)-lobed at the apex (ratio main-sinus length of the middle segment/middle-segment length = 0.15–0.21); petioles to 1.5 cm long, with patent to retrorse, eglandular hairs 0.2–0.3 mm long; stipules 3–4 by 1 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.5–2.2 cm long, with patent to retrorse, eglandular hairs 0.2–0.3 mm long; pedicel usually not overtopping the subtending leaf. *Sepals* 3.5–6 by 1.8–2 mm (ratio pedicel length/sepal length = 1.4–5.2), 3-nerved, mucronate (with mucro 0.5–0.8 mm long), with scarious margins 0.1 mm wide, densely hairy, with erect-patent, eglandular hairs 0.2–0.5 mm long on the abaxial side and margin, glabrous adaxially. *Petals* 9 by 3.5 mm (ratio petal length/petal width = 2.57), entire, glabrous on both sides and margin,

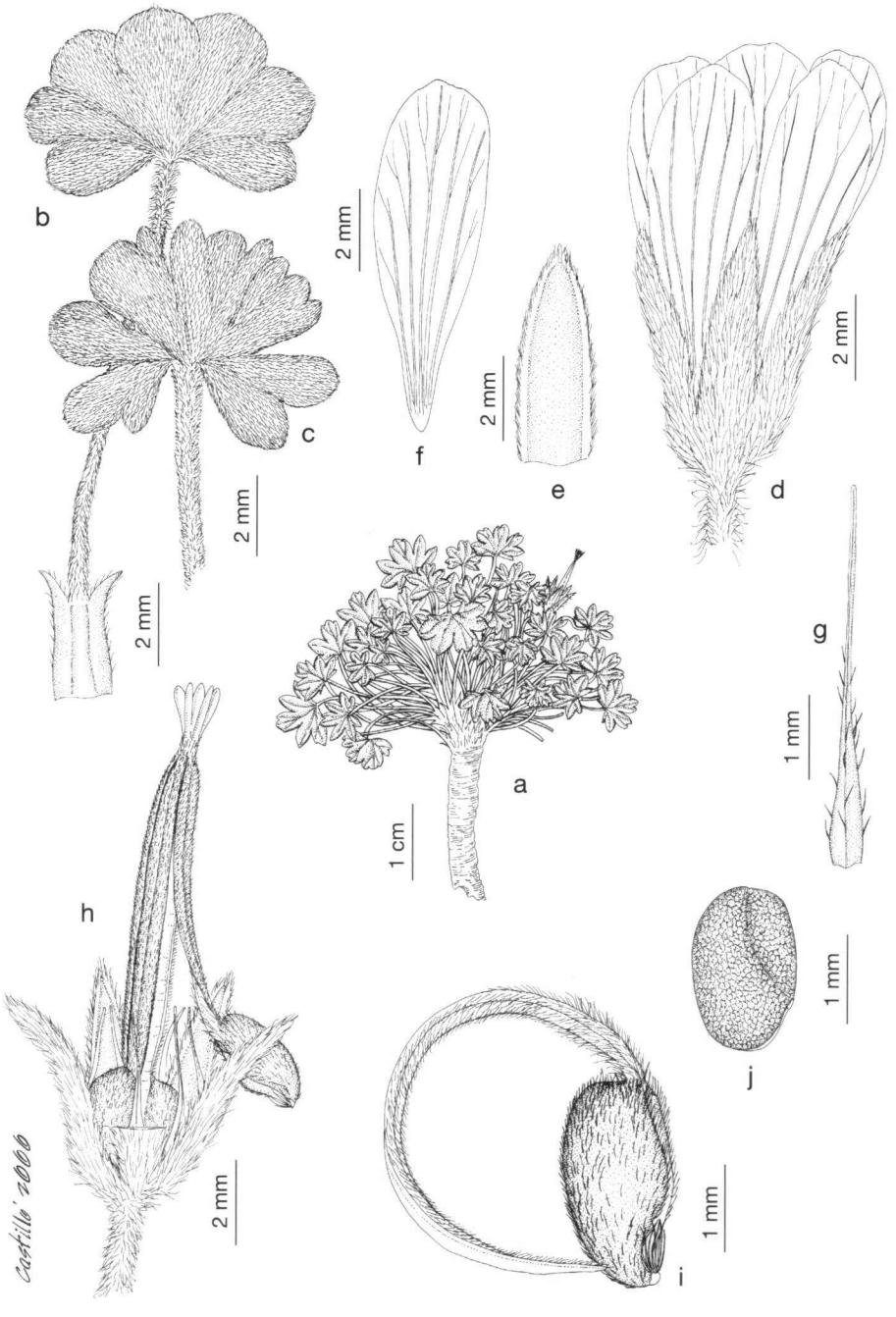


Fig. 26. *Geranium pavonianum* Briq. a. Habit; b & c. leaf; d. flower; e. sepal; f. petal; g. stamen; h. fruit; i. mericarp; j. seed (a, g–j: *Pavón 110*, G; b: *Smith et al. 9749*, F; c: *Smith et al. 9749*, MO; d–f: *Smith et al. 12332*, MO).

white. Filaments 2–3 mm long, not exserted, lanceolate, with eglandular hairs 0.2 mm long on the abaxial side and margin; anthers 0.5–0.7 by 0.5 mm, yellowish. Nectaries glabrous. Gynoecium 3 mm long, yellowish. *Fruit* 11–12 mm long; mericarps 3 by 1.4 mm, with patent, eglandular hairs 0.1–0.2 mm long; rostrum 8–8.5 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1–0.2 mm long; stigmatic remains 1.3–1.5 mm long (ratio fruit length/stigmatic remains length = 7.3–9), with 5 glabrous lobes. *Seeds* 1.9–2 by 1.1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — C Peru.

Habitat & Phenology — Puna grassland dominated by *Calamagrostis* on granitic outcrops. Altitude 4200–4600 m. Flowering unknown.

Note — *Geranium pavonianum* is a rare species endemic to C Peru. It is characterised by its densely hairy (not sericeous) palmatifid leaves, with 7 broadly obovate segments, usually entire. One collection (*Smith et al. 9749*, MO) shows many leaves with segments that are 3-lobed at the apex, but matches *G. pavonianum* otherwise. *Geranium sibbaldioides* subsp. *elongatum* has some resemblance to *G. pavonianum*. Upon closer inspection, however, the difference between them becomes apparent, with sepals and stipules ending in bristles and longer fruits in *G. sibbaldioides* subsp. *elongatum* versus sepals and stipules without bristles and shorter fruits in *G. pavonianum*. In addition, the ranges of *G. pavonianum* and *G. sibbaldioides* subsp. *elongatum* are completely non-overlapping.

16. **Geranium planum** Halloy — Fig. 27, Map 10

Geranium planum Halloy (1998) 467, 470 f. 4. — Type: *Halloy 1722* (holo LIL n.v.), Argentina, Tucumán, Cumbres Calchaquíes, between Cerro Isabel and Cerro Adriana, 5 March 1979.

Herbs 1 cm tall. *Rootstock* 9–20 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.2–0.5(–0.6) by 3.7–6.1 cm, orbicular in outline, cordate, palmatifid (divided for 0.68–0.72 of its length), sericeous on both sides, not coriaceous, nerves not projected; segments 5, entire, broadly lanceolate, 0.6–1 mm wide at the base; petioles to 0.6 cm long, sericeous, with antrorse, appressed, eglandular hairs 0.2–0.3 mm long; stipules 1.2–5 by 0.3–2 mm, lanceolate, papery, reddish, sericeous on both sides. Peduncles absent; pedicels 0.2–0.5 cm long, sericeous, with antrorse, appressed, eglandular hairs 0.1–0.2 mm long; pedicel not overtopping the subtending leaf. *Sepals* 4–4.5 by 1.6–2 mm (ratio pedicel length/sepal length = 0.5–1.2), 3–5-nerved, not mucronate, with scarious margins 0.2–0.3 mm wide, sericeous with erect-patent, eglandular hairs 0.2–0.3 mm long on the abaxial side and margin, glabrous adaxially. *Petals* unknown to us, white according to Halloy. Filaments 3–3.5 mm long, not exserted, lanceolate with an abruptly narrowed apex, with eglandular hairs 0.1–0.2 mm long on the abaxial side and margin; anthers unknown. Nectaries glabrous. Gynoecium unknown. *Fruit* 8–8.5 mm long; mericarps 2.2–2.8 by 1.2–1.5 mm, with antrorse, ± appressed, eglandular hairs 0.1–0.2 mm long; rostrum 5–6 mm long, without a narrowed apex, sericeous, with antrorse, appressed, eglandular hairs 0.2 mm long; stigmatic remains 0.8 mm long (ratio fruit length/stigmatic remains length = 10), with 5 glabrous lobes. *Seeds* 1.8–2 by 1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

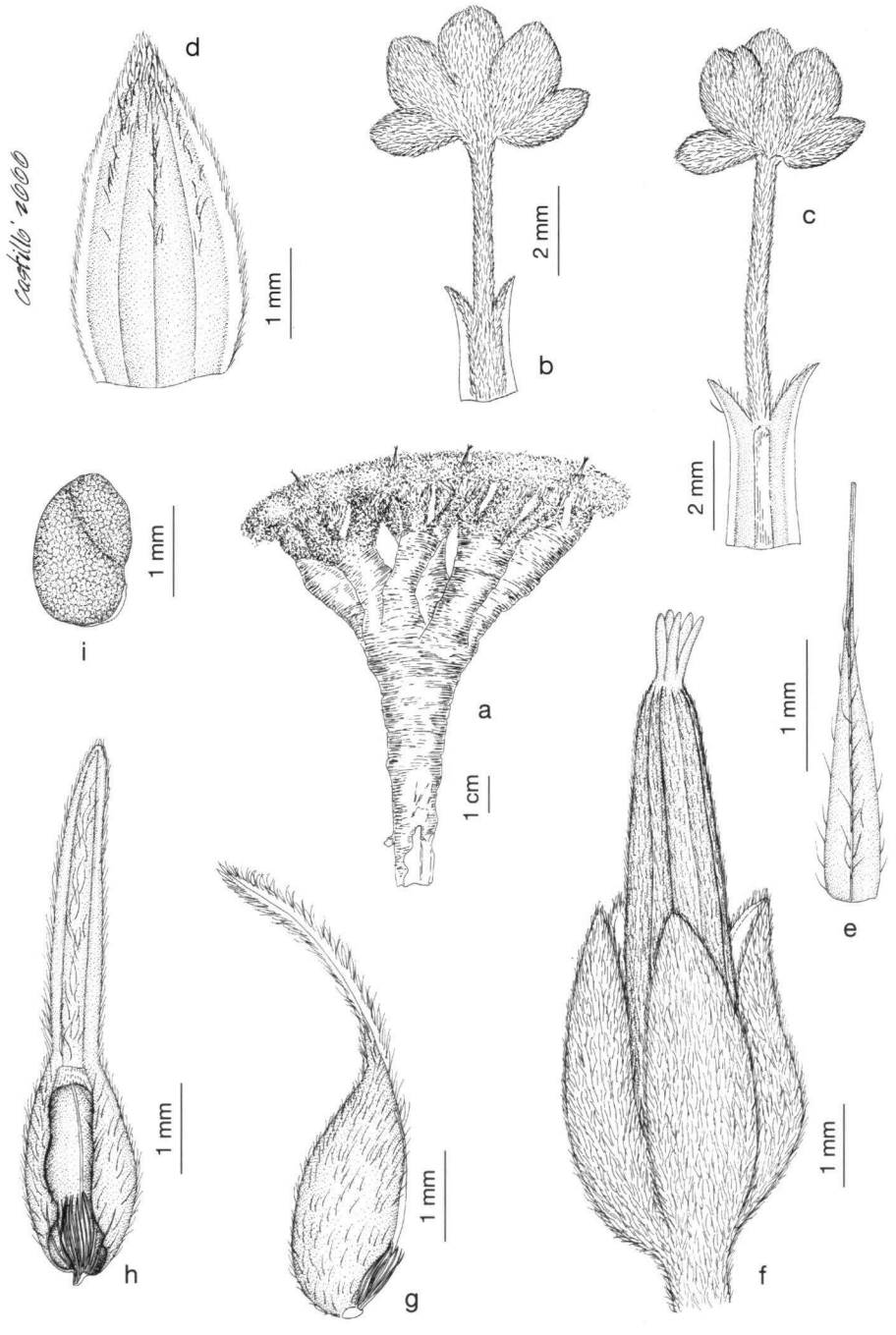


Fig. 27. *Geranium planum* Halloy. a. Habit; b. leaf (abaxial side); c. leaf (adaxial side); d. sepal e. stamen; f. fruit; g & h. mericarps; i. seed (all *Halloy 3362*, Halloy herbarium).

Distribution — N Argentina.

Habitat & Phenology — Gentle sloping or horizontal ground bordering the schistose peaks of Cerro Adriana and Cerro Isabel (Cumbres Calchaquíes range) in few separated populations. Altitude 4500–4600 m. Flowering: January.

Notes — *Geranium planum* is a recently described species endemic to N Argentina. It is the most southern record of sect. *Neoandina*. Among the *Geranium* sect. *Neoandina* species it resembles most closely *G. crassipes*, considering its palmatifid, short, sericeous leaves with entire segments. However, *G. planum* has leaves with 5 segments and sepals without a mucro versus leaves with 7 segments and sepals with mucro in *G. crassipes*. In addition, *G. crassipes* shows sepals with long, patent, hairs on the margin, which lack in *G. planum*.

We could not examine the type collection which was at LIL according to Halloy (1998). However, according A.M. Frías de Fernández (in litt.) no specimen of *G. planum* is kept at LIL. Fortunately, Dr. Halloy has provide me the only other collection of this species on which the present description is based. Some data of petals and androecium were not recorded since they are not present in the only available collection.

17. Geranium rhomboidale H.E. Moore — Fig. 28, Map 11

Geranium rhomboidale H.E. Moore (1951) 255, 256 f. 103. — Type: *Schultes 3238* (holo BH; iso GH), Colombia, Putumayo, Páramo de San Antonio, entre La Laguna de La Concha y el Valle de Sibundoy, 13 February 1942.

Herbs 2–4 cm tall. *Rootstock* 3–5 mm diam., ± vertical; with short vegetative stems. *Leaf* lamina 0.51–0.85(–1.2) by 0.55–1(–1.6) cm, polygonal to obtriangular in outline, rounded to cuneate, digitate with lateral segments upward (divided for 0.6–0.7 of its length), glabrous on both sides, with patent, eglandular cilia 0.4–0.8 mm long on the margin, each segment ending in 1 bristle 0.5–0.8 mm long, ± coriaceous, nerves not projected; segments 3(–5), obtriangular, with lanceolate lobes, 1.4–2.4 mm wide at the base, 3-lobed at the apex (ratio main-sinus length of the middle segment/middle-segment length = 0.11–0.26); petioles to 2.3 cm long, with retrorse to retrorse-appressed, eglandular hairs 0.2–0.5 mm long; stipules 10–13 by 1–1.5 mm, lanceolate (with a setaceous apex 4–5 mm long), papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.5–0.8 mm long. Peduncles absent; pedicels 0.6–1.2 cm long, with retrorse to retrorse-appressed, eglandular hairs 0.3–0.6 mm long; pedicel not overtopping the subtending leaf. *Sepals* 6–8 by 1.5–2.1 mm (ratio pedicel length/sepal length = 0.87–2), 3-nerved, mucronate (with mucro 0.5–0.9 mm long), with scarious margins 0.1 mm wide, with erect-patent, eglandular hairs 0.5–1 mm long on the margin (sometimes also on the base of the abaxial side), glabrous adaxially. *Petals* 8.5–10.6 by 2.2–3.2 mm (ratio petal length/petal width = 2.6–4.8), entire, glabrous, purplish. Filaments 2.5–3.5 mm long, not exserted, lanceolate, glabrous; anthers 0.6–0.7 by 0.5 mm, yellowish. Nectaries glabrous. Gynoecium 3–3.5 mm long, yellowish. *Fruit* 9–11 mm long; mericarps 1.6–2.2 by 1–1.2 mm, glabrous or with antrorse, ± appressed, eglandular hairs 0.1–0.2 mm long; rostrum 5.5–8 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 0.7–1.2 mm long (ratio fruit length/stigmatic remains length = 7.5–15.7), with 5 glabrous lobes. *Seeds* 1.4–1.5 by 0.8–0.9 mm; hilum 1/5 as long as the perimeter. Cotyledons entire.

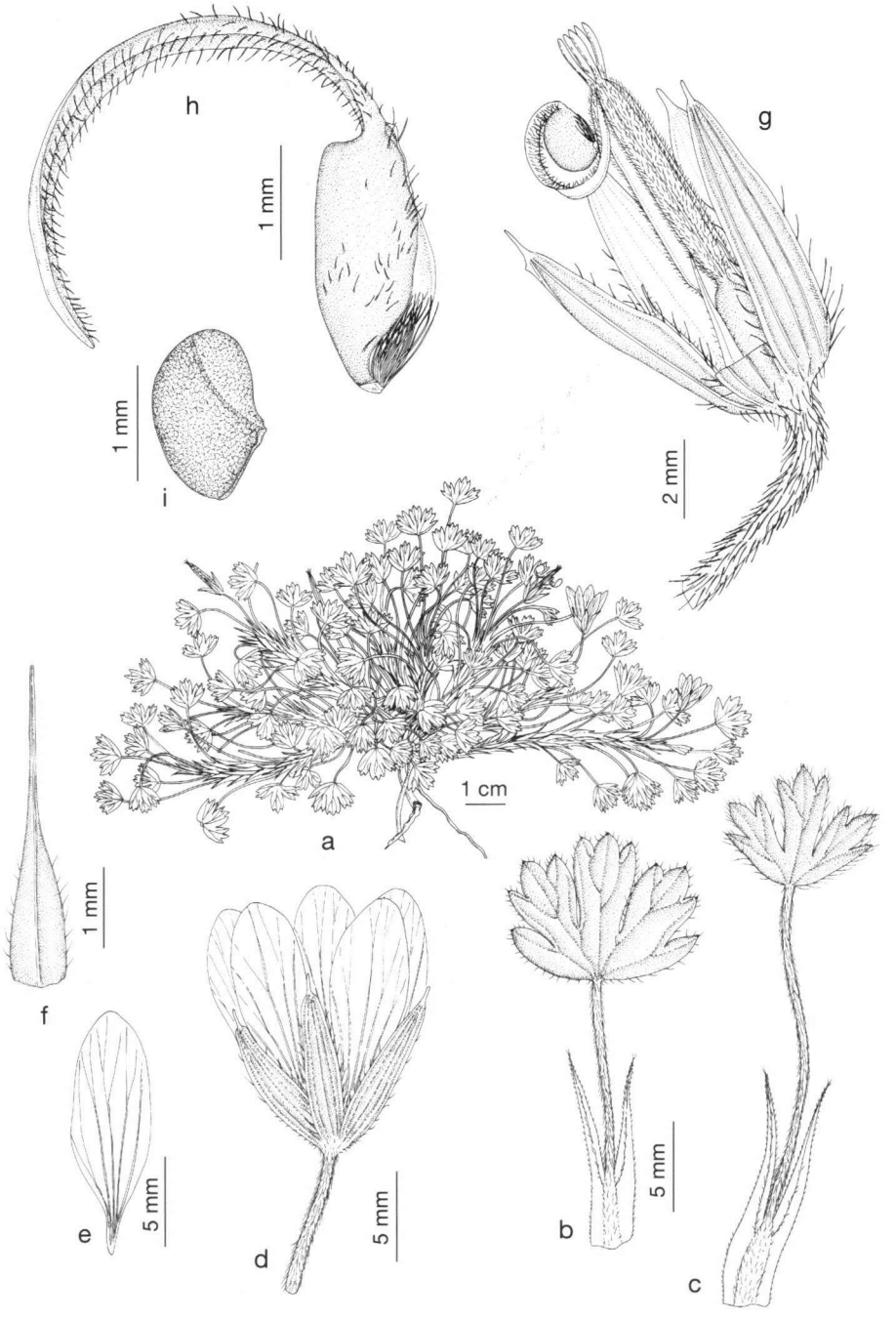
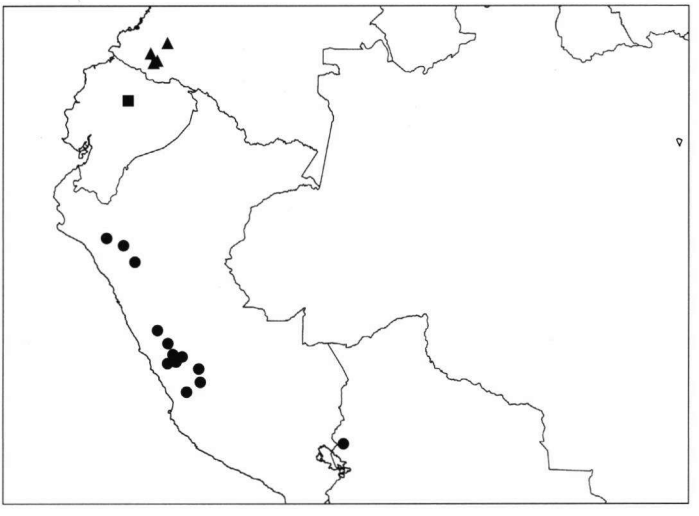


Fig. 28. *Geranium rhomboidale* H.E. Moore. a. Habit; b & c. leaves; d. flower; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a & b: *Alston 8347*, S; d–f: *Schultes 3238*, GH; c, g–i: *Schultes & Villarreal 7825*, US).



Map 11. Distribution of *Geranium rhomboidale* H.E. Moore (▲), *G. ruizii* Hieron. (●), and *G. sericeum* Willd. ex Spreng. (■).

Distribution — S Colombia.

Habitat & Phenology — On mosses under *Espeletia*, wet paramo. Altitude 2900–3600 m. Flowering: September to May.

Note — This species is characterised by the digitate leaf blade with usually three segments. The lateral segments are directed upward and the central segment is 3-lobed. The leaves are glabrous but with patent long cilia on the margin. As reported by Moore (1951: 257) *G. azorelloides*, *G. jahnii*, and *G. maniculatum* are closely resembling species. However, *G. jahnii* has very narrow leaves that are tridentate at the apex and with an articulated petiole, while *G. azorelloides* is quite similar to *G. jahnii* but with the petiole not articulated. From *G. maniculatum* it may be distinguished by its middle leaf segment 3-lobed (entire in *G. maniculatum*), and by its patent hairs 0.4–0.8 mm long on the leaf margin (glabrous or with short, antrorse hairs in *G. maniculatum*).

18. Geranium ruizii Hieron. — Fig. 29, Map 11

Geranium ruizii Hieron. (1895a) 31. — Type: *Ruiz & Pavón s.n.* (lectotype, designated by Knuth, 1912: 83, B†; isolectotypes BH-418700, BM, G, MA, MPU, P), Peru, Pasco, Cordillera del Diezmo [locality according to Geneva herbarium label].

Geranium dielsianum R. Knuth (1906) 563. — Type: *Weberbauer 3959* (lectotype, here designated, G; isolectotype BRSL), Peru, Cajamarca, Pass Coymolache.

Herbs 3–6 cm tall. *Rootstock* 6–8 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.7–1.45 by 0.9–1.7 cm, polygonal in outline, cordate, palmatifid (divided for 0.75–0.8 of its length), sericeous on both sides, not coriaceous, nerves not projected; segments 7, obtriangular, with lanceolate lobes, 1.2–1.5 mm wide at the base, 3-lobed at the apex (ratio main-sinus length of the middle segment/middle-segment length = 0.18–0.28); petioles to 3.5 cm long, sericeous, with patent to antrorse, eglandular hairs

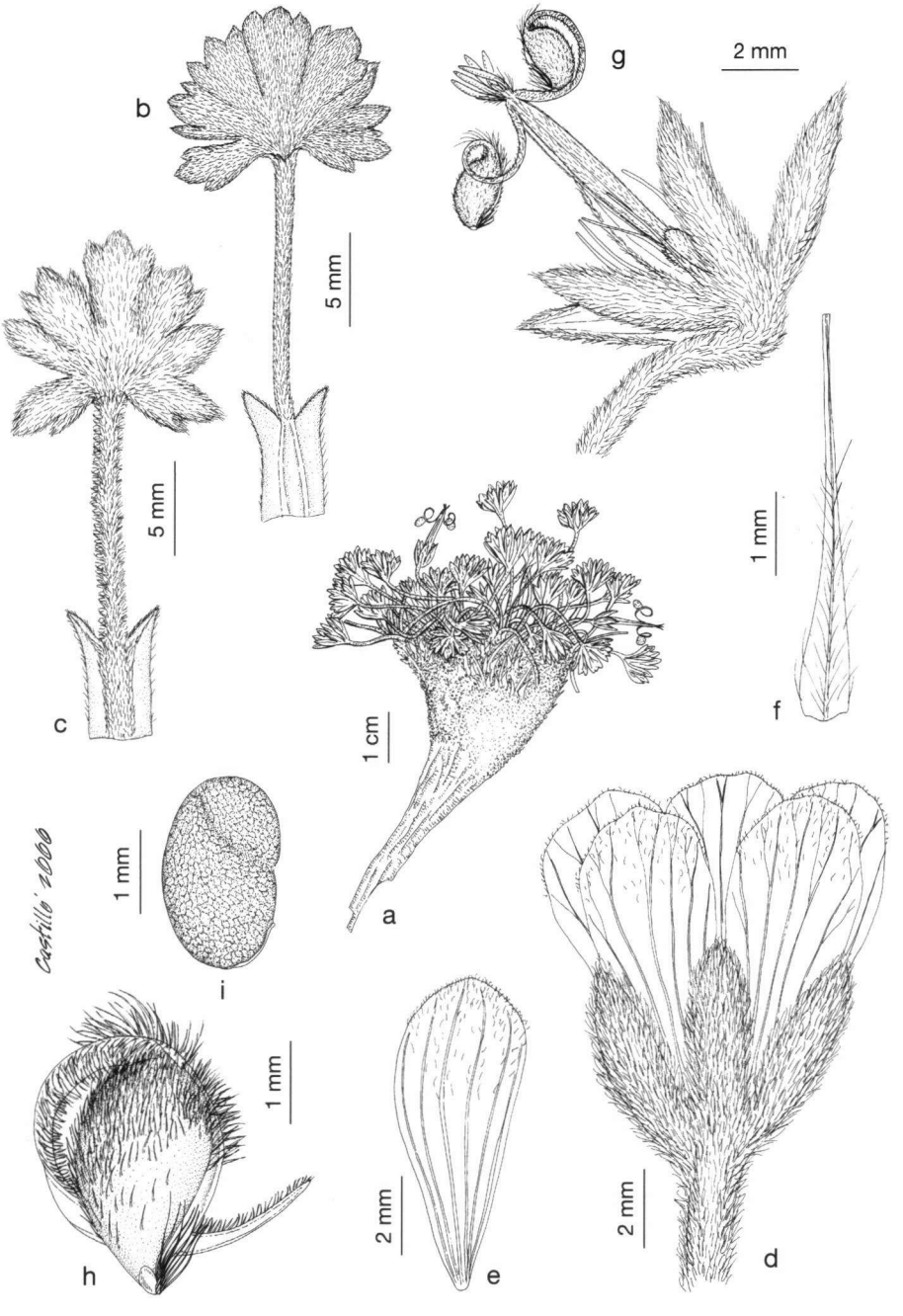


Fig. 29. *Geranium ruizii* Hieron. a. Habit; b. leaf (adaxial side); c. leaf (abaxial side); d. flower; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a, c, f–i: *Sullivan & Sullivan 804*, MO; b: *Asplund 11655*, S; d & e: *Pavon s.n.*, P).

0.5–1.5 mm long; stipules 9–11 by 1–2 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.7–4.5 cm long, with patent to antrorse, eglandular hairs 0.5–1.5 mm long; pedicel not overtopping the subtending leaf. *Sepals* 5.5–7 by 1.7–2 mm (ratio pedicel length/sepal length = 1.2–7.5), 3-nerved, mucronate (with mucro 0.5–1 mm long), with scarious margins 0.1 mm wide, sericeous with erect-patent, eglandular hairs 0.6–1.5 mm long on the abaxial side and margin, glabrous adaxially. *Petals* 10–14 by 4–7 mm (ratio petal length/petal width = 2–2.5), entire, glabrous, white. Filaments 3.5–4.5 mm long, not exserted, lanceolate, with eglandular hairs 0.3–0.5 mm long on the abaxial side and margin; anthers 0.8–1 by 0.5–0.6 mm, yellowish. Nectaries usually glabrous. Gynoecium 4–4.5 mm long, yellowish. *Fruit* 10–11 mm long; mericarps 2–2.5 by 1–1.5 mm, with erect-patent, eglandular hairs 0.3–0.6 mm long; rostrum 6–6.5 mm long, without a narrowed apex, woolly-sericeous, with patent, eglandular hairs 0.4–1.6 mm long; stigmatic remains 1.5–2.4 mm long (ratio fruit length/stigmatic remains length = 4.5–6.6), with 5 hairy lobes. *Seeds* 1.8 by 1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — Peru and N Bolivia.

Habitat & Phenology — Among rocks on exposed grassy slopes in puna. Altitude 3300–5000 m. Flowering: January to June.

Notes — *Geranium ruizii* can be distinguished from all other species treated here by its palmatifid leaves, sericeous on both sides and with the middle and usually also the lateral segments 3-lobed. It also has a sericeous petiole with patent to antrorse hairs. Knuth (1912: 78) differentiated *G. dielsianum* from *G. ruizii* on the basis of leaf size (longer in *G. dielsianum*). Additionally, *G. dielsianum* could be recognised by its "lateral as middle leaf-divisions mostly or all 3-dentate" against "lateral leaf-divisions often entire or 1-dentate" in *G. ruizii* (Macbride, 1949: 513). We have found, however, a continuous variation in leaf size. Entire lateral segments seems to occur sporadically, often among specimens with 3-lobed lateral segments. All these data suggest there is no basis for recognising *G. dielsianum*, which we have subsumed under *G. ruizii*.

In a collection from Peru (*Sánchez & Cabanillas 6735*, F, MA) the nectaries have some hairs at the apex, but match *G. ruizii* otherwise. The nectaries are usually glabrous in *G. ruizii*.

Most of the records of *G. ruizii* are from N and C Peru. One isolated locality, in Bolivia near the Peruvian border (*Menhofer 1795*, MA) suggest an insufficiency of collecting in the region between both areas. More problematic is the presence of *G. ruizii* in Colombia. A specimen kept at K (*Lobb 285*, K) is labelled as "Columbia". According to Chaudhri et al. (1972: 454), W. Lobb collected in S Colombia (mainly in Nariño), which would make likely the presence of *G. ruizii* in this country. However, no other collection has been found in any herbaria from Colombia (or Ecuador), and according to curator of COL (J.L. Fernández, in litt.) some other Lobb collections present similar problems.

19. **Geranium sericeum** Willd. ex Spreng. — Fig. 30, Map 11

Geranium sericeum Willd. ex Spreng. (1826) 70. — Type: *Humboldt s.n.* (lectotype, here designated, B-Willd.-12529; probably isolectotypes BH, HAL, P), without locality (isolectotypes of BH and P from Ecuador: Antisana).

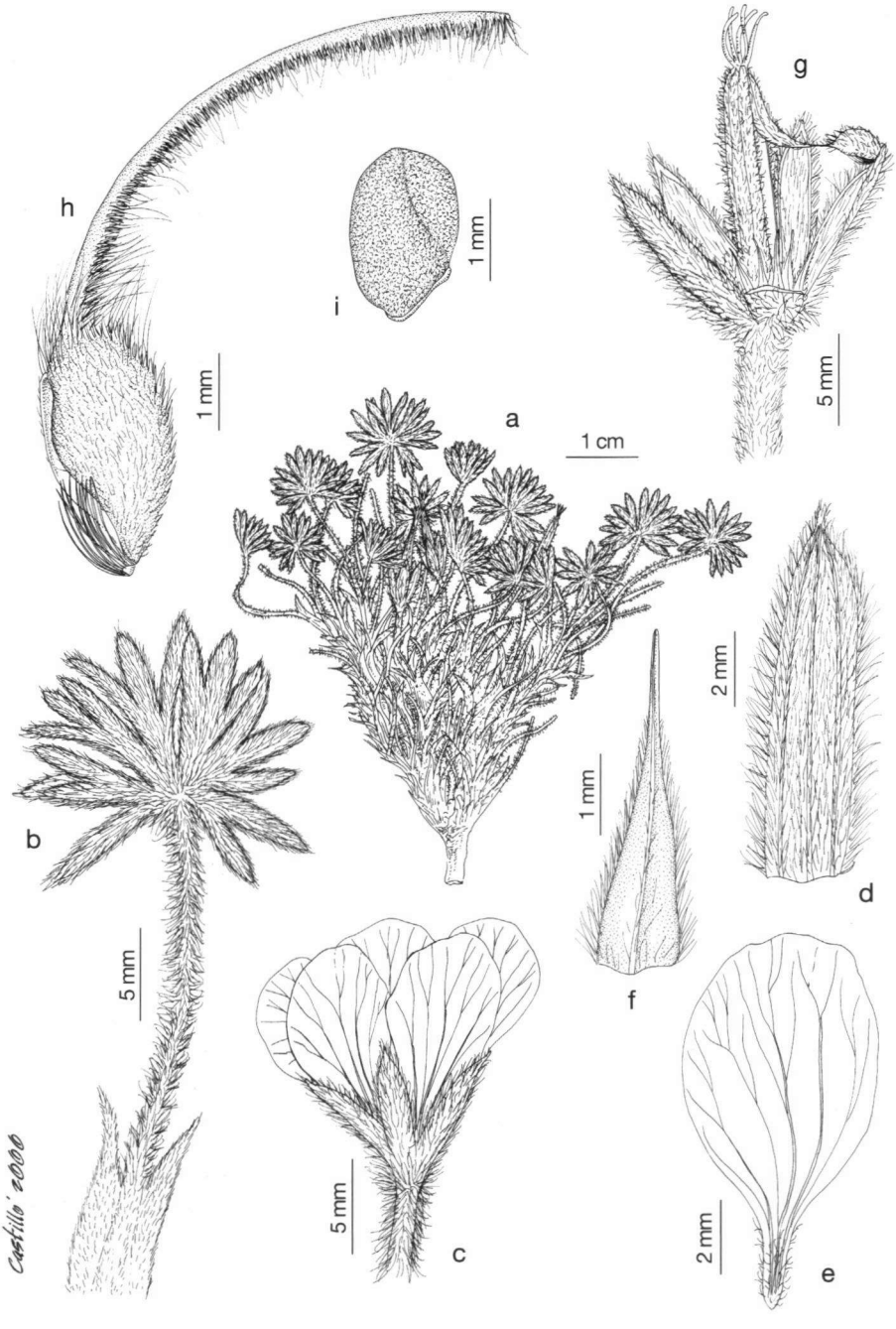


Fig. 30. *Geranium sericeum* Willd. ex Spreng. a. Fruiting branch; b. leaf; c. flower; d. sepal; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a, c: *Black 178*, AAU; b, d–h: *Løjtnant & Molau 15325*, AAU).

Herbs 2–4.1 cm tall. *Rootstock* 6–14 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.9–1.7 by 1.15–1.75 cm, polygonal in outline, cordate, palmatisect, sericeous on both sides, not coriaceous, nerves not projected; segments 7, obtriangular (with linear-lanceolate lobes), 0.3–0.5 mm wide at the base, 3-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.6–0.89); petioles to 3 cm long, woolly-sericeous, with patent to retrorse (not appressed), eglandular hairs 0.8–1.6 mm long; stipules 15–18 by 2–3 mm, lanceolate, papery, reddish, sericeous on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.1–0.5 cm long, woolly-sericeous, with patent, eglandular hairs 0.8–1 mm long; pedicel not overtopping the subtending leaf. *Sepals* 7–9 by 1.8–2.2 mm (ratio pedicel length/sepal length = 0.44–0.57), 3-nerved, mucronate (with mucro 0.3 mm long), with scarious margins 0.1 mm wide, woolly-sericeous, with antrorse, eglandular hairs 1–2 mm long on the abaxial side and margin, ± hairy adaxially. *Petals* 9–10.5 by 6 mm (ratio petal length/petal width = 1.5–1.75), entire, hairy on both sides (mainly on the base of the adaxial side), ciliate on the margin, purplish. Filaments 4–4.5 mm long, not exserted, lanceolate, with eglandular hairs 0.5–0.8 mm long on the abaxial side and margin; anthers 1 by 0.6 mm, yellowish. Nectaries glabrous. Gynoecium 4 mm long, yellowish. *Fruit* 11.5–14.5 mm long; mericarps 2.5–3.5 by 1.2–1.8 mm, woolly-sericeous, with erect-patent, eglandular hairs 0.8–1.5 mm long; rostrum 9–10 mm long, without a narrowed apex, woolly-sericeous, with patent, eglandular hairs 0.3–1.4 mm long; stigmatic remains 0.8–2 mm long (ratio fruit length/stigmatic remains length = 7.25–11), with 5 usually glabrous lobes. *Seeds* 2.2 by 1.3 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — Ecuador.

Habitat & Phenology — Grass paramo with open sandy areas, ravines and rock outcrops. Altitude 3900–4900 m. Flowering: throughout the year.

Notes — *Geranium sericeum* is endemic to Ecuador, restricted to a small area around Volcano Antisana. It is easily distinguished from other palmatisect-leaved species within its range by the possession of woolly-sericeous indumentum on lamina, petioles, peduncle, sepals, and fruit.

According to Fryxell (1991), *Sida radiciflora* C. Presl (Malvaceae) should be considered as a synonym of *G. sericeum*. Fryxell stated that Presl (1831–1835) described his *Sida* from Mt Chimborazo, Ecuador, and no original specimen was kept at PR. Thus, this author designated a collection by Née (MA-252584) as neotype of *S. radiciflora*, which is (in his view) *G. sericeum*. However, some new data contradict Fryxell's interpretation of *S. radiciflora*. Presl (1835: 106) described *S. radiciflora* from Guayaquil, not from Chimborazo. Additionally, according to Halfdan-Nielsen (ined.) there is a specimen collected by Haenke from Guayaquil, which is a *Sida* and which is presumably the type of *S. radiciflora* (PR-185995–591). Finally, an examination of Née's collection (MA-252584) reveals that this is *G. ecuadoriense* rather *G. sericeum*.

20. **Geranium sibbaldioides** Benth. — Fig. 31, Map 12

Geranium sibbaldioides Benth. (1845) 166. — Type: *Hartwig 126* (lectotype, here designated, K), Ecuador, Antisana.

Geranium cucullatum Kunth (1822) 231, nom. illeg., non L. (1753). — *Geranium ciliatum* Willd. ex Spreng. (1826) 71, nom. illeg., non Cav. (1787). — *Geranium bolivarianum* Dayton (1953)

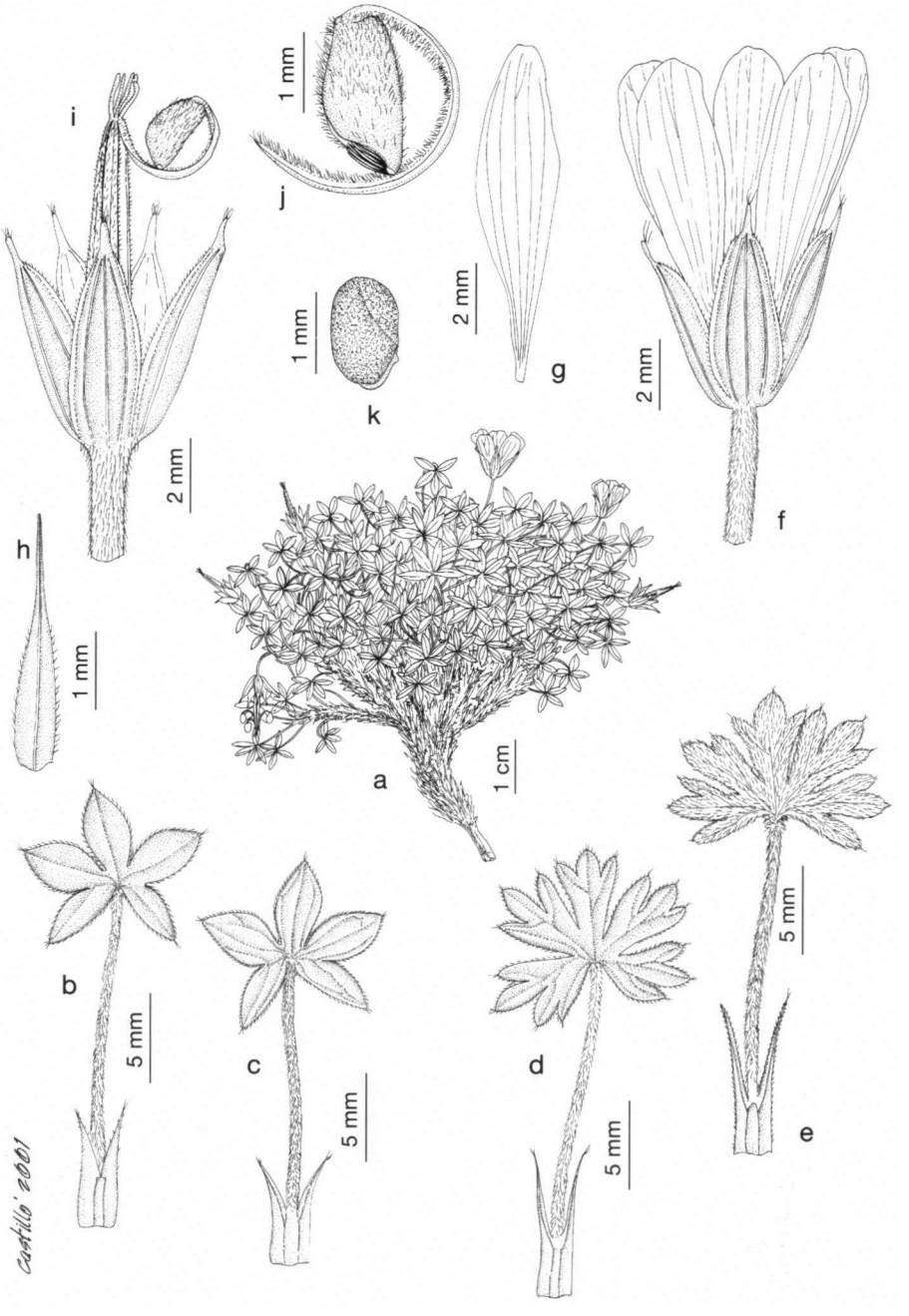


Fig. 31. a–c, f–k: *Geranium sibbaldioides* Benth. subsp. *sibbaldioides*. a. Habit; b. leaf (adaxial side); c. leaf (abaxial side); f. flower; g. petal; h. stamen; i. fruit; j. mericarp; k. seed (a–c, f–k: *Holm-Nielsen et al. 5422*, F). — d. *Geranium sibbaldioides* subsp. *beckianum* Aedo. Leaf (adaxial side) (*Solomon 18194*, LPB). — e. *Geranium sibbaldioides* subsp. *elongatum* (Wedd.) Aedo. Leaf (adaxial side) (*Moar 874*, COL).

245. — Type: *Humboldt & Bonpland s.n.* (lectotype, designated by Knuth, 1912: 88, B-Willd.-12531 photo!; isolectotypes H, HAL, P), Colombia, Cauca, Popayán, Almaguer.

Geranium igualatense R. Knuth (1930b) 88. — Type: *Rimbach 426* (holo B†), Ecuador, Tungurahua, Paramo des Igualata.

Geranium igualatense var. *laxius* R. Knuth (1930b) 89. — Type: *Rimbach s.n.* (no original material located), Ecuador, Tungurahua, Paramo des Igualata.

Geranium mogotocorense R. Knuth, see under subsp. *elongatum*.

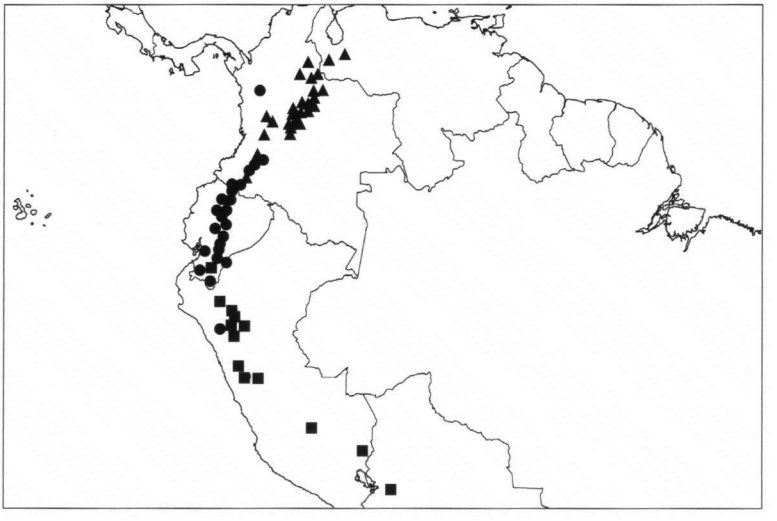
Geranium cuatrecasasii R. Knuth, see under subsp. *elongatum*.

Herbs 2–9 cm tall. *Rootstock* 2–4 mm diam., vertical; with short vegetative stems. *Leaf* lamina 0.5–1.3 by 0.6–1.6 cm, polygonal in outline, cordate, palmatifid (divided for 0.7–0.92 of its length), glabrous on both sides, with antrorse, eglandular cilia 0.1–0.2 mm long on the margin, each segment ending in 1–3 bristles 0.2–0.5 mm long, glabrous or hairy, not coriaceous, nerves not projected; segments 5, obtriangular to broadly lanceolate, 0.8–2 mm wide at the base, 1–3-lobed at the apex (ratio main-sinus length of the middle segment/middle-segment length = 0.32); petioles to 5 cm long, with retrorse, appressed (sometimes patent), eglandular hairs 0.1–0.7 mm long; stipules 6.5–12 by 1.5–2 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.2–0.3 mm long. Peduncles 0–0.4 cm long, with retrorse, appressed, eglandular hairs 0.2–0.3 mm long; bracteoles 5–7 by 1–1.5 mm, linear-lanceolate, with eglandular hairs on the abaxial surface and margin, glabrous adaxially, ending in 1–3 bristles 0.3–0.5 mm long; pedicels 0.35–3.9 cm long, with retrorse, appressed, eglandular hairs 0.2–0.5 mm long; pedicel and peduncle together often overtopping the subtending leaf. *Sepals* 4.5–8 by 1.5–2.2 mm (ratio pedicel length/sepal length = 1.9–2.7), 3-nerved, mucronate (with mucro 0.2–1.2 mm long), with scarious margins 0.1–0.2 mm wide, with scattered erect-patent, eglandular hairs 0.2–0.7 mm long on the base of abaxial side and margin, glabrous adaxially, ending in 1–3 bristles 0.4–0.5 mm long. *Petals* 8–11 by 2–3.2 mm (ratio petal length/petal width = 3.6–4), entire, glabrous on both sides and margin (sometimes ciliate on the basal margin), purplish. Filaments 2.5–3 mm long, not exserted, lanceolate, glabrous, or with few eglandular hairs 0.1–0.2 mm long on the abaxial side and margin; anthers 0.6–0.7 by 0.5–0.6 mm, yellowish. Nectaries glabrous. Gynoecium 3.5–4 mm long, yellowish. *Fruit* 8.5–10 mm long; mericarps 2–2.5 by 1–1.3 mm, with antrorse, ± appressed, eglandular hairs 0.1–0.3 mm long; rostrum 5.5–6.5 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 0.8–1.5 mm long (ratio fruit length/stigmatic remains length = 6.6–10.6), with 5 glabrous lobes. *Seeds* 1.6 by 1.1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution & Habitat — See under the subspecies.

Phenology — Flowering: throughout the year.

Notes — This species is extremely variable in indumentum and leaf shape throughout its area, from W Venezuela to N Bolivia. The original material was collected in Ecuador by Hartwig. This specimen and most of *G. sibbaldioides* collected in S Colombia and Ecuador have leaves with five entire segments, glabrous on both sides (with antrorse cilia on the margin); its petiole usually has retrorse, appressed hairs, and its sepals are almost glabrous (with few hairs towards the base). Some specimens sharing those characters have also been collected in N Peru. Specimens from W Venezuela and N and C Colombia usually have leaves hairy on one or both sides and sepals more



Map 12. Distribution of *Geranium sibbaldioides* Benth. subsp. *sibbaldioides* (●), *G. sibbaldioides* subsp. *beckianum* Aedo (■), and *G. sibbaldioides* subsp. *elongatum* (Wedd.) Aedo (▲).

or less hairy, their leaf segments are not always entire (many times the middle segment is entire and the lateral ones are 2- or 3-lobed; rarely the middle segment may be 3-lobed and obtriangular), and sometimes they have patent hairs on the petiole. Other *G. sibbaldioides* specimens from S Ecuador, Peru, and N Bolivia also show a different combination of features, since they have glabrous leaves (with antrorse cilia on the margin), with obtriangular 3-lobed segments, and sepals almost glabrous. These combinations of characters are related to different geographical areas, and consequently they have been recognised as subspecies. These combinations of characters, however, are not always constant, and a few samples are difficult to identify.

Geranium igualatense was described from *Rimbach 426* (B), which was destroyed during the Second World War. Unfortunately, no other duplicate of this collection has been found. Jørgensen & León-Yánez (1999: 492) considered it as synonym of *G. sibbaldioides*. This view seems suitable after examining the original description (Knuth, 1930b: 88).

a. subsp. **sibbaldioides**

Herbs 2–8 cm tall. *Leaf* lamina 0.5–1.1 by 0.6–1.3 cm, glabrous on both sides, with antrorse, eglandular cilia 0.1–0.2 mm long on the margin; segments broadly lanceolate, 0.9–1.2 mm at the base, 1- (or 2-)lobed at the apex; petioles with retrorse, appressed, eglandular hairs 0.1–0.3 mm long. Peduncles 0–0.4 cm long; pedicels 0.5–1.3 cm long, with retrorse, appressed, eglandular hairs 0.2–0.3 mm long. *Sepals* 4.5–6.2 by 1.5–2.2 mm, with mucro 0.5–1.1 mm long, with scattered erect-patent, eglandular hairs 0.2–0.3 mm long on the base of the abaxial side and margin, glabrous adaxially. *Petals* 8–11 mm long. *Fruit* 8.5–10 mm long.

Distribution — S Colombia, Ecuador, and N Peru.

Habitat — Pajonal, grassy or boggy paramo, or *Polylepis* forest. Altitude 2700–5000 m.

Note — *Geranium sibbaldioides* subsp. *sibbaldioides* has been sometimes confused with *G. campii* and *G. maniculatum*, two similar species. For their discrimination see the discussion under those species.

b. subsp. **beckianum** Aedo

Geranium sibbaldioides subsp. *beckianum* Aedo (2000) 184. — Type: *Beck 19987* (holo MA-628702), Bolivia, La Paz, Nor Yungas, pasando Unduavi hacia Cotapata, 3 May 1993.

Herbs 2–6 cm tall. *Leaf* lamina 0.7–1.3 by 0.8–1.4 cm, glabrous on both sides, with antrorse, eglandular cilia 0.1–0.2 mm long on the margin; segments obtriangular (with lanceolate lobes), 0.9–1.3 mm at the base, 3-lobed at the apex; petioles with retrorse, appressed, eglandular hairs 0.1–0.3 mm long. Peduncles 0–1.2 cm long; pedicels 0.9–3.9 cm long, with retrorse, appressed, eglandular hairs 0.2–0.3 mm long. *Sepals* 4.5–6 by 1.6–2 mm, with mucro 0.7–1.2 mm long, with scattered erect-patent, eglandular hairs 0.2–0.3 mm long on the base of the abaxial side and margin, glabrous adaxially. *Petals* 9–11.5 mm long. *Fruit* 8–10.5 mm long.

Distribution — Ecuador, Peru, and Bolivia.

Habitat — Natural grassland, humid pajonal, shrub paramo, or open forest. Altitude 3000–4275 m.

Note — A collection of subsp. *beckianum* (*Barbour 3423*, F, MO) from Peru shows rather more divided leaves. Otherwise it is similar to other specimens of subsp. *beckianum*.

c. subsp. **elongatum** (Wedd.) Aedo

Geranium sibbaldioides subsp. *elongatum* (Wedd.) Aedo (2000) 184. — *Geranium cucullatum* var. *elongatum* Wedd. (1861) 285. — *Geranium sibbaldioides* var. *elongatum* (Wedd.) J.F. Macbr. (1934) 7. — Type: *Goudot s.n.* (lectotype, here designated, P; isolectotype G), Colombia, Cundinamarca, páramo de Usaguin, 1844.

Geranium mogotocorense R. Knuth (1930b) 88. — Type: *Killip & Smith 17626* (holo US-1353188), Colombia, Santander, Vetas, Páramo de Mogotocoro, 18 January 1927.

Geranium cuatrecasasii R. Knuth (1933) 143. — Type: *Cuatrecasas 2277* (lectotype, here designated, MA-252455), Colombia, Tolima, Alto del Condor, 14 May 1932.

Herbs 4–9 cm tall. *Leaf* lamina 0.5–1.1(–1.3) by 0.7–1.4(–1.6) cm, pilose, with ± scattered subpatent, eglandular hairs on both sides (sometimes only adaxially), each segment ending in 1–3 bristles 0.3–0.5 mm long; segments lanceolate, sometimes obtriangular (with lanceolate lobes), 0.8–2 mm at the base, 1(–3)-lobed at the apex; petioles with retrorse, appressed (sometimes patent) eglandular hairs 0.3–0.7 mm long. Peduncles absent; pedicels 0.35–1.4(–3) cm long, with patent or retrorse, appressed, eglandular hairs 0.3–0.5 mm long. *Sepals* 5–8 by 1.5–2.2 mm, with mucro 0.2–0.6 mm long, with erect-patent, eglandular hairs 0.3–0.7 mm long on the abaxial side and margin, glabrous adaxially. *Petals* 5–9(–13) mm long. *Fruit* 8.5–10.5 mm long.

Distribution — Colombia and Venezuela.

Habitat — Open grassy paramo, or *Sphagnum* bog. Altitude 1990–4400 m.

Notes — *Geranium cucullatum* var. *elongatum* was described by Weddell (1861) as a plant with hairy leaves. However, the original material recorded by this author is

heterogeneous, covering all the variability of *G. sibbaldioides*: a) glabrous leaved specimens from Ecuador corresponding to *G. sibbaldioides* subsp. *sibbaldioides* (*Jameson 496*, E!, P!); b) glabrous leaved specimens from Peru (i.e., *Lechler 2518*, HAL!, P!, W!) corresponding to *G. sibbaldioides* subsp. *beckianum*; and c) hairy leaved specimens from Colombia (*Goudot s.n.*, P!), on which we have typified *G. cucullatum* var. *elongatum* because it is in accordance with the protologue and with the sense of Knuth's (1912) monograph. Consequently, the name for specimens from W Venezuela and Colombia becomes *G. sibbaldioides* subsp. *elongatum*.

A specimen of subsp. *elongatum* with exceptionally long petals (13 mm) was collected by *Rangel et al. 1582* in Colombia (Boyacá, Sierra Nevada del Cocuy). It can be differentiated from *G. paludosum* (a related species with long petals) by its leaves with entire and lanceolate segments, hairy on both sides.

21. **Geranium stramineum** Triana & Planch. — Fig. 32, Map 13

Geranium stramineum Triana & Planch. (1873) 112. — Type: *Goudot s.n.* (lectotype, here designated, P), Colombia, Tolima, pic Tolima, Quebrada de los Venados, 1844.

Geranium confertum Standl. (1916) 111. — Type: *Pittier 1107* (holo US-531305), Colombia, Cauca, Páramo de Buena Vista, January 1906.

Geranium angelense Halfd.-Niels. (1996) 269, 270 f. 2. — Type: *Halfdan-Nielsen et al. 21* (holo C; iso AAU, QCA n.v., QCNE n.v.), Ecuador, Carchi, Páramo del Angel, base de Volcán Chiles, Lagunas Verdes, 16 November 1991.

Geranium guamanense Halfd.-Niels. (1996) 271 f. 3. — Type: *Øllgaard & Balslev 10064* (holo AAU; iso MO, NY), Ecuador, Napo, road Quito-Baeza, Páramo de Guamaní, 7–9 October 1976.

Herbs perennial, 2–12 cm tall. *Rootstock* 4–6 mm diam., ± vertical; sometimes with short vegetative stems. *Leaf* lamina 1.1–2.3 by 1.2–2.6 cm, orbicular in outline, cordate, palmatifid (divided for 0.57–0.8 of its length), glabrous to pilose with antrorse, appressed, eglandular hairs on both sides, ± coriaceous, nerves ± projected on the abaxial side, sunken adaxially; segments 7, obtriangular, with lanceolate lobes, 2–4 mm wide at the base, 3-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.13–0.21); petioles to 10 cm long, glabrous or pilose, with patent, eglandular hairs 0.2–1 mm long; stipules 10–60 (!) by 4–6 mm, obtuse (with a setaceous apex 3–6 mm long), scarious, stramineous, glabrous on both sides, ending in 1–3 bristles 0.5 mm long. Peduncles absent; pedicels 1.1–2 cm long, glabrous or pilose, with patent, eglandular hairs 0.2–1 mm long; pedicel not overtopping the subtending leaf. *Sepals* 8–9 by 2.5–3.5 mm (ratio pedicel length/sepal length = 1.6–2.5), 3-nerved, mucronate (with mucro 0.5–0.8 mm long), with scarious margins 0.1 mm wide, with erect-patent, eglandular hairs 0.5–1 mm long on the abaxial side (sometimes glabrous) and margin, glabrous adaxially. *Petals* 9–14 by 3.5–5 mm (ratio petal length/petal width = 2.5–2.7), entire, glabrous, purplish, sometimes white. Filaments 3.5–5 mm long, not exserted, lanceolate with an abruptly narrowed apex, glabrous, or with eglandular hairs 0.1–0.2 mm long on the abaxial side and margin; anthers 0.6–0.8 by 0.5 mm, purplish. Nectaries glabrous. Gynoecium 4 mm long, purplish. *Fruit* 10–12 mm long; mericarps 2–2.1 by 1.1–1.3 mm, with antrorse, ± appressed, eglandular hairs 0.1–0.4 mm long on the surface and eglandular hairs 0.5–0.7 mm long on the margin; rostrum 6–8 mm long, without a narrowed apex, with

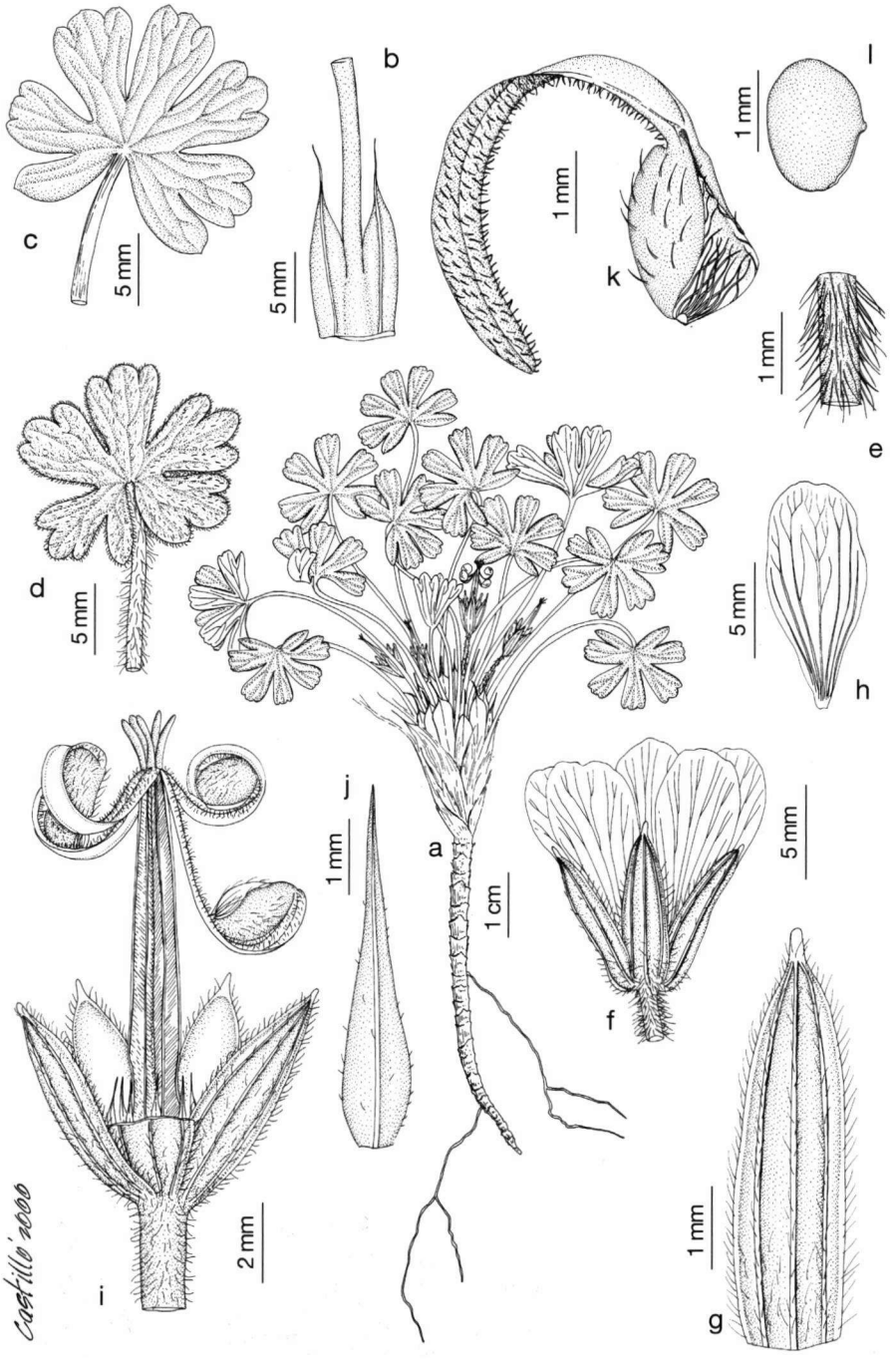
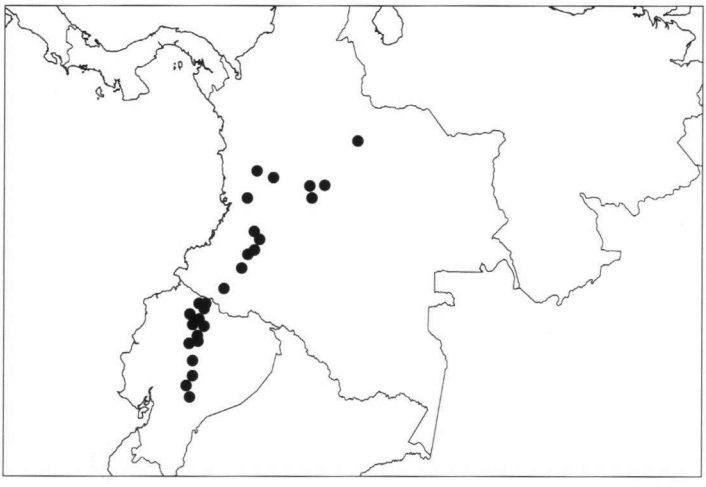


Fig. 32. *Geranium stramineum* Triana & Planch. a. Habit; b. stipules; c & d. leaves; e. peduncle; f. flower; g. sepal; h. petal; i. fruit; j. stamen; k. mericarp; l. seed (a–c: *MAF 61*, AAU; d: *Barclay 4057*, COL; e–h: *Idobro et al. 3181*, COL; i–l: *Archibald 4048*, E).



Map 13. Distribution of *Geranium stramineum* Triana & Planch.

erect-patent, eglandular hairs 0.1–0.2 mm long; stigmatic remains 1.5–2 mm long (ratio fruit length/stigmatic remains length = 5.5–7.3), with 5 glabrous lobes. *Seeds* 1.5–1.6 by 1–1.1 mm; hilum 1/4 as long as the perimeter. Cotyledons entire.

Distribution — Colombia and Ecuador.

Habitat & Phenology — Grass or boggy paramo. Altitude 1750–4275 m. Flowering: throughout the year.

Notes — *Geranium stramineum* can be distinguished from all other species treated here by its stramineous and scarious stipules that with time becomes scrapped at the margin. These stipules are obtuse with a setaceous apex 3–6 mm long. In sect. *Neoandina* the stipules are usually papery, reddish, lanceolate, without a setaceous apex, although they sometimes end in 1–3 bristles.

Geranium stramineum can be glabrous or with more or less abundant hairs on the petiole and on the leaf lamina. Hairy forms have been described as *G. confertum*, *G. angelense*, and *G. guamanense*. However, many transitional specimens joint glabrous to hairy forms, which makes me reluctant to accept these forms as deserving specific recognition. For instance, *Barclay 6399* (MO) has a glabrous petiole and hairs only on the leaf margin, *Halfdan-Nielsen & León 74* (QCA) has a hairy petiole and hairs on the leaf margin and on the nerves of the abaxial side. In the collection by *Lozano et al. 4591* (COL) there are glabrous specimens and specimens that are quite hairy on the petiole and the lamina, whereas in a duplicate at F all specimens are hairy. The sepal and petal length are variable and do not show any relation with the indumentum. Moreover, hairy and glabrous forms both occur all over the range of this species. Consequently, these forms are here not accorded taxonomic recognition.

22. Geranium tovarii Aedo — Fig. 33, Map 14

Geranium tovarii Aedo (2000) 184. — Type: *Hutchinson & Tovar 4258* (holo F; iso CAS, E, G, GH, M, MO, NY, P, S), Peru, Lima, Huarochiri, lago Aguascocha, Mina Caprichosa, above Casapalca, 1 March 1964.

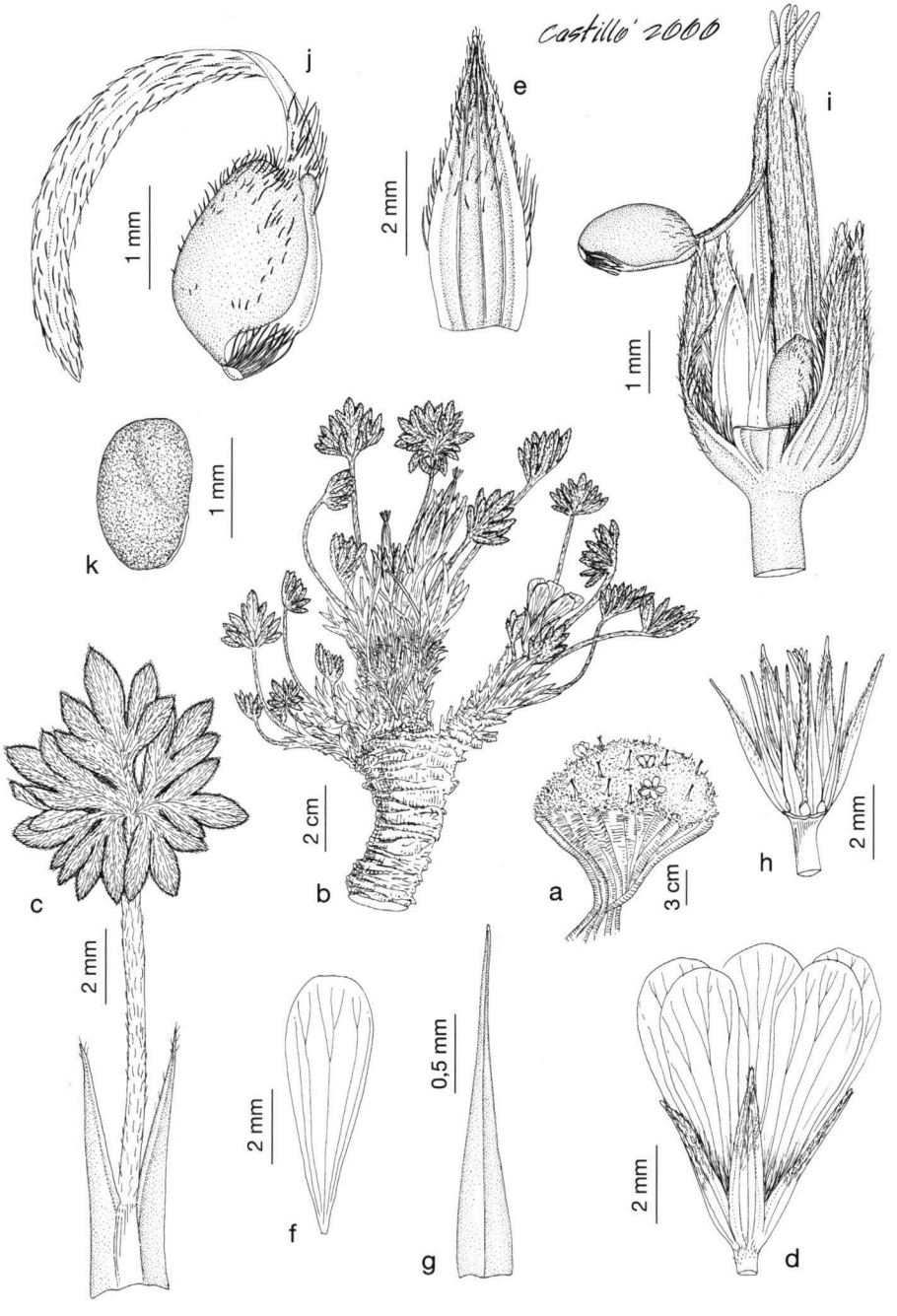
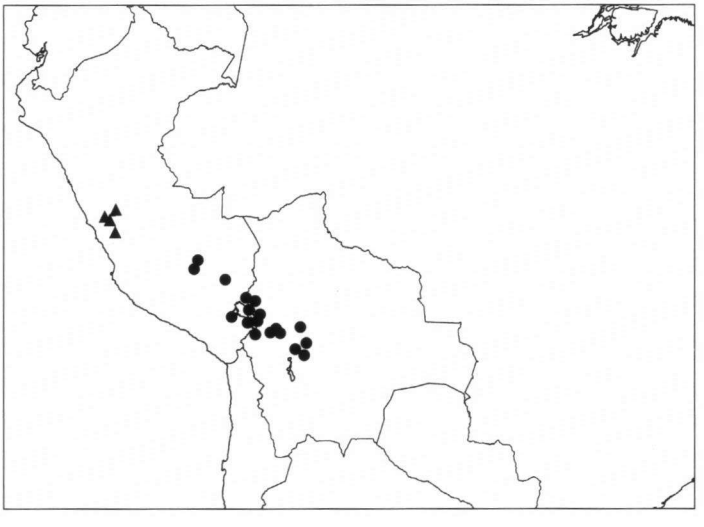


Fig. 33. *Geranium tovarii* Aedo. a. Habit; b. fruiting and flowering branch; c. leaf; d. flower; e. sepal; f. petal; g. stamen; h. androecium and nectaries; i. fruit; j. mericarp; k. seed (a–c, e, g, i: *Hutchinson & Tovar 4258*, F; d, f, h: *Hutchinson & Tovar 4258*, UC; j, k: *Hutchinson & Tovar 4258*, M).

Herbs 0.7–3.4 cm tall. *Rootstock* 10–13 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.18–1.05 by 0.22–0.92 cm, polygonal in outline, cordate, palmatisect, sericeous on both sides, not coriaceous, nerves not projected; segments 7, rhombic, with linear-lanceolate lobes, 0.4–0.6 mm wide at the base, 5- or 6-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.33–0.63); petioles to 2.3 cm long, sericeous, with antrorse, appressed, eglandular hairs 0.2–0.4 mm long; stipules 7–8 by 1 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.22–0.35 cm long, glabrous or with scattered antrorse, appressed, eglandular hairs 0.2–0.3 mm long; pedicel not overtopping the subtending leaf. *Sepals* 4–6 by 1.1–1.7 mm (ratio pedicel length/sepal length = 0.36–0.87), 3-nerved, mucronate (with mucro 0.1–0.3 mm long), with scarious margins 0.2 mm wide, with erect-patent, eglandular hairs 0.2–0.4 mm long on both sides, and patent, eglandular hairs 1–1.2 mm long on the margin. *Petals* 4–7 by 1.8–7.6 mm (ratio petal length/petal width = 2.2–2.7), entire, glabrous, purplish, sometimes white. Filaments 2–2.5 mm long, not exserted, lanceolate, glabrous; anthers 0.6–0.7 by 0.5 mm, yellowish. Nectaries glabrous. Gynoecium 2.6–3.5 mm long, yellowish. *Fruit* 7.5–8.2 mm long; mericarps 1.9–2.5 by 1–1.1 mm, with antrorse, ± appressed, eglandular hairs 0.2–0.3 mm long; rostrum 4–4.5 mm long, without a narrowed apex, with antrorse, appressed, eglandular hairs 0.2–0.3 mm long; stigmatic remains 0.9–1.5 mm long (ratio fruit length/stigmatic remains length = 5.3–9.1), with 5 glabrous lobes. *Seeds* 1.3–1.4 by 1 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — C Peru.

Habitat & Phenology — Rocky outcrops or dry grassland in puna. Altitude 4200-4780 m. Flowering: January to March.



Map 14. Distribution of *Geranium tovarii* Aedo (▲) and *G. weddellii* Briq. (●).

Note — *Geranium tovarii* is a rare endemic to C Peru. Of the *Geranium* species that grow in S America it resembles most closely *G. weddellii*, from which it is easily distinguished by its much shorter petals, longer hairs on the margin of the sepals, glabrous nectaries, and a fruit without a narrowed apex. The deeply divided, sericeous leaves are quite similar in both species. Upon closer inspection, however, the difference between them become apparent, with a 5- or 6-lobed versus an always 3-lobed middle segment in *G. tovarii* and *G. weddellii*, respectively. In addition, the ranges of *G. tovarii* and *G. weddellii* are completely non-overlapping.

23. Geranium weddellii Briq. — Fig. 34, Map 14

Geranium weddellii Briq. (1908) 183. — Type: *Mandon 785* (lectotype, designated by Knuth 1912: 80, G; isolectotypes MPU, NY, P, W), Bolivia, Sorata, Guatata, March 1858.

Geranium palcaense R. Knuth (1915) 68. — Type: *Herzog 2097* (holo L; iso BH-418695), Bolivia, Cerro de Palca, May 1911.

Herbs 1.1–3.5 cm tall. *Rootstock* 6–12 mm diam., vertical; without vegetative stems. *Leaf* lamina 0.4–1.1 by 0.51–1.1 cm, polygonal in outline, cordate, palmatisect, sericeous on both sides, not coriaceous, nerves not projected; segments 7, rhombic, with linear-lanceolate lobes, 0.2–0.5 mm wide at the base, 3-lobed in the distal half (ratio main-sinus length of the middle segment/middle-segment length = 0.36–0.46); petioles to 1.7 cm long, sericeous, with antrorse, appressed, eglandular hairs 0.2–0.3 mm long; stipules 4–7 by 0.5–1 mm, lanceolate, papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially. Peduncles absent; pedicels 0.5–1.2 cm long, sericeous, with antrorse, appressed, eglandular hairs 0.3 mm long; pedicel overtopping the subtending leaf. *Sepals* 6–7.9 by 2–3 mm (ratio pedicel length/sepal length = 0.7–2), 3-nerved, mucronate (with mucro 0.3–0.4 mm long), with scarious margins 0.3 mm wide, hairy to sericeous on the abaxial side (with erect-patent, eglandular hairs 0.3–0.5 mm long), and ± hairy adaxially. *Petals* 11–15 by 4.5–6 mm (ratio petal length/petal width = 2.4–2.6), entire, glabrous, purplish, sometimes white. Filaments 5–6 mm long, not exserted, lanceolate, with eglandular hairs 0.2–0.3 mm long on the abaxial side and margin; anthers 1.1–1.3 by 0.6–0.8 mm, yellowish. Nectaries with a tuft of hairs at the top, dorsally glabrous. Gynoecium 5.5–6.5 mm long, purplish. *Fruit* 13–13.5 mm long; mericarps 2.6–3 by 1.5–1.7 mm, with antrorse, ± appressed, eglandular hairs 0.2–0.3 mm long; rostrum 9–10 mm long, with a narrowed apex 1–1.5 mm long, hairy to sericeous, with antrorse, appressed, eglandular hairs 0.2–0.3 mm long; stigmatic remains 1.5–2 mm long (ratio fruit length/stigmatic remains length = 6.7–8.6), with 5 glabrous lobes. *Seeds* 2.2 by 1.4–1.6 mm; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — S Peru and N Bolivia.

Habitat & Phenology — Stony or grassy places. Altitude 3125–4600 m. Flowering: November to April.

Note — *Geranium weddellii* is easily distinguished from other similar sympatric species by its small and palmatisect, sericeous leaves with 3-lobed middle segments and its sericeous petioles with antrorse, appressed hairs. The differences between *G. weddelli* and *G. tovarii* are addressed in the discussion under the latter species.

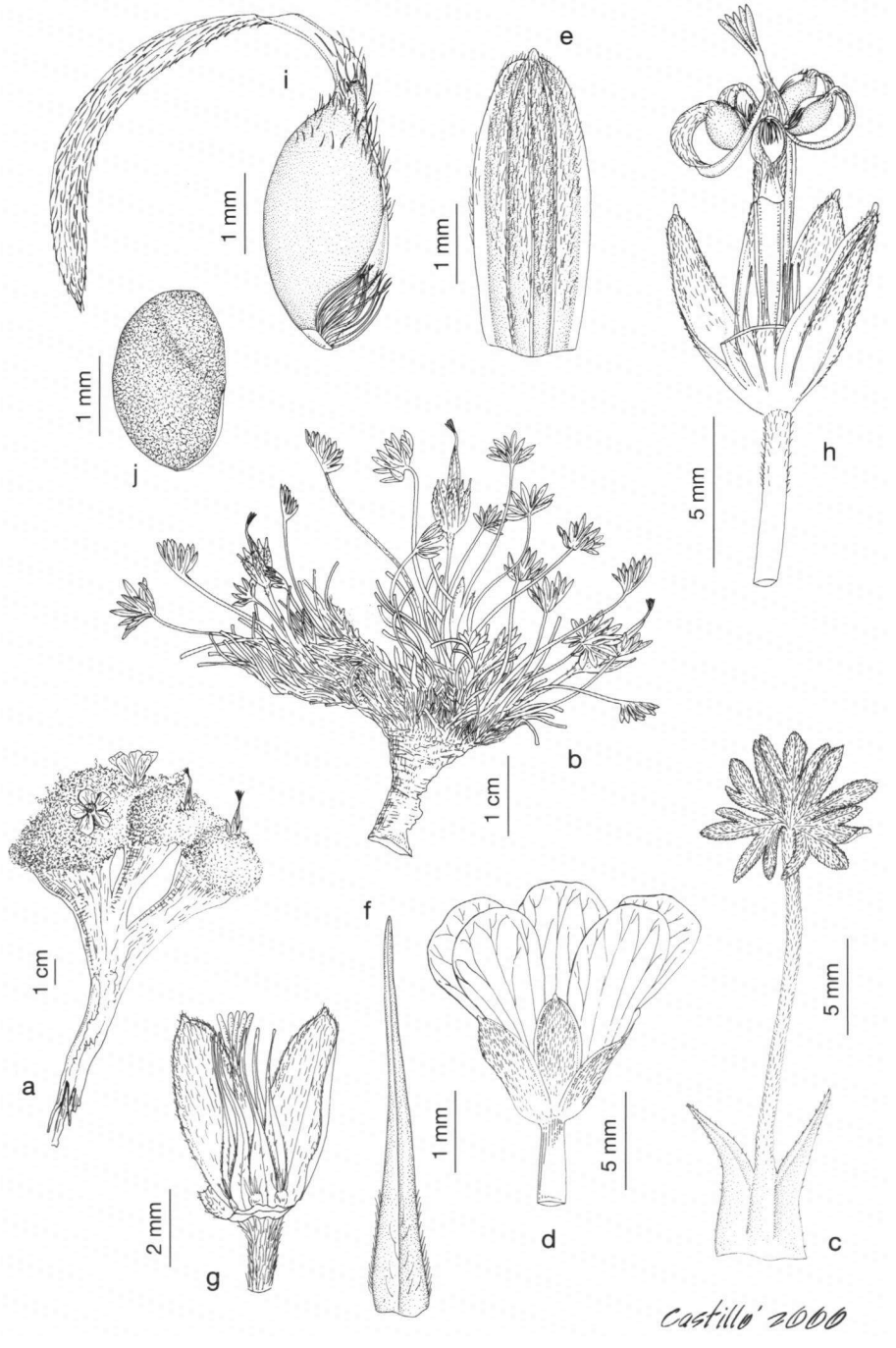


Fig. 34. *Geranium weddellii* Briq. a. Habit; b. fruiting branch; c. leaf; d. flower; e. sepal; f. stamen; g. androecium and nectaries; h. fruit; i. mericarp; j. seed (a: *Solomon 11385*, MO; b, i, j: *Davis et al. 1569*, F; c: *Mandon 785*, G; d, f, g: *Vuilleumier 341*, LPB; h, e: *Davis et al. 1569*, GH).

GERANIUM section PARAMENSIA

Geranium sect. *Paramensia* R. Knuth (1931) 55. — Type: *Geranium jahnii* Standl.

Shrubby with rootstock ± horizontal, not tuberculate, not turnip-shaped, without fusiform-swollen roots; aerial stem erect, ligneous, glabrous, densely clothed with imbricate persistent stipules and petioles; without vegetative stems. Basal *leaves* unknown; lamina of caulinar leaves obtriangular or lanceolate in outline, cuneate, entire or tridentate, with an abscission zone between lamina and petiole, glabrous (sometimes with eglandular cilia), coriaceous, and with or without projecting nerves; segments 1–3, entire, lanceolate (when present); cauline leaves alternate; stipules lanceolate, free, papery, reddish, glabrous or hairy. *Inflorescence* in 1-flowered cymules, solitary or grouped at the end of each branch; peduncles and pedicels hairy; bracteoles linear-lanceolate, glabrous or hairy; pedicel and peduncle together overtopping the subtending leaf. *Sepals* ovate, smooth, not accrescent, 3-nerved, mucronate, with scarious margins, hairy. *Petals* erect-patent, ± obovate, entire, with or without claw, hairy at least on the basal margin, purplish. *Stamens* 10, both whorls bearing anthers; filaments not exserted, lanceolate, yellowish, almost glabrous. Nectaries hemispherical, glabrous. *Fruit* of the seed-ejection type; mericarps smooth, without longitudinal rib, without basal beak, with a basal callus, without a basal prong, usually with eglandular hairs, brownish; rostrum without a narrowed apex; stigmatic remains with 5 glabrous lobes. *Seeds* ellipsoid, finely reticulate, brownish; hilum 1/6 as long as the perimeter. Cotyledons entire.

Notes — This section comprises two species of shrubby habit, one endemic to Venezuela and the other from Ecuador. It may be readily distinguished from other sections in S America by its leaves with an abscission zone between lamina and petiole. The basal part of the stem lacks leaf laminas and is densely clothed with imbricate persistent stipules and petioles. Similarities between sect. *Paramensia* and sect. *Neurophyllodes* (endemic from Hawaii) have already been suggested (Standley, 1915: 600). Both sections have a shrubby habit and unlobed, parallel-veined leaves rather than the palmate leaves and herbaceous habit typical of the genus. The most important feature shared by both groups is, however, the presence of an abscission zone (in the apex of the petiole in sect. *Paramensia* and in the base of the petiole in sect. *Neurophyllodes*). This highly specialised feature, otherwise unknown in *Geranium*, suggests a common origin (Standley, 1915: 600; Aedo et al., 1998b: 213). The strong resemblance between the leaves of *G. jahnii* and *G. cuneatum* (from sect. *Neurophyllodes*) is also remarkable, with an obtriangular outline and some teeth at the apex. In sect. *Neurophyllodes* the flowers are arranged in compound cymes forming large corymbose inflorescences that project beyond the leaves (as in *G. multiflorum* A. Gray, *G. cuneatum* Hook., and *G. hanaense* A.C. Medeiros & H. St.John), in terminal, 3- or 4-flowered cymes (as in *G. hillebrandii* Aedo & Muñoz Garm. and *G. kauaiense* (Rock) H. St.John), or in axillary 1–4-flowered cymes (as in *G. arboreum* A. Gray).

According to Pax et al. (1997: 76) the phylogenetic analysis of *rbc*L sequences suggests an American derivation of sect. *Neurophyllodes*. Unfortunately, these authors only studied *G. richardsonii* Fisch. & Trautv. (from USA) and *G. vulcanicola* Small and *G. subulato-stipulatum* R. Knuth (from Mexico). However, these authors indicate that morphological considerations render other S American groups (as sect. *Neoandina*) as their potential ancestors.

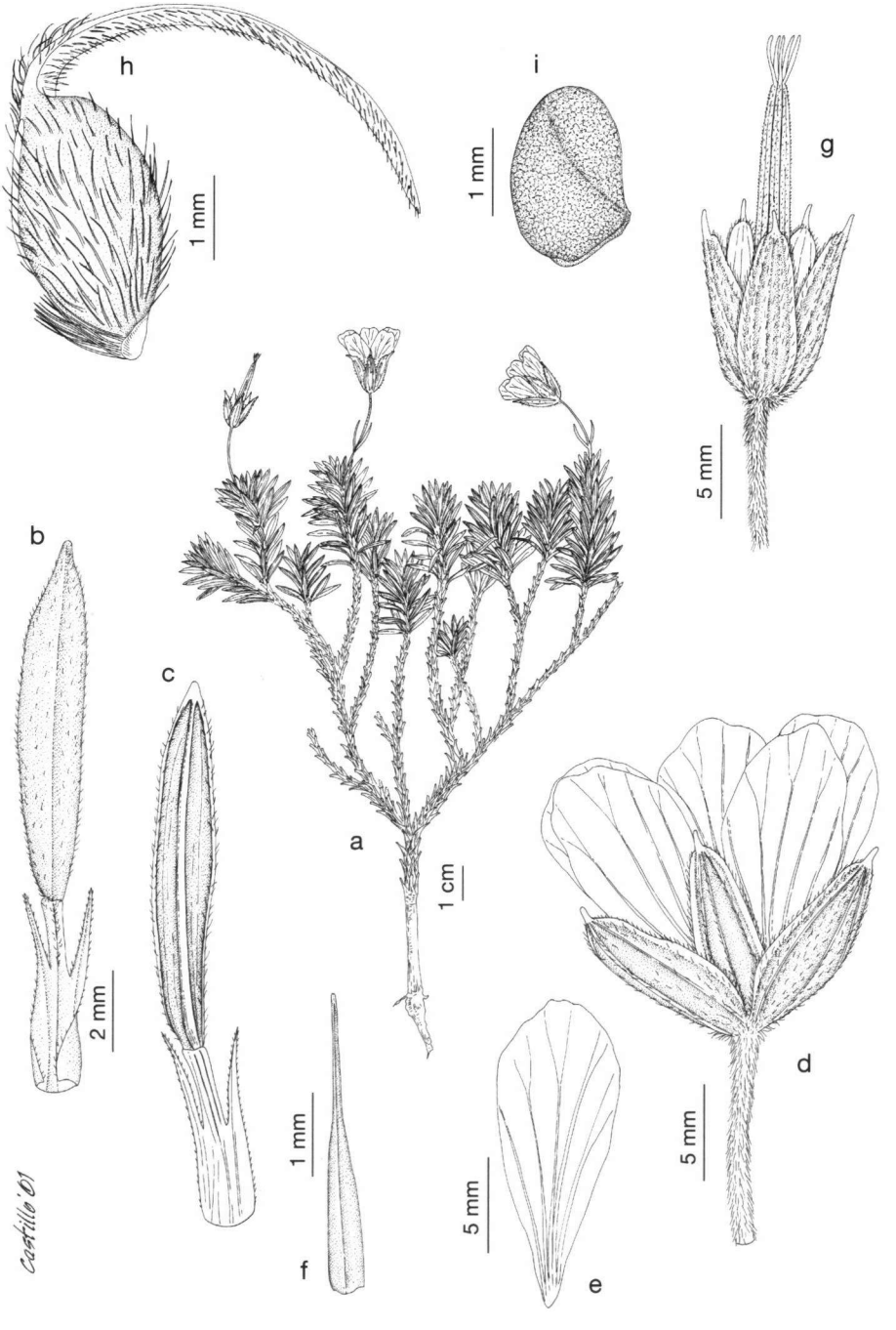


Fig. 35. *Geranium exallum* H.E. Moore. a. Flowering branch; b. leaf (adaxial side); c. leaf (abaxial side); d. flower; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a–f: *Prieto 279*, NY; g–i: *Prieto 279*, BH).

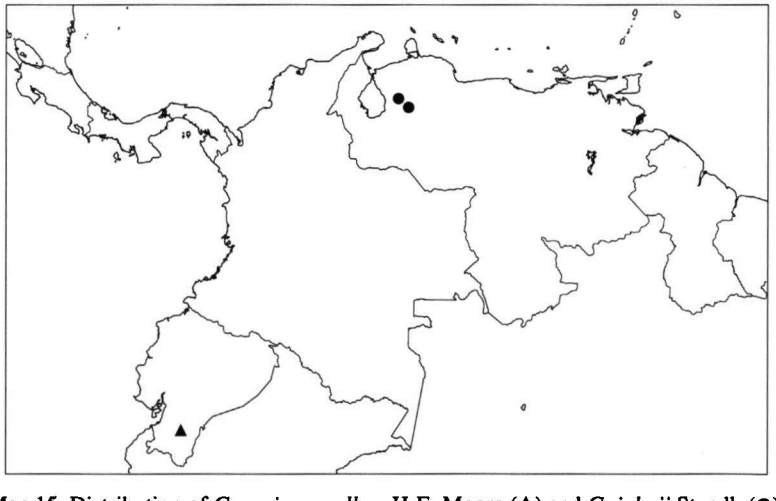
24. Geranium exallum H.E. Moore — Fig. 35, Map 15

Geranium exallum H.E. Moore (1961) 142, 143 f. 1A. — Type: *Prieto 279* (holo NY!; iso BH! K!), Ecuador, Azuay, between Oña and the Río Yacuambi, 10–19 September 1945.

Shrubby 6–20 cm tall. *Rootstock* 2–4 mm diam.; aerial stem 3–6 cm diam. *Leaf* lamina 0.8–1 by 0.22–0.3 cm, lanceolate in outline, cuneate, entire, glabrous on both sides, with antrorse, eglandular cilia 0.1–0.3 mm long on the margin, coriaceous, nerves not projected; petioles to 0.45 cm long, glabrous; stipules 3–4 by 0.5–0.7 mm, papery, reddish, glabrous on both sides, with antrorse, eglandular hairs 0.1–0.2 mm long on the margin. Cymules 1-flowered, solitary at the end of each branch; peduncles 0.5–1.3 cm long, with retrorse, appressed, eglandular hairs 0.2–0.3 mm long; bracteoles 5–7.5 by 0.8–1 mm, linear-lanceolate, glabrous on both sides, with eglandular hairs on the margin; pedicels 0.9–1.6 cm long, with retrorse, appressed, eglandular hairs 0.2–0.3 mm long; pedicel and peduncle together overtopping the subtending leaf. *Sepals* 7.5–10 by 2.5–3.5 mm (ratio pedicel length/sepal length = 1.2–1.5), 3-nerved, mucronate (with mucro 0.8–1 mm long), with scarious margins 0.2–0.3 mm wide, with ± patent, eglandular hairs 0.2–0.7 mm long on both sides (mainly on nerves and margin). *Petals* 11–13 by 6–7 mm (ratio petal length/petal width = 1.8–1.9), entire, without claw, glabrous except for a few marginal hairs at the base, purplish. Filaments 4–5 mm long, not exserted, lanceolate, glabrous except for a few marginal hairs 0.2–0.4 mm long; anthers 1.5 by 1 mm, colour unknown. Nectaries glabrous. Gynoecium 4 mm long, yellowish. *Fruit* 17 mm long; mericarps 3.2 by 1.5 mm, with erect-patent, eglandular hairs 0.3–0.7 mm long; rostrum 11 mm long, without a narrowed apex, with erect-patent, eglandular hairs 0.1 mm long; stigmatic remains 3 mm long (ratio fruit length/stigmatic remains length = 5.6), with 5 glabrous lobes. *Seeds* 2.2 by 1.2 mm, finely reticulate, uniformly, brownish; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — Ecuador.

Habitat & Phenology — Unknown habitat. Altitude 2700 m. Flowering: September.



Map 15. Distribution of *Geranium exallum* H.E. Moore (▲) and *G. jahnii* Standl. (●).

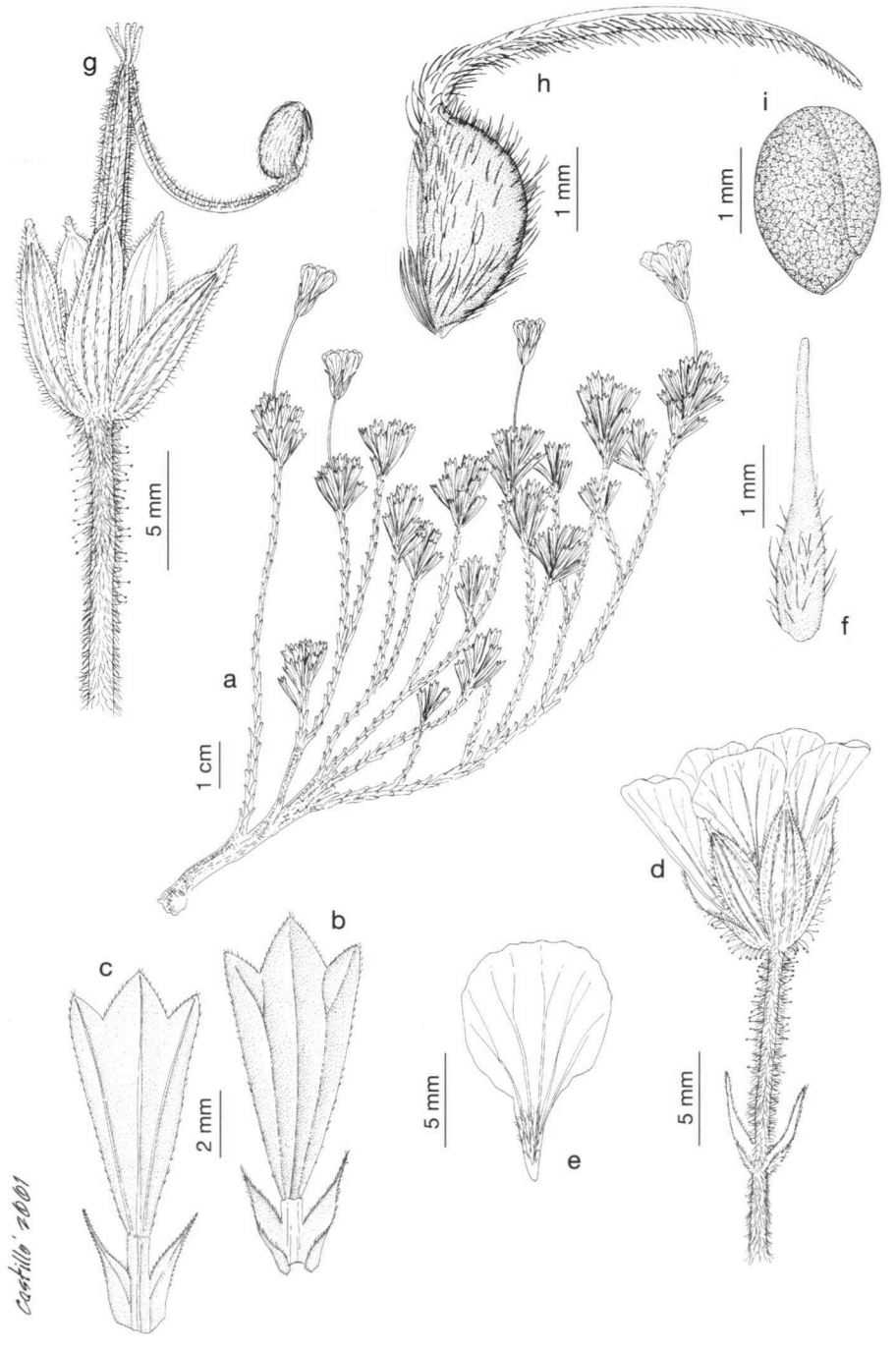


Fig. 36. *Geranium jahnii* Standl. a. Habit; b. leaf (adaxial side); c. leaf (abaxial side); d. flower; e. petal; f. stamen; g. fruit; h. mericarp; i. seed (a, d–f: *Duno & Riina 781*, MA; b & c: *Duno & Riina 748*, MA; g–i: *Duno & Riina 597*, MA).

Note — *Geranium exallum* is a rare endemic to S Ecuador, known only from the type. It is easily distinguished from other *Geranium* species by its coriaceous, lanceolate and entire leaves, which as pointed out by Moore (1961: 141) is far unique in the genus. This species resembles most closely *G. jahnii*, considering its shrubby habit, its stem densely clothed with imbricate persistent stipules and petioles, and its leaves with an abscission zone between the lamina and petiole. However, *G. jahnii* has obtriangular leaves, tridentate at the apex, glabrous, and pedicels with glandular hairs versus lanceolate, entire leaves with marginal cilia and pedicels without glandular hairs in *G. exallum*. Additionally the stipules have a setaceous apex in *G. jahnii*, lacking in *G. exallum*.

25. **Geranium jahnii** Standl. — Fig. 36, Map 15

Geranium jahnii Standl. (1915) 601. — Type: *Jahn 34* (holo US-602229!), Venezuela, Trujillo, Páramo del Jabón, 2 October 1910.

Shrubby 8–13 cm tall. *Rootstock* 3–4 mm diam., ± horizontal; aerial stem 2–3 cm diam. *Leaf* lamina 6.2–8 by 2–2.5 cm, obtriangular in outline, cuneate, tridentate (divided for 0.15–0.17 of its length), glabrous, coriaceous, nerves projected; segments 3, entire, lanceolate, 1.2–1.4 mm wide at the base; cauline leaves alternate; petioles to 0.35 cm long, with retrorse, appressed, eglandular hairs 0.1 mm long; stipules 5.5–6.5 by 0.7–1 mm, lanceolate (with a setaceous apex 2–2.5 mm long), papery, reddish, with eglandular hairs on the abaxial surface and margin, glabrous adaxially. Cymules 1-flowered, grouped at the end of each branch; peduncles 4 cm long, with patent, eglandular hairs 0.1–0.3 mm long; bracteoles 3.5 by 0.5 mm, linear-lanceolate, with eglandular hairs on the abaxial surface and margin, glabrous adaxially; pedicels 7–8 cm long, with patent, eglandular hairs 0.1–0.3 mm long, and patent glandular, hairs 0.4–0.6 mm long; pedicel and peduncle together overtopping the subtending leaf. *Sepals* 6.5–7 by 2.5 mm (ratio pedicel length/sepal length = 0.9–1.1), 3-nerved, mucronate (with mucro 0.7 mm long), with scarious margins 0.3–0.4 mm wide, with patent, eglandular hairs 0.3 mm long, and patent, glandular hairs 0.4–0.7 mm long on the abaxial side and margin, glabrous adaxially. *Petals* 13 by 8 mm (ratio petal length/petal width = 1.6), entire, with claw 2 mm long, hairy on the base of the abaxial side and margin, glabrous adaxially, purplish. Filaments 3.5–4 mm long, not exserted, lanceolate, glabrous except for a few marginal hairs 0.2–0.3 mm long; anthers 1.1 by 0.6 mm, colour unknown. Nectaries glabrous. Gynoecium 4 mm long, yellowish. *Fruit* 14 mm long; mericarps 3.1 by 1.8 mm, with antrorse, ± appressed, eglandular hairs 0.1–0.4 mm long; rostrum 10 mm long, without a narrowed apex, with eglandular, ± patent hairs 0.1–0.3 mm long; stigmatic remains 1 mm long (ratio fruit length/stigmatic remains length = 14), with 5 glabrous lobes. *Seeds* 2.4 by 1.5 mm, finely reticulate, uniformly, brownish; hilum 1/6 as long as the perimeter. Cotyledons entire.

Distribution — Venezuela.

Habitat & Phenology — Unknown habitat. Altitude 3000–3350 m. Flowering: April to August.

Note — *Geranium jahnii* can be distinguished from all other species treated here by the distinctly obtriangular, tridentate leaves with an abscission zone between the lamina and the petiole. The differences and similarities between *G. jahnii* and *G. exallum* are addressed in the discussion under the latter species.

EXCLUDED NAMES

Geranium bangii Hieron. (1895b) 314. — Type: *Bang 788* (lectotype, designated by Knuth, 1912: 85, B†; isolectotypes BM, E, F, GH, K, MO, NY, W), Bolivia, Oruro, Capi, March 1890.

After examining the type, we concluded that this name should be considered as a synonym of *G. sessiliflorum* Cav., thus belonging to *Geranium* sect. *Andina* R. Knuth.

Geranium cucullatum var. *typicum* R. Knuth (1906) 568, nom. inval. (see Art. 24.3 ICBN).

Geranium exili Standl. (1936) 220, nom. nud.

Geranium mandonii A.W. Hill, nom. nud. (in sched., K!).

Geranium microphyllum Briq. (1908) 183, nom. nud.

Geranium multipartitum var. *typicum* R. Knuth (1906) 566, nom. inval. (see Art. 24.3 ICBN).

Geranium neopumilum Aedo & Muñoz Garm. (1997) 726. — *Geranium pumilum* R. Knuth (1912) 88, nom. illeg., non (Willd.) Poir. (1812). — Type: *Stuebel 185e* (holo B†), Ecuador, Cerro Antisana, 1871.

According to Knuth (1912: 88) this species should be included in sect. *Andina* (sect. *Neoandina* in the present work). This view is also followed by Jørgensen & León-Yánez (1999: 492), who synonymised *G. neopumilum* to *G. sibbaldioides*. Type material kept at B was destroyed during the Second World War. In addition, no material of this species has been located in any of the studied herbaria. Knuth (1912: 89) described this species as having glandular hairs on the peduncles. We have not found this feature in any of the species included in sect. *Neoandina*. Moreover, we have examined two specimens of *G. sibbaldioides* from Cerro Antisana, which have only eglandular hairs. Thus, it could be concluded that *G. neopumilum* is an extremely rare species of sect. *Neoandina* collected once. It is also possible that, however, *G. neopumilum* is a reduced (stemless) form of *G. antisanae* R. Knuth, belonging to sect. *Diffusa* R. Knuth. Note that the original material of *G. antisanae* is *Stuebel 185n* (B†), also from Cerro Antisana.

Geranium pflanzii R. Knuth (1912) 576. — Type: *Pflanz 206* (holo B†; photo: G, GH, MO, NY), Bolivia, Palca-La Paz, 1908.

According to the photographs of the type material it should be considered as a synonym of *G. sessiliflorum* Cav., thus belonging to sect. *Andina* R. Knuth.

Geranium potentilloides Willd. ex Spreng. (1826) 70, nom. nud., pro syn.

Geranium sessiliflorum Cav. (1787) 198, t. 77, f. 2. — Type: *Commerson s.n.* (lectotype, designated by Garilleti, 1993: 91, MA-475750; isolectotype P), Chile, Estrecho de Magallanes.

This species is a representative of sect. *Andina* R. Knuth.

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IDENTIFICATION LIST

The number after each collection refers to the corresponding species in the text and to the following list of species. Three mixed collections have been located: *Heinrichs 962b* (including *G. humboldtii*, *G. maniculatum*, and *G. sibbaldioides* subsp. *sibbaldioides*), *Jørgensen et al. 1237* (including *G. campii* and *G. sibbaldioides* subsp. *beckianum*), and *Macbride 4401* (including *G. multipartitum*, *G. sibbaldioides* subsp. *beckianum*, and *G. stramineum*).

Geranium
1. *azorelloides*
2. *campii*
3. *costaricense*
4. *crassipes*
5. *digitatum*
6. *ecuadoriense*
7. *foreroi*
8. *humboldtii*
9. *jaekelae*
10. *macbridei*
11. *maniculatum*
12. *multipartitum*
13. *nivale*
14. *paludosum*
15. *pavonianum*
16. *planum*
17. *rhomboidale*
18. *ruizii*
19. *sericeum*
20a. *sibbaldioides* subsp. *sibbaldioides*
20b. *sibbaldioides* subsp. *beckianum*
20c. *sibbaldioides* subsp. *elongatum*
21. *stramineum*
22. *tovarii*
23. *weddellii*
24. *exallum*
25. *jahnii*

Acosta Solís 7618: 20a; 8157: 11; 8167: 20a; 8341: 20a; 8394: 12; 8743: 11; 10554: 20a — Aguirre 302: 21 — Aizpuru 3692CA: 12 — Almeda & Nakai 4763: 3 — Alston 7238: 20c; 8347: 17 — Anderson & Mori 224: 3 — André 690: 12; 3950: 6; 4455: 2 — Anthony & Tate 292: 12; 293: 19 — Antonio 1560: 3 — Archibald 4048: 21 — Asplund 7057: 11; 7908: 12; 8378: 6; 9618: 12; 9820: 20a; 9935: 20a; 11643: 9; 11655: 18; 17512: 20b.

Balls 6462: 23 — Balslev 1013: 6 — Balslev & Steere 3217: 2 — Balslev & Vries 3648: 20a — Balslev et al. 3959: 19; 3960: 12; 69179: 12; 69179A: 8; 69290: 12 — Barbour 3423: 20b — Barclay 4117: 20c; 4251: 20c; 4515: 20c; 4635: 20a; 5106: 20a; 5128: 11; 5256: 20c; 5752: 20a; 7492: 20c — Barclay & Juajibioy 5751: 20a; 5806: 20a; 5955: 20a; 5983: 1; 6227: 20c; 6373: 20c; 6399: 21; 6637: 7; 8008: 12; 8128: 12; 8666: 2; 8779: 21; 8781: 20a; 8851: 21; 8894: 12; 9167: 12; 9225: 8; 9466: 17; 10475: 20c — Barfod & Pennington 41258: 8; 41258A: 12 — Beck 3957: 23; 7197: 23; 13065: 1; 19987: 20b; 21989: 23; 21990: 23; 22493: 23 — Becker & Terrones 306: 20a — Bejarano 9: 20c — Benavides 4576: 20a — Benoist 2410: 12 — Bernal 244: 20c — Bernal & Llano 220: 20c — Bernal et al. 204: 20c — Bernardi 10856: 20c — Bernardi et al. 17134: 20c — Betancour & Churchill 2439: 20c — Black 178: 19 — Boeke 582: 12 — Bornmüller 183: 8 — Brandbyge 41142: 6; 42247: 6 — Buchtien 610: 20b — Burger & Stolze 5265: 3.

Camp 399: 2; 1633: 20b; 2088: 12; E-5138: 2 — Cárdenas 3879: 23 — Castroviejo et al. 12149: 20c — Cazalet & Pennington 5348: 20a; 5757: 12; 5758: 8 — Ceballos et al. 661: 23 — Cerón et al. 4396: 8; 11830: 20b — Chávez 3292: 23 — Cleef 890: 20c; 1094: 20c; 1202: 20c; 1529: 20c; 1782: 20c; 2119: 20c; 2263: 20c; 2574: 21; 2757: 20c; 4370: 21; 4918: 20c; 5379: 20c; 5574: 20c; 5699: 20c; 5757: 20c; 6109: 20c; 6191: 20c; 6530: 21; 6878: 20c; 7047: 20c; 7334: 20c; 7352: 20c; 7453: 20c; 7491: 20c; 7677: 20c; 7936: 21; 7984: 20c; 8128: 20c; 8548: 20c; 9079: 20c; 9368: 20c — Cleef & Duncan 3164: 20c — Cleef & Florschütz 5484B: 21; 5509: 20c — Cleef & Huber 4824A: 21 — College West Indies Exped. 22: 14 — Core 411: 11; 905: 20a; 1451: 20c — Cuatrecasas 373: 20c; 1216: 20c; 1314: 20c; 1546: 20c; 1588: 20c; 2066: 20c; 2274: 20c; 2275: 20c; 2277: 20c; 5578: 20c; 5926: 21; 9351: 21; 9507: 20c; 9550: 20c; 9772: 20c; 11741: 17; 14629: 20a; 14716: 21; 18965: 21; 19048: 20c; 19048a: 20a; 20083: 12; 20550: 12; 20580: 20c; 23151c: 20c; 23185: 20c — Cuatrecasas & Mora 26915: 21 — Cuatrecasas & Romero 24555: 14; 24578: 14 — Cuatrecasas & Willard 26271: 21; 26273: 21; 26343: 1 — Cuatrecasas et al. 12053: 20c.

Davidse & Herrera 29409: 3 — Davis et al. 1569: 23 — Díaz Piedrahita & Jaramillo 1900: 20c — Díaz Piedrahita et al. 2468: 12; 2469: 21 — Dorr & Valdespino 6480: 6 — Drew E-185: 20a — Duno & Riina 597: 25; 748: 25; 781: 25 — Duque 566: 1 — Dwyer & Idrobo 8174: 20c.

Ellemann 2741: 2 — Ellenberg 4052: 22; 5006: 20b — Eriksen & Larsen 45446A: 12 — Espinosa 2040: 20a; 2187: 12; 3090: 17 — Evans 20163: 20c.

Fábrega 466: 20a — Fagerlind & Wibom 979: 6; 980: 6; 1397: 20a; 1440b: 20a — A. Fernández 2956: 21 — J.L. Fernández Alonso et al. 5155: 20c; 6134b: 20c; 6140: 20c; 6335: 21 — A. Fernández Pérez & Jaramillo 432: 20c — Feuerer 7275a: 23; 8188: 23 — Filskov et al. 37491: 12 — Forero & Kirkbride 635: 7 — Fosberg 20258: 20c; 20741: 21; 20761: 20c; 20785: 20c; 20828: 20c — Fosberg & Giler 22852: 2 — Franco 841: 20c — Franco & Rangel 73: 20c; 327: 20c — Freire et al. 2118: 12 — Fuertes & Aguirre 6: 20c.

García Barriga 16178: 20c — García Barriga & Jaramillo 19811: 20c — García Barriga et al. 18592: 17 — Garwood et al. 1275: 3 — Garzón 164: 20c — Garzón et al. 63: 20c; 84: 20c — Gavilanes & Funk 871: 20a — Gay 1208: 5; 2109: 20b — Gentry & Blaney 64382: 20a — Gentry & Ortiz 74367: 8 — Gentry et al. 23174: 20b; 30526: 21; 39757: 18; 47740: 20a — Gilli 55: 6 — Grant 10638: 1 — Grubb et al. 106: 20c; 123: 20c; 173: 20c; 605: 12; 682: 19.

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233: 12 — Huertas & Camargo 6584: 20c — Humbert 30846: 4; 30850: 22; 30852: 4 — Humbert et al. 26886: 20c; 26888: 20c; 27068: 21 — Humboldt & Bonpland 2240: 8 — Hutchinson & Tovar 4258: 22 — Huttel 385: 6.

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