

Taxonomic revision of *Solanum* sect. *Chamaesarachidium* (Solaneae, Solanaceae)

Gloria E. Barboza

Barboza, G. E. Taxonomic revision of *Solanum* sect. *Chamaesarachidium* (Solaneae, Solanaceae).

The delimitation of *Solanum* sect. *Chamaesarachidium* Bitter, as well as its relationship with sect. *Episarcophyllum* Bitter and certain species of sect. *Solanum*, is presented. Three species are included in *Solanum* sect. *Chamaesarachidium* (*S. annuum* C. V. Morton, *S. chamaesarachidium* Bitter, and *S. gilioides* Rusby), which are described in detail and illustrated. The following combination of characters defines *Solanum* sect. *Chamaesarachidium*: the small annual habit, the pinnatifid to pinnatisect leaf blade, the inflorescence opposite or subopposite to the leaves, the number of flowers per inflorescence (3-14), the campanulate corolla, the very small anther size (1.1-2.7 mm long), the accrescent fruiting calyx with a well-marked venation, the absence of sclerosomes in the pericarp, the tuberculate seed coat, and the Andean habitat.

G. E. Barboza, Instituto Multidisciplinario de Biología Vegetal-CONICET and Universidad Nacional de Córdoba, Casilla de Correo 495, 5000. Córdoba, Argentina. E-mail: gbarboza@imbiv.unc.edu.ar

Introduction

During the revision of the species of *Solanum* sect. *Solanum* from South America, the examination of herbarium collections in many European and American herbaria and the observation of living material led me to circumscribe a small group of *Solanum* species from the high altitudes of the Andean mountains. These species belong to sect. *Chamaesarachidium* and are closely related to sect. *Episarcophyllum* Bitter and certain species with accrescent fruiting calyx of sect. *Solanum*.

Fifty years after Bitter (1917) proposed sect. *Chamaesarachidium*, Cabrera (1971) stated that *S. nicandricalyx* resembles *S. chamaesarachidium*. Morton (1976) agreed with the affinity between both taxa, but assigned *S. nicandricalyx* to sect. *Episarcophyllum*. Later, Nee (1999) placed these species in subsect. *Chamaesarachidium* within sect. *Solanum*, while Hunziker (2001) accepted the sectional rank for both of them, adding one more species, *S. micrantherum*. On his part, Child (1984) included *S. annuum* C. V. Morton (the valid name for *S. micrantherum*) and *S. gilioides* Rusby (the valid name for *S. nicandricalyx*) in sect. *Parasolanum* Child, created to accommodate 10-12 species from the temperate New World.

All three species of *Solanum* sect. *Chamaesarachidium* share the following combination of characters: the habit (small annual procumbent herbs), the division of the leaf blade (pinnatifid to pinnatisect, rarely entire margin), the position of the inflorescence (opposite or subopposite to the leaves), the number of flower per inflorescence (3-14), the corolla shape (always campanulate), the anthers size (very small: 1.1-2.7 mm long), the fruiting calyx (accrescent and with a strong venation), the absence of sclerosomes in the fruit, the seed coat (tuberculate), and the habitat (common in the Argentinian and Bolivian Andean plateau). The exclusive characters of sect. *Chamaesarachidium* are the peculiar ornamentation of the seeds and the accrescent, profusely reticularly veined fruiting calyx.

This paper provides a survey of novel characters for a deeper understanding of the relationships in this poorly known South American section.

Material and methods

This revision is based on the examination of over 80 herbarium specimens or field collections, and on pickled material preserved in FAA (formalin-acetic acid-ethanol). Trichomes were analyzed from epidermal peels of the different organs.

Pollen material was obtained from anthers of herbarium specimens or plants in the field fixed in FAA (flowers just before anthesis). Samples for light microscope study were acetolysed according to the method of Erdtman (1960), and mounted in glycerine jelly. For scanning electron microscopy (SEM), non-acetolysed grains were dehydrated in an alcohol series, pipetted on to a SEM stub in a few drops of 96 % alcohol, and allowed to dry. Samples were coated with gold/palladium and examined using a JEOL JSM 35CF microscope (Insibio-Conicet).

The measurements given are based on 20 non-acetolysed pollen grains of 5 collections (marked with an asterisk in the sections herein entitled *Additional specimens examined*) from each species. Descriptive terminology follows Punt et al. (1994).

Seeds were soaked in water and sterilized in a 5-10 % commercial bleaching agent. The seeds were then washed twice, air dried and coated with gold/palladium for SEM. Light microscope preparations were stained with safranin and Cresil Blue. Pictures were taken with an Axiophot microscope.

Discussion of selected characters

Trichomes

Stems, leaves, peduncle, pedicels and calyx have simple, uniseriate, non-glandular or glandular trichomes. The non-glandular hairs may be unicellular and striate (Fig. 3 M) or

multicellular (4-10-celled) and verrucose (Fig. 3 H, 4 E, 5 J). In *S. annuum*, conspicuous protuberances bearing long non-glandular trichomes are very common on the stems. The glandular trichomes may be short (stalk bi-celled and smooth, head multi-celled, Fig. 3 L, 4 D, 5 D), or long (stalk multicellular smooth, Fig. 4 I, 5 C, or verrucose, Fig. 4 K, head always unicellular).

The pubescence of the calyx is variable. Non-glandular trichomes are found in the three species of sect. *Chamaesarachidium*, but both the long verrucose and the short glandular hairs may also appear in *S. chamaesarachidium*, while only the shorter hairs are mixed with the non-glandular ones in *S. gilioides* and *S. annuum*. The vestiture of the corolla varies from papillose on the margin to densely hairy on the outer surface. The staminal filaments always have abundant hairs, being exclusively non-glandular in *S. annuum* and glandular in the other two species (Fig. 4 I, 5 C). Finally, the style is pubescent along its basal half or 2/3, with verrucose or striate non-glandular hairs in *S. annuum* (Fig. 3 M), or only with short papillae in *S. chamaesarachidium* (Fig. 4 J) or with a mix of glandular and non-glandular hairs in *S. gilioides* (Fig. 5 G, H).

Androecium

The androecium deserves special comment. A dorsal and basal connectival prolongation is present in the anthers of *S. chamaesarachidium* (Fig. 4 A, C) and sometimes also in the ones of *S. gilioides* (Fig. 5 L), while it is absent in *S. annuum* (Fig. 3 I). When the appendix is present, it is a non-glandular structure which is free from the filament (Barboza & Hunziker 1991). This situation is very different to what happens in sect. *Campanulisolanum* (Barboza & Hunziker in press) and sect. *Delitescens* (Barboza & Hunziker 1991; Hunziker 2001), in which the appendix is always glandular and well-fused to the filament in the latter section. The presence and the size of the connectival appendix are useful characters at specific level in sect. *Chamaesarachidium*,

unlike the case of the other two sections, in which this connectival appendix is a key character to define each of them.

Pollen morphology

The pollen morphology of *Solanum* sect. *Chamaesarachidium* is quite homogenous. Pollen grains are shed as monads, trizonocolporate, subspheroidal and small to medium-sized (26.40 ± 3.62). The outline in ecuatorial view is circular (Fig. 1 A, D), and in polar view it is circular to convexly triangular. The colpi are long (18-30 μm), the membrane is irregularly and densely microgranular (Fig. 1 D) and the ends acute (Fig. 1 C). The endoapertures are circular (pore diameter: 5.7-8.5 μm , Fig. 1 D) or subcircular (7-10.5 x 5.7-10 μm). The polar area is small (polar area index: 0.14-0.17). The exine is densely microgranulate (Fig. 1 B-D).

Quantitative data in μm for the three taxa of this section (P, E, P/E) are included in Table 1.

Table 1. Measurements of *Solanum* sect. *Chamaesarachidium* pollen grains in μm

Taxa	<i>E</i> (P)	Min-Max	<i>P</i>	Min-Max	<i>E</i> (E)	Min-Max	<i>P/E</i>	Min-Max
<i>S. annuum</i>	29.72 \pm 2.90	22.85-35.71	28.84 \pm 2.90	22.72-35.50	28.85 \pm 2.98	22.85-37.13	1.00 \pm 0.06	0.85-1.23
<i>S. chamaesarachidium</i>	24.01 \pm 1.29	21.42-28.56	25.37 \pm 1.40	22.85-28.56	23.69 \pm 1.27	21.42-25.70	1.07 \pm 0.06	1.00-1.27
<i>S. gilioides</i>	24.32 \pm 2.43	19.99-31.42	23.73 \pm 1.71	21.42-27.13	24.67 \pm 0.81	22.85-25.70	0.96 \pm 0.07	0.86-1.06

E (P) = equatorial diameter in polar view; *P* = polar diameter; *E* (E) = equatorial diameter in equatorial view; *P/E* = polar/equatorial diameter.

The shape varies according to the species. It is prolate spheroidal in *S. chamaesarachidium*, mostly oblate spheroidal in *S. gilioides* and oblate spheroidal to subprolate in *S. annuum*.

The exine ornamentation is very similar to that of other sections of subgenus *Solanum*, such as sect. *Campanulisolanum* (Barboza & Hunziker in press), and sect. *Solanum* (Edmonds

1984), and also to that of other subgenera (Sharma 1974; Anderson & Gensel 1976; Gbile & Sowunmi 1979), which, once more, reinforces the great homogeneity of the exine sculpturing within *Solanum*.

Ovules

The single ovule per locule in *S. annuum* (Fig. 3 N) is an outstanding feature in section *Chamaesarachidim* and an exception at the generic level. The ovary in the other two species bears more than 10 ovules and less than 25 in total, which is also a low rate for the genus.

Fruiting calyx

The fruiting calyx has three remarkable characters: the texture, the venation and the accrescence. Being membranaceous in anthesis, the calyx becomes a papery and scarious whitish envelope when fruiting in the three species. A manifest and strongly raised reticulate venation is clearly observable in *S. chamaesarachium* (Fig. 4 P) and *S. gilioides* (Fig. 5 A, N) and comparatively less developed in *S. annuum* (Fig. 3 A). The accrescence is a distinctive feature, since the calyx lobes grow differently in each species, enlarging considerably and fusing at their bases (Fig. 5 A). In *S. gilioides*, in a process that becomes evident soon after the anthesis, the very acuminate calyx lobes enlarge outstandingly in length, which results in an inflated calyx, which is closed at the top and amply exceeds the length of the fruit (Fig. 5 A, N); on the contrary, in *S. chamaesarachidium* and *S. annuum*, the enlargement of the lobes occurs more in width than in length, the lobes being more or less rounded in *S. annuum* (Fig. 3 A) and broadly ovate or elliptic in *S. chamaesarachidium* (Fig. 4 P). In these two species, the appressed calyx is open at the top and partially encloses the berry.

Seed

The seed is also very peculiar. Many rounded or acute projections arise from the seed surface (Fig. 1 E, F), giving a tuberculate pattern to the seed in the three species. Anatomically, the structure of the young seed coat is multi-layered (6-10 layers), consisting of an outer epidermis, 4-8 parenchymatous layers, and an inner layer specially differentiated from the rest by its form and content, the endothelium. In a further stage, some remarkable changes are noticeable in all these layers (Fig. 2 A). The epidermal cells show a pronounced radial elongation, especially the ones at the margin (Fig. 2 B); their inner tangential walls and part of the radial ones thicken and lignify, while the rest of the radial walls and the outer tangential wall remain thin and cellulosic. The content of these cells is rich in starch (Fig. 2 A, B), and their nuclei are large. From the parenchymatous layers, many proliferations of cells arise, becoming so pronounced that they take the form of tubercles (Fig. 2 C). Ten to thirteen epidermal cells and some subepidermal parenchymatous cells take part in the formation of each tubercle. In later stages, when the embryo is approaching maturity, the thickenings and lignification of the outer epidermal cell walls become more pronounced, while the starchy content has been consumed, and most of the parenchymatous layers has disappeared, leaving only a thin layer of crushed and disorganized tissue. The inner surface of the endothelium becomes cutinized and this layer seems to take up now a protective function, instead of the initially nutritive one (Fig. 2 D).

Affinities

Solanum sect. *Episarcophyllum* and some species of sect. *Solanum* are the closest relatives of this small group of plants.

The species of *Solanum* sect. *Episarcophyllum* grow mostly in the same habitat and are in appearance very similar to those of sect. *Chamaesarachidium*; however, these species differ in

many characters: they are perennial plants with thick rhizomes and generally with erect aerial stems up to 1 m tall; the leaves are fleshy, dentate-sinuate to lobulate, usually with revolute interlobular sinuses; the inflorescences are terminal (exceptionally extra-axillary); the corolla is sub-rotate or infundibuliform-stellate; the narrowly elliptical anthers usually measure (3) 4-6 mm long; the fruiting calyx is scarcely accrescent and leaves the berry uncovered; the venation is deeply immersed in the mesophyll; the fruit bears generally numerous stone grains; and the seed coat is honey-combed or smooth (Del Vitto & Petenatti 1999; Hunziker 2001).

The affinity with sect. *Solanum* refers to a small group of glandular-viscid species of this section, which grow in disturbed habitats as weeds. In these species (such as *S. tweedianum* Hook., *S. physalifolium* Rusby, *S. sarrachoides* Sendtn., etc.), the calyx is also accrescent, but the venation is hardly evident. However, they can be easily distinguished from those of sect. *Chamaesarachidium* for their extra-axillary short-racemose inflorescences, the semi-stellate or rotate corollas, the presence of sclerosomes in the pericarp, and the rough or reticulate seed coat (Edmonds 1983; Edmonds & Chweya 1997).

Taxonomic Treatment

Solanum section Chamaesarachidium Bitter, Repert. Sp. Nov. Regni Veg. 15: 93 (1917). Type species: *Solanum chamaesarachidium* Bitter

Small annual herbs, very branched at the base; stems herbaceous, longitudinally ridged or narrowly winged, pubescent. Leaves simple, solitary, petiolate or sessile, the blade narrowly elliptical, ovate or obovate in outline, apex acute, base cuneate-attenuate to very attenuate, margin entire or pinnatifid to pinnatisect. Inflorescences opposite or subopposite to the leaves, pedunculate, simple racemose or more rarely bifurcate, few or multi-flowered (3-14 flowers). Pedicels articulate at the base. Calyx lobes sometimes unequal, apex obtuse, acute or acuminate.

Corolla campanulate, pubescent outside and glabrous inside, 3.5-8.5 mm long, 7-8 (11) mm in diam. at anthesis, the lobes ca. 1 mm long. Filaments inserted near the corolla base, their free portion pubescent, as long as or longer than the sector fused to the corolla; anthers ellipsoidal, small [1.1-2.5 (2.7) mm long x 0.6-1.1 mm lat], basi-ventrifixed or basifixed, with large pores that continue in a longitudinal slit, thecae almost completely joined together and scarcely separated at the apex. Gynoecium ca. 2.75-5.4 (6.1) mm long; ovary glabrous; style cylindrical, straight or curved at its apex, pubescent in the 2/3 or 1/2 basal, equalling the anthers or exserted; stigma capitate, scarcely lobed at the base and wider than the style. Fruit globose or ellipsoidal, scarcely or multi-seeded (1 or 2 or up to 25 blackish seeds); pericarp thin; sclerosomes absent; calyx accrescent, papery-scarious and with noticeable reticulate venation; fruiting pedicels always deflexed. Seeds globose or trans-ovoidal in outline; seed coat tuberculate. Embryo annular or coiled; cotyledons shorter than the rest of the embryo, and one of them longer than the other; endosperm abundant.

Solanum sect. *Chamaesarachidium* comprises three species: *S. annuum*, *S. chamaesarachidium*, and *S. gilioides*.

KEY TO THE SPECIES OF *SOLANUM* SECT. *CHAMAESARACHIDIUM*

1. Inflorescence generally simple, 8-12-flowered, or, more rarely, when bifurcate each branch 4-7-flowered, the rachis long (up to 9 cm); anthers 1.2-2.5 (2.7) mm; ovary with only 2 ovules; fruiting calyx with venation not so evident; berry one- or two-seeded. Leaf blades dimorphic, entire or minutely serrate and markedly pinnatipartite to pinnatisect 1. *S. annuum*
1. Inflorescence always simple, 2-5-flowered, the rachis short (not more than 3 cm long); anthers 1.1-1.8 (2.5) mm; ovary with more than 10 ovules; fruiting calyx with venation well-marked

- and reticulate; berry with 8-25 seeds. Leaf blades not dimorphic, pinnatifid to pinnatipartite, rarely pinnatisect or entire 2
2. Calyx lobes broadly elliptic or ovate, slightly acute; anthers with a conspicuous connectival dorsal prolongation; ovary globose; style with very short striate papillae; berry globose, (5) 7-10 mm diam., fruiting calyx growing more in width than in length, its lobes quite broad and rounded, partially enclosing the berry 2. *S. chamaesarachidium*
2. Calyx lobes linear or narrowly triangular, very acute; anthers sometimes with a small connectival dorsal prolongation; ovary ellipsoidal, style with long smooth glandular trichomes and non-glandular verrucose ones; berry ellipsoidal, ca. 6 mm long x 4.2 mm wide, fruiting calyx growing more in length than in width, its very acuminate lobes completely enclosing the berry 3. *S. gilioides*

1. *Solanum annuum* C. V. Morton

A revision of the Argentine species of *Solanum*: 102, Fig. 7 I-K, 9 (1976). Type: Argentina.

Prov. Salta. Depto. Rosario de Lerma, Campo Quijano, 2700 m, 17 Jan 1929, Venturi 8507 (US! holotype, photo-US at CORD!).

Solanum micrantherum Cabrera, Hickenia 1 (31): 168, Fig. 4 (1978). Type: Argentina. Prov.

Catamarca. Depto. Andalgalá, El Candado, 16 Feb 1917, Jörgensen 978 (SI! holotype, fragment CORD!; GH!, US! isotypes).

Annual herbs, 5-30 (50) cm high. Stems moderately pubescent with conspicuous protuberances bearing non-glandular trichomes, slender, ascending. Leaves ovate to elliptic, the blade 2.3-7 x 0.8-4 cm, dimorphic, some of them smaller and with entire or minutely serrate margins, others

larger and strongly pinnatipartite to pinnatisect (occasionally, only entire leaves are present), both types with scarce to abundant antrorse trichomes on the lamina. Petiole not more than 6 mm or subsessile. Inflorescence simple racemose, 8-12-flowered or more rarely bifurcate (each branch 4-7-flowered); rachis up to 9 cm long; peduncle (1.5) 2-5.2 cm long. Pedicels (1) 2-9 mm long, pubescent. Calyx 2.4-3.5 (3.8) mm long, the lobes obtuse, slightly unequal (1 or 2 larger), broadly ovate, as long as or shorter than the tube, (0.7) 0.8-1.3 mm long x 1.5 mm wide. Corolla (4) 5-6.2 (8.1) mm long, 7-8 (10) mm in diam. at anthesis, lilac, with conspicuous interlobular membranes; lobes with abundant non-glandular trichomes on outer surface and margins. Filaments inserted ca. 1.1 mm above the corolla base, their free portion pubescent (multicellular verrucose non-glandular hairs), 0.8-1.55 (1.9) mm long; anthers 1.2-2.5 (2.7) x ca. 0.75 mm, without a connectival dorsal prolongation. Gynoecium 4.7-5.4 (6.2) mm long; ovary subglobose; ovules 2; style articulate, 3.5-4.5 (5.5) mm long, and 1.3-1.5 (1.8) mm beyond anthers, curved near the apex, pubescent (striate hairs); stigma 0.3 x 0.5 mm. Berry globose, small, ca. 2.5 mm in diam., few-seeded (1 or 2), calyx partially investing the berry, the lobes more or less rounded (3.2-3.7 mm long x 3.2-4.7 mm wide); pedicels thin, 2.5-4 mm long. Seeds 2.6 x 2.1 mm; embryo annular. n = 12 (Moscone, Darwiniana 31: 266, fig. 3 A. 1992, sub nom. *Solanum nicandricalyx*).
- Fig. 3.

Phenology. Flowers collected mainly from January to March. Fruiting from February to probably April.

Distribution and habitat. Endemic from the biogeographical Prepuna and Puna Provinces in northern Argentina (Prov. Jujuy, Salta, Tucumán, and Catamarca). It occurs at high elevations (2100-3300 m).

Additional specimens examined. Argentina. Catamarca: Andalgalá, Capillitas, Bettfreund 281 (LP); El Candado, Jørgensen s. n. (Herb. Osten 11518) (G); between Río Lampacillo and Río Potrero, Sleumer 1841* (CORD, LIL); Cuesta de la Negrilla, Sleumer 2684 (LIL). Jujuy: Capital, between León and Nevado Chañi, Las Cuevas, Fabris et al. 4094 & 4120* (LP); Humahuaca, West 6316 p.p. (GH); Tilcara, Casa Colorada, Sleumer 4104 (LIL); Tumbaya, Volcán, Cabrera et al. 21732* (LP). Salta: Cachi, Cuesta del Obispo, Novara 6227 (MCNS); Rosario de Lerma, Chorrillos, Novara 4895 (G, MCNS); Santa Victoria, Lizoite, Meyer & Bianchi 33401 (LIL). Tucumán: Tafí, Colalao del Valle, Quebrada de Managua, Castellón 2596 (LIL); El Infiernillo, Castellón 13127 p.p. (LIL); Cuesta de Guasamayo, Schreiter 4828 (LIL); Abra de los Arrieros, Schreiter 5429 (LIL); El Molle, A. T. Hunziker, Barboza & Moscone 24886 & 24901* (CORD); Quebrada de Managua, Subils & Bernardello 2665 & 2667 (CORD); Quebrada El Mollar, Subils & Bernardello 2674 (CORD); Quebrada del Pantanillo, Subils & Bernardello 2682 (CORD).

Solanum annuum was placed in sect. *Dulcamara* p.p. by Morton (1976) taking its pedunculate, multi-flowered inflorescence into account; on his part, Cabrera (1978) stated the probable inclusion of *S. micrantherum* in sect. *Campanulisolanum*, considering its campanulate corolla. However, many other characters, such as the habit (small annual herbs vs. shrub or perennial herbs), the anther size (1.2-2.7 mm long vs 3.5-5 mm long), the number and ornamentation of the seeds (two tuberculate seeds vs. many foveolate seeds), among other features, contradict the respective positions of these two authors.

2. *Solanum chamaesarachidium* Bitter

Repert. Sp. Nov. Regni Veg. 15: 94 (1917). Based on *Chamaesaracha boliviensis* Dammer, Bot. Jahrb. Syst. 49: 215 (1913) (non *Solanum boliviense* Dunal). Type: Bolivia. Depto. La Paz:

Between Palca and La Paz, 4200 m, Mar 1908, Pflanz 145 (B-destroyed holotype, photo 2710-B at F!, CORD!, NY!).

Procumbent herbs, (3) 5-15 cm high. Stems prostrate, pubescent with long, flexuose, non-glandular trichomes. Leaves narrowly elliptical, obovate or ovate, the blade 1.5-4 x 0.6-2 cm, the margins pinnatifid to pinnatipartite, with 3-4 pairs of opposite unequal acute or rounded segments, both surfaces with abundant antrorse trichomes. Petiole 0.7-1.5 (2.5) cm. Inflorescence simple racemose, 2-4-flowered; peduncle 0.5-2 cm long. Pedicels (2) 6-15 mm long. Calyx 2.5-4 mm long, pubescent (the same trichomes of the stem and other glandular ones), the lobes broadly elliptic or ovate, slightly acute, ca. 1.5 times longer than the tube, 1.3-2 mm long. Corolla 3.5-6.2 mm long x ca. 6 mm in diam at anthesis, white or violet; lobes with non-glandular trichomes on outer surface and papillose on the margins. Filaments inserted 0.6-1.1 mm above the corolla base, their free portion pubescent with long and abundant smooth glandular trichomes, 0.5-1.5 mm long; anthers 1.1-1.65 x 0.7-1.1 mm, with a noticeable connectival dorsal prolongation (ca. 0.3 mm long). Gynoecium 2.75-3.5 mm long; ovary subglobose, 0.8-1.25 mm long; style exerted, pubescent in its 2/3 basal (very short striate papillae), 1.7-2 mm long; stigma 0.2 mm long x 0.4 mm wide. Berry globose, (5) 7-10 mm diam., multi-seeded (8-17 or up to 25 seeds); calyx strongly latitudinally accrescent, appressed to the berry and partially covering it, lobes broadly ovate (3.5-9 mm long x 6.4-12 mm wide). Seeds 1.9-2.4 mm long x 1.5-2 mm wide, embryo coiled. - Fig. 4.

Phenology. Flowering mainly from January to March. Fruiting from February to May.

Distribution and habitat. *Solanum chamaesarachidium* is confined to southern Peru, Bolivia (La Paz) to northern Argentina (Jujuy, Salta, Tucumán, Catamarca, and La Rioja)

inhabiting the Prepuna to Altoandina biogeographical Provinces, at high elevations (2100-4900 m).

Additional specimens examined. Peru. Cuzco: Chumbivilcas, Núñez & Delgado V. 7943 (AAU, NY). Puno: Juliaca, Stafford 455 (BM). Bolivia. La Paz: cultivated plots of land, Buchtien 772 (NY, US); Aroma, between El Alto and Pocota, Ceballos et al. Bo. 47 (SI); Ayo-Ayo, Lara & Hervé s.n. (LPB 13); Escoma, Camacho, etwa 10 kilometer südlich Escoma, Feuerer 5657 a (NY); Ingavi, Titicani-Tacaca, Villavicencio 318 (LPB, NY); 20 km S Guaqui, Villavicencio 916a (LPB); Murillo, Patacamaya, Arce s.n. (LPB 549); Laguna de las Animas, Beck 4580 (CORD, LPB, NY); Omasuyos, La Paz-Huarina road, Krapovickas & Fuchs 7070 (LIL); Pacajes, Calacoto, Asplund 2826 (LPB, S). Argentina. Jujuy: Capital, Las Cuevas, Fabris et al. 4075 (LP); Cochinoca, just along E of Abra Rechaite, Taylor et al. 11307 (SI); Humahuaca, Mina Aguilar, Cabrera et al. 19783 (BM, K, LP, SI); Ciénaga de Zarzo, Fabris 6860 (LP); between Molino and Mina Aguilar, J. H. Hunziker et al. 10515 (SI); near Iturbe, Negritto, Barboza & Matesevach 353* (CORD); Quebrada de La Soledad, Okada 3059 (LP); between Iturbe and Humahuaca, Soriano 680 (SI); Cerro La Soledad, Venturi 8622* (SI, US); Javi, Cajas a Abra de Lizoite, Kiesling et al. 3873 (SI); passing the detour towards Abra de Lizoite, Negritto, Barboza & Matesevach 394 (CORD); ca. 3 km from the slopes of Abra del Lizoite, Negritto, Barboza & Matesevach 428 (CORD); Ciénaga Grande, Tolaba 1631 (MCNS); Abra Colorada, Tolaba 1655 (MCNS); Rinconada, ruta Mina Pirquitas a Peñas Blancas, Zuloaga et al. 6011 (SI); Tilcara, Alto de la Laguna Negra, Cabrera & Hernández 14078 (LP, SI); passing San Gregorio, Sleumer 3574 (SI); Casa Colorada, Sleumer 4102 (LIL); Tumbaya, Abra de los Pives, Cabrera 18534 (LP); road to Abra de Lipán, Cabrera et al. 30546 (SI). Catamarca: Andalgalá, Cerro Yutuyaco, Jörgensen 1638 (GH, SI, US); C. Yutuyaco a Capillitas, Sleumer 2748 (LIL); Belén, Nacimientos de San Antonio, Legname & Vervoorst 158 (LIL). La Rioja: Chilecito, Quebrada J. Díaz, Kurtz 13739

(CORD); La Mesada, Kurtz 13806 (CORD); Famatina, La Encrucijada, Krapovickas 6219 (BAB); Mina San Juan, Kurtz 13659 (CORD); Mina Italia, Kurtz 14792* (CORD); Real Viejo, Kurtz 14724* (CORD). Salta: La Caldera, Quebrada del Río Potrero Castillo, Sleumer & Verveorst 3019 (LIL); Los Andes, Abra del Acay, Novara 4936 (MCNS); Rosario de Lerma, Chorrillos, Novara 4885 (MCNS); Santa Rosa de Tastil, Palací 378 (MCNS); Quebrada de Tastil, Varela & Del Castillo 1391 (MCNS). Tucumán: Chicligasta, Estancia Las Pavas, Venturi 3112 (GH, LIL, SI); Tafí, Cumbre del Cajón, Schreiter 4835* (LIL); Cumbres Calchaquíes, Sparre 9494 (LIL).

Solanum chamaesarachidium resembles *S. gilioides* very much; therefore, sometimes it is difficult to distinguish them; the main differences are in the calyx: in the flower, the calyx lobes of *S. gilioides* are linear or narrowly triangular and grow considerably in length when fruiting, instead of the marked growth in width of the ovate calyx lobes of *S. chamaesarachidium*.

3. *Solanum gilioides* Rusby

Mem. Torrey Bot. Club 4: 228 (1895). Type: Bolivia. Depto. Cochabamba. Vic. Cochabamba, 1891, Bang 938 p.p. (NY!, plants on right hand holotype; GH!, NY!, US! isotypes).

Solanum nicandricalyx Cabrera., Bol. Soc. Argent. Bot. 13 (4): 326, Fig. 1 (1971). Type:

Argentina. Prov. Jujuy. Depto. Tilcara, Falda Grande, Cerro de Guairahuasi, 3400 m, 4 Mar 1961, Cabrera & Hernández 14026* (LP! holotype, fragment & photo-LP at CORD!).

Prostrate herbs, 5-15 cm high. Stems slender, moderately pubescent to glabrescent. Leaves narrowly elliptical or ovate; blade (2) 3-6.5 x (0.8) 1-2.4 cm, pinnatipartite, rarely pinnatisect or pinnatifid or entire, with 3-5 pairs of opposite or alternate unequal oblong or triangular

segments, both surfaces with abundant antrorse trichomes especially on the nerves. Petiole 6-10 mm or subsessile. Inflorescence simple, racemose, 2-5-flowered; peduncle (0.4) 1-2 (3) cm long. Pedicels (2) 5-10 mm long, pubescent. Calyx (2.5) 3-4.5 (5.2) mm long, pubescent with the same antrorse trichomes of the stem and scarce, very small glandular ones, the lobes linear or narrowly triangular, very acute, 1.3-1.8 times longer than the tube, 1.8-3.5 mm long. Corolla (4.7) 5-8.5 mm long, 7-8 (11) mm in diam. at anthesis, light blue or violet; lobes with abundant non-glandular trichomes, their margins papillose. Filaments inserted 1-3 mm above the corolla base, their free portion pubescent with long smooth glandular trichomes, 1.1-1.8 mm long; anthers 1.1-1.8 (2.5) x 0.6-0.7 mm, with a connectival dorsal prolongation (ca. 0.2 mm long), or sometimes completely absent. Gynoecium 3.1-4 mm long; ovary ellipsoidal; style slightly curved near the apex, pubescent in its $\frac{1}{2}$ basal (trichomes similar to the ones of the filaments mixed with non-glandular trichomes), 2-3.2 mm long, and ca. 0.4 mm beyond anthers; stigma 0.2-0.3 mm long, 0.5 mm wide. Berry ellipsoidal, small, ca. 6 mm long x 4.2 mm wide, multi-seeded (9-17 seeds); calyx strongly accrescent, inflated, growing much more in length than in width, amply exceeding the berry; lobes very acuminate (12-13.5 mm long x 7-7.5 mm wide); pedicels thickened at apex, 6-7 mm long. Seeds 1.7-2.2 mm long x 1.4-1.7 mm wide, embryo annular. Fig. 5

Phenology. Flowering mainly from February to April. Fruiting from March to April.

Distribution and habitat. *Solanum gilioides* is also common in the Puna Province from southern Peru to northern Argentina (Prov. Jujuy, Salta, and Tucumán), growing above 3000 m.

Additional specimens studied: Peru. Puno: Huerta bei Puno, Ellenberg 2977 (U). Argentina. Jujuy: Capital, Las Cuevas, Fabris 4092 (LP); Humahuaca, Tres Cruces, Legname s.n. (LIL

540005); Valle Grande, Cerro Hermoso, Fabris et al. 5398* (LP); Finca Pozuelos, Fabris & Crisci 6932* (LP); Yavi, Abra del Lizoite, Negritto, Barboza & Matesevach 429* (CORD). Salta: Iruya, Pantipampa, Tolaba et al. 1155* (MCNS). Tucumán: Tafí, Infiernillo, Petersen & Hjerting s.n. (L).

Acknowledgements - I am deeply indebted to late Prof. Armando T. Hunziker for introducing me to botanical investigation and for his constant encouragement and guidance during my research on Solanaceae. I also thank the curators and assistants of the herbaria at AAU, BAB, BM, CORD, G, GH, K, L, LIL, LP, LPB, MCNS, NY, S, SI, U, US for the access to the material, L. Ribulgo for the illustrations and Agencia Córdoba Ciencia, Secretaria de Ciencia y Tecnología (University of Córdoba), Consejo Nacional de Investigaciones Científicas y Técnicas (Argentina), and the Royal Botanic Gardens of Kew for the grants that allowed me to visit European and American herbaria.

References

- Anderson, G. J. & Gensel, P. G. 1976. Pollen morphology and the systematics of *Solanum* section *Basarthrum*. - *Pollen et Spores* 18: 533-552.
- Barboza, G. E. & Hunziker, A. T. 1991. Estudios sobre Solanaceae XXXI. Peculiaridades del androceo de interés taxonómico en *Solanum*. - *Kurtziana* 21: 185-194.
- Barboza, G. E. & Hunziker, A. T. Revision of *Solanum fiebrigii* and *Solanum sinuatiexcisum*, and their inclusion in sect. *Campanulisolanum*. - In press.
- Bitter, G. 1917. Solana nova vel minus cognita XVI. - *Repert. Spec. Nov. Regni Veg.* 15: 93-98.
- Cabrera, A. L. 1971. Especies nuevas o críticas de la flora jujeña. I. - *Bol. Soc. Argent. Bot.* 13: 325-336

- 1978. Especies nuevas o críticas del género *Solanum* de la provincia de Jujuy, Argentina. - *Hickenia* 1 (31): 161-171.
- Child, A. 1984. Taxonomic studies in *Solanum* L. 2. Two new infrageneric taxa for the subgenus *Solanum*. - *Feddes Repert.* 95: 141-150.
- Del Vitto, L. A. & Petenatti, E. 1999. Notas en *Solanum* (Solanaceae) de Argentina II. Aportes al conocimiento de la Sect. *Episarcophyllum*. - *Kurtziana* 27: 319-326.
- Edmonds, J. 1983. Seed coat structure and development in *Solanum* L. section *Solanum* (Solanaceae). - *Bot. J. Linnean Soc.* 87: 229-246.
- 1984. Pollen morphology of *Solanum*. - *Bot. J. Linnean Soc.* 88: 237-251
- & Chweya, J. A. 1997. Black Nightshades. *Solanum nigrum* L. and Related Species. - IPGRI, Rome.
- Erdtman, G. 1960. The acetolysis method, a revised description. - *Svensk Bot. Tidskr.* 54: 561-564.
- Gbile, Z. O. & Sowunmi, M. A.. 1979. The pollen morphology of Nigerian *Solanum* species. - In: Hawkes, J. G., Lester, R. N. & Skelding, A. D. (eds.), *The Biology and Taxonomy of the Solanaceae*. *Linnean Soc. Symp., Ser. 7*: 335-3422. Academic Press, London.
- Hunziker, A. T. 2001. *Genera Solanacearum. The Genera of Solanaceae Illustrated, Arranged According to a New System.* - A. R. G. Gantner Verlag K.-G., Ruggell.
- C. V. Morton, C. V. 1976. *A Revision of the Argentine Species of Solanum.* - Academia Nacional de Ciencias, Córdoba-Argentina.
- Moscone, E. 1992. Estudios sobre cromosomas meióticos en Solanaceae de Argentina. - *Darwiniana* 31: 261-297.

- Nee, M. 1999. Synopsis of *Solanum* in the New World. - In: Nee, M., Symon, D. E., Lester, R. N. & Jessop, J. P. (eds), Solanaceae IV. Advances in Biology and Utilization. Royal Botanic Gardens, Kew, pp. 285-333.
- Punt, W., Blackmore, S., Nilsson, S. & Le Thomas, A. 1994. Glossary of Pollen and Spore Terminology. - Laboratory Paleobotany & Palynology Foundation, Utrecht.
- Sharma, B. D. 1974. Contribution to the palynotaxonomy of genus *Solanum* L. - J. Palynol. 10: 51-68.

Numerical list of taxa

1. *Solanum annuum* C. V. Morton
2. *S. chamaesarachidum* Bitter
3. *S. gilioides* Rusby

List of Exsiccatae

- Arce s.n. (2).
- Asplund, E., 2826 (2).
- Bang, M., 938 p.p (3).
- Beck, S., 4580 (2).
- Bettfreund, 281 (1).
- Buchtien, O., 772 (2).
- Cabrera, A. L., 18534 (2).
- Cabrera, A. L. & Hernández, 14026 (3); 14078 (2).
- Cabrera, A. L., Crisci & Kiesling, 19783 (2).
- Cabrera, A. L. et al., 21732 (1); 30546 (2).
- Castillón, L., 2596, 13127 p.p. (1).
- Ceballos, A. et al. Bo., 47 (2).
- Ellenberg, H., 2977 (3).
- Fabris, H., 4092 (3); 6860 (2).
- Fabris, H., Cano & Tello, 4075 (2); 4094 & 4120 (1).

Fabris, H. & Crisci, 6932 (3).
Fabris H., Schnack & Crisci, 5398 (3).
Feuerer, T., 5657 a (3).
Hunziker, A. T., Barboza & Moscone, 24886 & 24901 (1).
Hunziker, J. H. et al., 10515 (2).
Jørgensen, P., s.n., Herb. Osten 11518 (1); 978 (1); 1638 (2).
Kiesling, R. et al., 3873 (2).
Krapovickas, A., 6219 (2).
A. Krapovickas & Fuchs 7070 (2).
Kurtz, F., 13659, 13739, 13806, 14724, 14792 (2).
Lara, R. & Herve s.n. (2).
Legname, P., s.n. (LIL 540005) (3).
Legname, P. & Vervoorst 158 (2).
Meyer, T. & Bianchi, 33401 (1)
Negritto, M. et al., 353, 394, 428 (2); 429 (3).
Novara, L., 4885 (2); 4895 (1); 4936 (2); 6227 (1).
Núñez, P. & Delgado V., 7943 (3).
Okada, 3059 (2).
Palací, 378 (2).
Petersen & Hjerting s.n. (3).
Pflanz, K., 145 (2).
Schreiter, R., 4828 (1); 4835 (2); 5429 (1).
Sleumer, H., 1841, 2684 (1); 2748, 3574, 4102 (2); 4104 (1).
Sleumer, H. & Vervoorst, 3019 (2).
Sparre, B., 9494 (2).
Soriano, A., 680 (2).
Stafford, 455 (2).
Subils, R. & Bernardello, 2665, 2667, 2674, 2682 (1).
Taylor et al., 11307 (2).
Tolaba, J., 1631, 1655 (2).
Tolaba, J., Ragno & Quiroga, 1155 (3).

Varela, F. & Del Castillo, 1391 (2).

Venturi, S., 3112 (2); 8507 (1); 8622 (2)

Villavicencio, X., 318, 916a (2).

West, 6316 p.p. (1)

CAPTIONS

Fig. 1. SEM micrographs of pollen and seeds of *Solanum* sect. *Chamaesarachidium*. A, B. *S. gilioides*. C, D. *S. annuum*. E, F. *S. chamaesarachidium*. A: Equatorial view of a pollen grain. - B: Detail of the microgranulate exine. - C: Polar area (observe the small polar area). - D: Pollen apertures (the membrane of the colpus with granular elements). - E: Seed, showing the projections of the seed coat. - F: Detail of the seed tubercles. (A, B: Fabris & Crisci 6932; C, E: Hunziker et al. 24901; D, F: Kurtz 13806). Scale bars. A-D = 1 μ m; E = 100 μ m; F = 10 μ m.

Fig. 2. Seed coat structure in *Solanum* sect. *Chamaesarachidium*. A, B. *S. gilioides*. C. *S. annuum*. D. *S. chamaesarachidium*. A: Detail of the young seed coat showing the outer epidermis with starch (arrow), the parenchymatous layers and the endothelium (arrow). - B: Marginal epidermal cells of the seed coat showing the thickened and lignified cell walls and the starchy content (arrows). - C: Tubercle formation in a young seed (observe the proliferation of the parenchymatous layers). D. Tubercle in a mature seed. (A, B: Negritto et al. 429; C: Hunziker et al. 24901; D: Kurtz 13806). Scale bar. A-D = 25 μ m

Fig. 3. *Solanum annuum*. A: Fruit. - B: Plant. - C: Embryo. - D: Corolla opened to show the insertion of stamens. - E: Flower. - F: Gynoecium. - G: Styler apex and stigma. - H: Non-glandular verrucose trichome of the calyx. - I, J: Anthers, in dorsal and ventral view respectively. - K: Seed, observe the tuberculate seed coat. - L: Glandular trichome of the calyx. - M: Non-glandular striate trichome of the style. - N: Longitudinal section of the ovary showing the single ovule per locule. (Hunziker et al. 24901). Scale bar = 4 mm (A, D, E), 4 cm (B), 2 mm (C, F), 1 mm (G-K, N), 100 μ m (L, M).

Fig. 4. *Solanum chamaesarachidium*. A-C: Dorsal, ventral and lateral view of an anther, respectively. - D, E: Glandular and non-glandular trichomes of the calyx. - F: Inside view of a corolla sector. - G: Plant. - H: Flower bud. - I: Smooth glandular hair of the filaments. - J: Papilla of the style. - K: Verrucose glandular hair of the calyx. - L, M: Seed, lateral view and transverse section (note the protuberances of the seed coat). - N: Embryo. - O: Gynoecium. - P: Fruit, upper view. (Krapovickas 6219). Scale bar = 1 mm (A-C), 60 μm (D), 250 μm (E, I), 1.5 mm (F, H, L-O), 2 cm (G), 100 μm (J, K), 3 mm (P). Taken from Hunziker (2001) with some modifications.

Fig. 5. *Solanum gilioides*. A: Fruit. - B: Plant. - C, D: Glandular trichomes of the filaments and calyx, respectively. - E: Flower. - F: Embryo. - G: Gynoecium. - H: Styler apex and stigma. - I: Calyx. - J: Non-glandular verrucose trichome of the calyx. - K, L: Anthers, ventral and dorsal view, respectively. - M: Seed. - N: Fruit (part of the calyx has been removed to show the berry). - O: Corolla opened to show the insertion of stamens. (Negritto et al. 429). Scale bar = 8 mm (A, N), 3 cm (B), 150 μm (C, D, J), 4 mm (E, I, O), 1 mm (F, H, K-M), 2 mm (G).







